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Towards improved understanding and management of parasite transmission in the rangelands of Asia

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Towards improved understanding and management of parasite transmission in the rangelands of Asia

Munib Khanyari

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Doctor of Philosophy (PhD) in the Faculty of Life Sciences

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Abstract

Rangelands are co-grazed by domestic and wild ungulates, potentially leading to disease transmission, which is complicated by climate change and altering livestock management. Gastro-intestinal nematodes (GINs) are key determinants of ungulate health. I investigated the impacts of environmental and social factors on GIN cross-transmission between ungulates in the temperate and montane Asian rangelands - a relatively data-poor system, with limited scientific-veterinary infrastructure. First, I built an iterative framework, demonstrating the value of combining ecological and social information to inform disease management. Subsequently, I worked in three areas shared by wild and domestic ungulate hosts. In India, the montane rangeland of Kibber is home to sedentary Bharal *Pseudois nayaur* and livestock, while Pin has sedentary Ibex *Capra sibirica* and migratory livestock. The temperate rangeland of Ural, Kazakhstan is home to migratory saigas and sedentary livestock. I conducted fieldwork in each place and developed GIN transmission models, building from simpler to more complex systems and methods. In Kibber, gradual accumulation of infective GIN larvae over summer governed pasture infectivity. The most effective intervention was early-season suppression of GIN infection in livestock using temperature cues. In Pin, I highlighted the importance of social factors affecting GIN transmission and found that a *c.*30 day intervention before the migratory livestock leave Pin achieved the highest infection attenuation. In Ural, I examined interconnections between multi-scale social-ecological factors affecting ungulate health. Then, I modelled parasite transmission, likely future changes, and evaluated parasite reduction interventions. Increased livestock, but not climate change, resulted in increased infection for saigas. Early-season suppression of infection in livestock reduced predicted parasite loads in saigas. Working on a similar goal across three sites revealed contextualising parasite transmission models in an interdisciplinary understanding of local socio-ecological systems is key. The thesis provides a scientific foundation for aligning herder livelihoods with wildlife conservation.

Dedication

This thesis is to dedicated to Rahman Bab and my *Khala*. You both watch over me from the stars, without you, I was, and am, incomplete.

This thesis is also dedicated to those herders that venture out onto the pastures across trans-Himalayan India and the Kazakh steppe each morning, you inspire me!

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To my friends and colleagues up in Spiti and Ladakh, you are my inspiration. You make it hard for me to distinguish between friends and family. Dorjay, we have shared moments that words can’t describe. Let’s not get lost in the mountains, the next time? Rinchen, you make me laugh and you make me believe in friendship. Dhamal (Tanzin Thukten), one day I will climb the mountains faster than you! Shri (Kesang Chunit), walking the mountains with you gives me a source of peace. Kamal (Tandup Cherring), you have endured so much, yet you teach me the value of patience and hard work. Lama ji (Tanzin Tsewang), you have a heart of gold, we need more like you in the world.

To my friends and colleagues in Kazakhstan, thank you for accepting me. Albert, you are an inspiration. We have been through tough times together, thank you for being the personification of calm, even in the eye of the storm. Renat and Borjan, my brothers, you accepted me even when I was an outsider, thank you! To my friends and colleagues in Nature Conservation Foundation, without you, I am nothing. Kullu, you have literally taken me under your wing and molded me into a researcher. Thank you for being a friend and a mentor. I would not be half the researcher and person I am without you. Your support during my thesis has been endless, thank you! Abhirup Khara, I have shared beautiful moments with you, thank you for always being critical yet supportive. One day, I will make black tea that you will actually like. Jenise Patel, you are a true friend and we still have a score to settle: let's go back and find blue sheep in Rupin? Manvi Sharma, you have been such a well-wisher and ego-booster with your kind comments, thank you so much! Charu ji, running with you has been more than ticking off kilometers; I have learned so much about myself, my work and life from you, thank you! Prasen, my brother, we have shared special moments in the mountains with each other. All I can say is that it is just the start of a journey together.

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Nothing I have done in this thesis, would be possible without the inputs, hospitality and friendship of the various communities I worked with. The people of Pin and Kibber, living on literally the roof of the world, you make me value the comforts and privileges in my life, thank you! The *Kinnaura* livestock herders, you taught me the importance of work ethic. You continue to do your work even through all the hardship, thank you! The *Okhotzomprom* rangers in Kazakhstan, doing your duties out in the vast Kazakh steppe, often far from family and friends, thank you for what you do!

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Thank you Richard Wall for being so generous in his support throughout my PhD. Last, but far from the least, E.J. and Eric. You took me under your wing, you placed trust me in, you nurtured me. For the remainder of my life, I will remain in debt to you both, because you both are so tireless in your pursuit to build young researchers' careers. You both are so humble and each word you say inspires me. Under your supervision, I become a better version of myself. Thank you, thank you, thank you!

Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the *University's Regulation and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Munib Khanyari

Signed: [redacted] Date: 30/10/2021

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List of abbreviations

ACBK – Association for the Conservation of Biodiversity of Kazakhstan

AUC – Area Under the Curve

^{0}C – Degree Celsius

DAV – Daily Access Viewer

EPG – Eggs per Gram

FECs – Fecal Egg Counts

FLOTAC – Flotation Technique

FMD(V) – Foot and Mouth Disease (Virus)

GINs- Gastro-intestinal Nematodes

GLOWORM-FL – Global-Worm-Full-Life-Cycle

IUCN – International Union for the Conservation of Nature

$L3_h$ – Infective larvae on herbage

mm – millimeter

MME – Mass Mortality Event

NCF – Nature Conservation Foundation

NDVI – Normalized difference vegetation index

NIR – Near infrared

PPR(V) – Peste des Petit Ruminants (Virus)

- Chapter 1-

General Introduction

Camping under a starry night sky out in the Western Kazakh steppe

1.1 Problem Statement

Over one-third of the world's land area is used to graze livestock (Reid et al., 2008). The global food economy is heavily based on livestock products and over 752 million of the world's poor (living on less than 2US$ a day) rear livestock today (Otte et al., 2012). These numbers are likely to increase, with the human population set to reach 9 billion by 2030 (Otte et al., 2012**)**. Such trends are driving human land use towards increased proximity with wildlife habitats (Daszak et al., 2001). Therefore, spatio-temporal overlap between livestock and wildlife, especially ungulates, is a reality across the globe. This is especially true for rangelands, as the primary resource of interest for both domestic and wild ungulates is pasture. This leads to resource competition between the two and potential for disease spill-over (Berger et al., 2013). Transmission of disease at the interface of livestock and wild ungulates is important as it can impact agricultural economics, especially of resource-poor farmers (Reid et al., 2008) and wildlife conservation (Smith et al., 2009).

Gastro-intestinal nematodes (GINs) are determinants of fitness in wild and domestic ungulates (Gulland, 1992; Perry & Randolph, 1999). They are known to impact milk production, growth rates, fertility, and susceptibility to other diseases (Albon et al., 2002; Thumbi et al., 2013). Transmission is usually facilitated through indirect contact by sharing of pasture and water points (Morgan et al., 2004). Indirect contact is ideal for transmission of GINs that can often infect different definitive host species and have one or more environmental stage to complete their life cycle (Zajac, 2006). Often GINs get overlooked as their impact can be subtle and clinical signs hard to detect. In pastoralist settings, the monitoring of performance parameters such as growth and milk production, which would betray negative subclinical impacts of GIN on animal health, is usually sporadic or absent. Nonetheless, they are universally present. Contextualizing this within the knowledge that nearly 2/3 of the GINs found in livestock are also found in wild ungulates, highlights the connectedness of the fates of livestock and wild ungulates (Walker & Morgan, 2014). Also, as a part of GIN life history is driven by environmental conditions, changes in climate are likely to impact them to a great extent (Harvell et al., 2002). The development, survival and behaviour of the free-living stages and thus the availability of infective stages for transmission are highly dependent on weather and micro-climatic conditions (Morgan & van

Dijk, 2012). For example, there is evidence that recent increases in temperature in the UK have resulted in changes in the phenology of GINs on pasture and in the incidence of disease due to GIN infection in livestock (van Dijk et al., 2008). Consequently, the impact of climate change on GIN-host dynamics is of increasing concern (Rose et al., 2016). Nonetheless, even today our understanding of disease mechanisms and management at the livestock-wildlife interface remains limited (Rhyan & Spraker, 2010).

One key component of developing this understanding is the exploration of mechanisms of transmission using models parameterised with field data. Existing mathematical models of nematode transmission in animals generally consider a single host population that is continually present, and parasite vital rates that are predictably dependent on air temperature. These models aren't effective when considering host migration, multiple host populations, and climatic stochasticity, all of which are common in nature (Morgan et al., 2006). Additionally, many attempts to understand disease transmission fail to incorporate critical social information that drives livestock movement and health, such as use of traditional pasture management techniques (Escarcha et al,. 2018). These social factors are key in determining both the possibility and the magnitude of disease transmission in a multiple host mixed-use system.

In order to explore the complexities of GIN transmission, Rose et al., (2015) developed the GLOWORM-FL model. This simulates the effect of climate on the free-living stages of GIN parasites, thereby enabling an exploration of the potential effects of climate change on GIN transmission. The model framework presented in Rose et al., (2015) builds on previous work (Smith, 1990; Grenfell et al., 1995), including that aimed to better understand GIN transmission in multiple ungulate host systems (Morgan et al., 2007), by incorporating recent advances in understanding of the behaviour and ecology of GINs on pasture to predict the climate-dependent seasonal dynamics of GIN infection. In order to have effective and adaptive management a better understanding of these parasites is needed and the GLOWORM-FL model is an attempt in doing so. Nonetheless, it has immense scope for being adapted and improved. Not only do disease models need to be robust enough to incorporate appropriate amounts of ecological complexity of the systems, to be effective for stakeholders (such as resource-poor herders), they also need to integrate existing practices and understand human factors driving rangeland grazing and livestock health. Many existing models of GIN transmission allow for simulation of management practices, but none yet incorporate the contextual human factors driving these practices, nor have they been widely used to help design antiparasitic intervention strategies in complex ecological settings.

Considering all of this, stakeholders such as conservationists and policy-makers are realising the importance of understanding the interactions between disease in wildlife, livestock and humans, to both conserve species and support local communities in improving wellbeing and livestock productivity (Zinsstag et al., 2011). The World Health Organization has encouraged an approach to designing and implementing programmes, policies, legislation and research in which multiple sectors communicate and work together to achieve better public health outcomes. This "One Health" approach is so far limited in its real-world application, however, at least beyond zoonotic diseases for which connections between humans and animal health are obvious. More diverse case-studies are needed to understand the complex pathways linking wild and domestic animal health and human wellbeing, not least through pastoralist practices and livelihoods. There is also a need to understand the impact on these disease-mediated interactions of environmental and social changes, particularly in migratory systems (Daszak et al., 2001). This is particularly needed in data-poor systems of the world, those that are characterized by being remote, having limited scientific-veterinary infrastructure and services, and perhaps an underestimation of GIN presence and impact relative to other diseases (Kosmala et al., 2016).

1.2 Theoretical underpinnings for research on parasite transmission at the wildlife-livestock interface

There are several theoretical and empirical studies addressing the mechanisms affecting parasite transmission, particularly at the wildlife-livestock interface. In table 1.1, I synthesise a few particularly useful lenses through which researchers have studied parasite transmission in landscapes with domestic and wild hosts. These studies can be categorised according to three themes (displayed by differing colours): i) the scale at which research is conducted, ii) the consequences of movement for host-pathogen interactions and iii) the impact of changes in an ecosystem on disease transmission. In this thesis, I don't set out robustly to test any of the theories or hypotheses proposed by these studies, but use them as guidance to better understand the parasite transmission in my study sites. This helps to delimit the conceptual framing of my study. These themes demonstrate that host scale, movement and perturbation have been examined for diseases in general, and are likely to be important – yet understudied – for GIN emergence and transmission.

Table 1.1. Themes, theories and hypotheses underpinning research into disease transmission at the livestock-wildlife interface, with explanations and key references. Items in bold articulate the overarching themes and key references

Theme	Explanation and key references
Host-scale: **Population and individual levels of disease transmission**	Population-level phenomena like host density and seasonal migration, affect disease transmission. Assumes that disease transmission at the population level can be indicative of the individual level phenomenon. This approach doesn't reveal mechanisms at the individual level that could impact observed patterns of disease transmission at the population level. Alternative approach is to investigate how individual characteristics, (eg. the likelihood of an individual making a contact leading to possible transmission), combine to impact infection in populations. While this provides detailed information on factors affecting transmission of a given parasite, they are usually complicated to conduct, often requiring a lot of time and resource investment. Key references: (Fenton et al., 2002; Galvani & May, 2005; Tompkins et al., 2011)
Movement: **Escape hypothesis**	The "escape" hypothesis notes that harmful parasites may be one of the evolutionary drivers of seasonal migration. However, migration and disease interactions are highly complex and studies have shown that migratory behaviour can lead to having higher levels of parasites.

	Key references: (Avgar et al., 2014; Teitelbaum et al., 2018)
Changes: **Perturbation and pathogen-pool hypothesis**	Perturbations like land-use change force perturbations in pathogen dynamics in hosts (eg. changes in species richness, abundance and contact rates), which facilitate the emergence and/or transmission of diseases in sympatric hosts. Perturbation can also lead to reduced disease incidence. Alongside, exposure to novel diseases, from a diverse pool of disease causing organisms to which certain hosts have not had prior exposure to is possible. Key references: (Lloyd-Smith et al., 2009; Murray & Daszak, 2013)

1.3 Research Aims and Objectives

Emerging from the problem statement, the aim of the thesis was to ***investigate the impact of environmental and social factors on GIN transmission dynamics between interacting domestic and wild ungulate hosts, exhibiting varying spatio-temporal dynamics, in temperate Asian rangelands.*** By addressing this aim, I will fill a major gap in empirical understanding of disease dynamics in this particular geography, and more widely for multi-host, spatio-temporally varying systems where controlling GIN disease is important both socio-economically and for wildlife conservation.

The schematic in figure 1.1 shows the conceptual underpinning of the thesis. The conceptual model explains the mechanism behind parasite (GIN) transmission in a mixed-used spatio-temporally dynamic landscape. Two key components of transmission are i) host overlap and ii) presence of transferable GINs. These are influenced in multiple host rangeland settings in various ways. A key factor driving host contact patterns is seasonality in forage availability, which in turn drives host movement (eg. Bekenov et al., 1998). For livestock, traditional herding systems have evolved movement strategies to track variability in forage (Ghoshal, 2017). However, herding systems can impact livestock movement (hence contact patterns with co-hosts) through means that are not driven by forage alone (Escarcha et al., 2018). The presence of transferable GINs is governed by climatic variability because part of GINs' life-history occurs outside the host, on pasture. In addition to climate driving parasite availability, social factors such as anthelmintic treatment of livestock and pasture management techniques affect the presence and abundance of transferable GINs (eg. Barone et al., 2020). Understanding parasite transmission requires empirical understanding and models incorporating both host movement (overlap) and climatic variation for GINs (Rose et al., 2015).

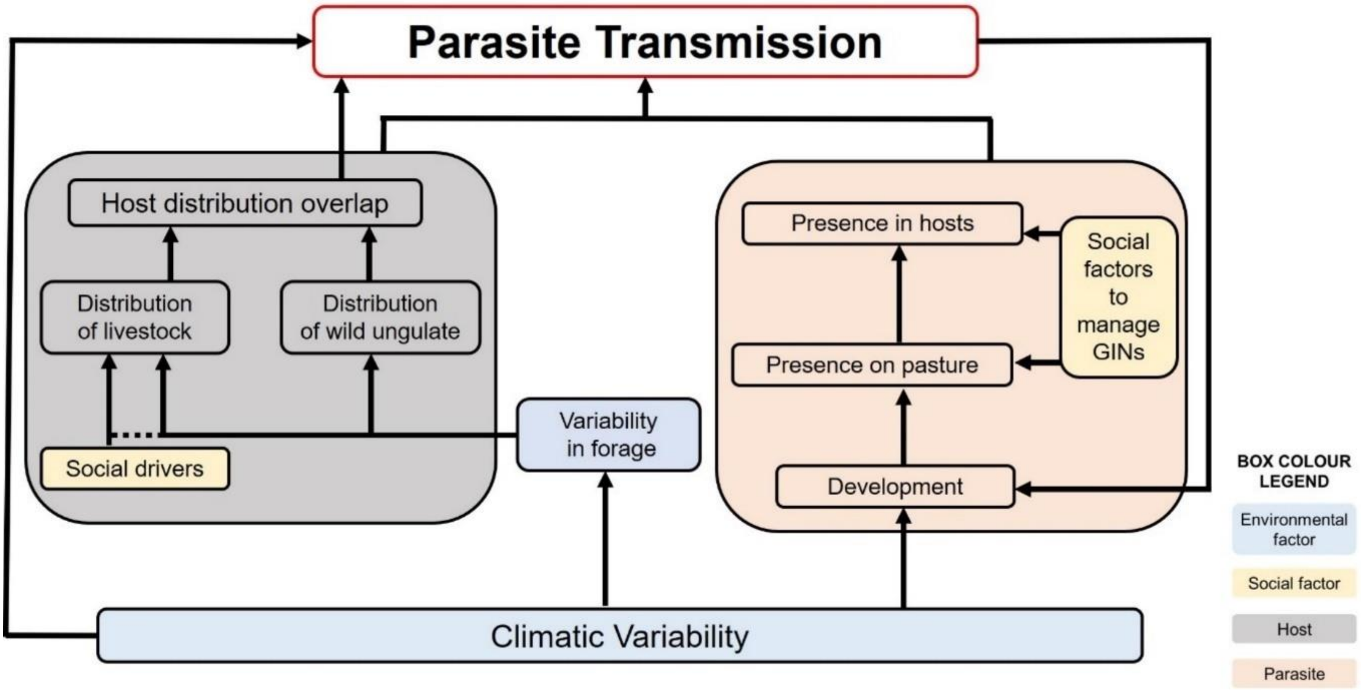


Figure 1.1 Simplified conceptual framework of the thesis.

The thesis has five objectives, which together address the aim and are connected to each other as shown in figure 1.2:

1. Build a disease risk prioritization framework to assess disease spill over risk from livestock to wildlife in rangelands;
2. Understand the relationships between multi-scale factors affecting host health in rangelands;
3. Investigate the impacts of social factors on host health and GIN transmission;
4. Model GIN transmission between sedentary ungulate hosts, through a social-ecological lens, and evaluate the likely effectiveness of potential interventions;

5. Model GIN transmission between hosts displaying movement, investigate likely changes in transmission dynamics due to movement and accompanying socio-ecological changes, and evaluate the likely effectiveness of potential interventions.

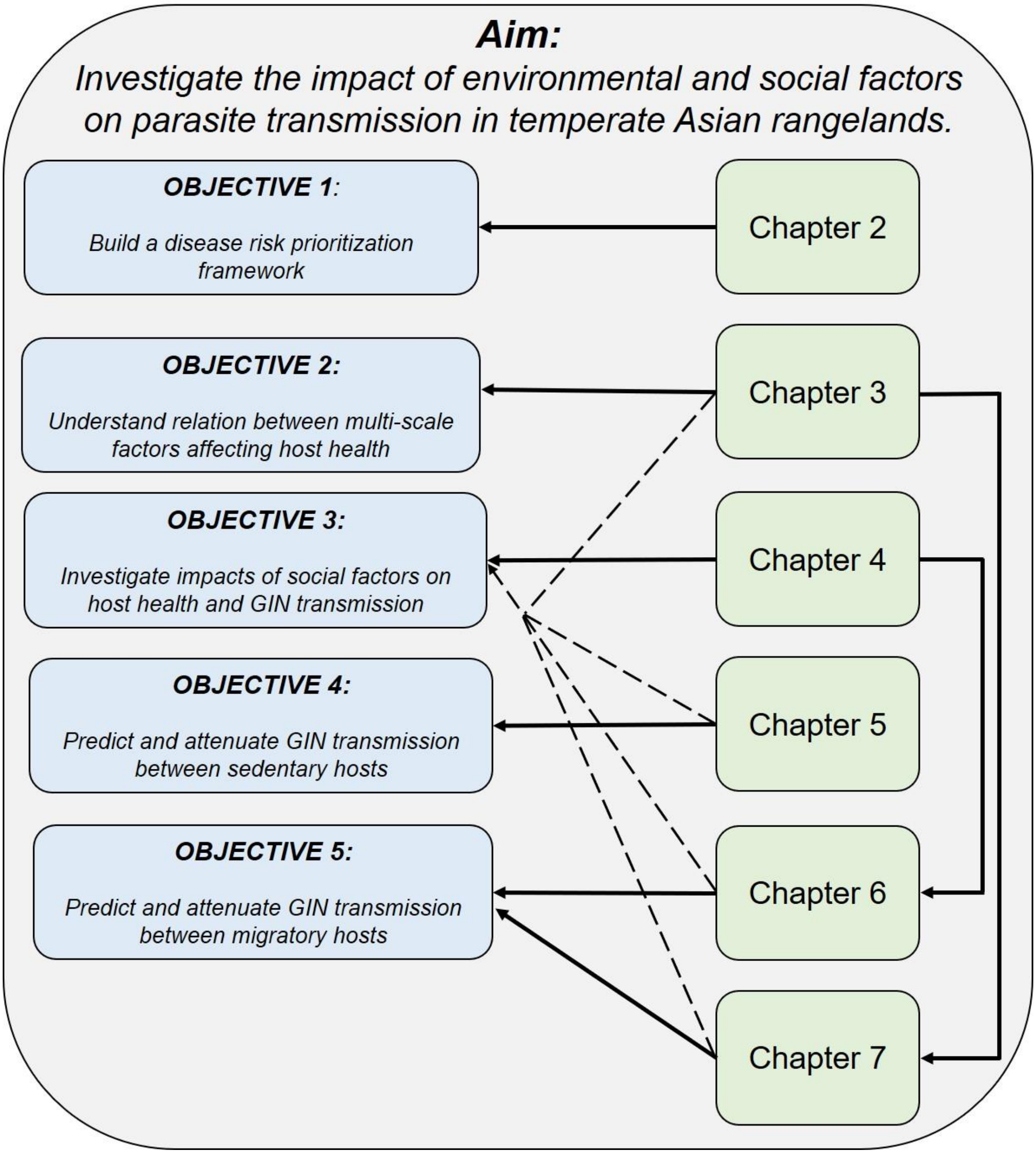


Figure 1.2. A schematic displaying the connections between different objectives and chapters. Solid lines indicate direct connections, whereas dashed lined indicate partial connection (eg. a section of a chapter contributes to a certain objective). *Note*: Objective 3 permeated through all the subsequent chapters hence the dotted lines.

1.4 Study Area: Selection, Comparability and Feasibility

1.4.1 Rationale for working across the temperate Asian rangelands

Globally, diseases are increasingly becoming a problem for wildlife, humans and their livestock (Daszak et al., 2000; Smith et al., 2009). Besides the direct impacts of diseases on individual animals and people, and hence the need to control disease events, their increasing global occurrence is correlated to anthropogenic disturbance of ecosystems, biodiversity loss and changes in the way people and animals interact (Daszak et al., 2001; Allen et al., 2017).

Currently, areas within South and South East Asia, Central Europe, sub-Saharan Africa, Central America, and parts of South America are considered as global disease risk hotspots, particularly for zoonoses and emerging infectious diseases (Jones et al., 2008; Allen et al., 2017). Evidently, these projections rely on information about past spill-overs and outbreaks (Jones et al., 2008). Altering ecological and socio-economic conditions in regions that were previously considered as relatively 'low risk', however, could transfer them to a higher risk category of disease transmission. One such region is the temperate rangelands of Asia; regions covered by the temperate and montane grasslands and shrublands across Asia (as defined by Olson et al., 2001; Fig. 1.3). Compared to tropical and other (non-Asian) temperate systems, this region has seen a relative paucity of research on disease transmission, particularly between wildlife and livestock (Allen et al., 2017). Nonetheless there are several factors disposing the Asian mountains and steppe to potential disease risk.

Local ecological factors

Often it is assumed that the predominantly cold and dry landscapes of Asia's temperate rangelands have relatively lower abundance and richness of pathogens than the warmer lower latitudes (Ostrowski & Gilbert, 2016). However, the relative importance of pathogen abundance and richness to the emergence of disease, compared to other risk factors, is largely unknown. It is also possible that lower intrinsic levels of immunity in animal populations, perhaps because of lower rates of pathogen exposure or coevolution of host-pathogen relationships compared to the tropics, could render this landscape vulnerable to disease (Ostrowski & Gilbert, 2016).

Recent studies of wild animals in this region, especially mammals, detail behavioural characteristics that could increase their disease exposure beyond what might be expected from the traditional view of these species. Asiatic ibex *Capra sibirica* and blue sheep *Pseudois nayaur*, are found extensively across the Central and South Asian mountains. They are gregarious species, exhibiting social behaviour, along with seasonally compromised body condition linked to strong seasonality and/or resource competition with sympatric livestock. These are important factors in regulating and spreading pathogens (Mishra et al., 2004; Ostrowski & Gilbert, 2016).

These characteristics are rather similar for various species of wild ungulates inhibiting the temperate grasslands of Asia (often referred to as the steppe) such as saiga antelopes *Saiga tatarica*, Mongolian gazelle *Procapra gutturosa* and Khulan *Equus hemionus*. In fact, the devastating Peste des Petits Ruminants Virus (PPRV) outbreak in Mongolian saigas *Saiga tatarica mongolica* was attributed to a spill-over from livestock, particularly exacerbated by compromised body condition due to exploitative competition and severe winter (Pruvot et al., 2020a). Additionally, many of the Asian steppe ungulates are known to migrate long distances in large groups, with calving at set times of the year (eg. Bekenov et al., 1998). Crucially, phylogenetic, dietary and habitat similarities between wild ungulates and domestic livestock in this region, like in most rangelands of the world, can facilitate pathogen spill-over or spill-back between these groups. This has serious implications for disease risk not only in wild and domestic animals, but also in the exposure risk of humans to these pathogens (Walker et al., 2017; Rohr et al., 2019).

Local social-ecological factors

Across the Asian temperate rangelands, human density is relatively low. However, these landscapes are especially extensively used by people and their livestock, representing one of the largest rangeland systems on the globe (Berger et al., 2013; Kerven et al., 2016). Large sections of society in this region are agro-pastoralists and live in close proximity to wildlife (Robinson & Milner-Gulland, 2003; Mishra et al., 2004), with relatively high abundance of livestock (Berger et al., 2013); which are often migratory (Kerven et al., 2016; Ghoshal, 2017). These factors create a close connectivity between humans, livestock, and wildlife and their seasonal movements and interactions create a regional connectivity: key to the emergence and spread of disease through creating tight contact patterns (Wiethoelter et al., 2015).

Poaching and wildlife trade - both legal and illegal - are present in this region (Kuhl et al., 2009; Li & Lu, 2014). This has implications for disease transmission via the increased direct contact of humans and wildlife and the ecosystem-level impacts associated with depletion of hunted species (Choisy & Rohani, 2006). Agricultural practices in Asia's temperate rangelands are currently changing, particularly towards intensification; new areas are being converted to cultivation of cash crops (e.g. Dara et al., 2020), reducing the diversity of crop and livestock species and breeds (e.g. Mishra et al., 2001) and increasing livestock densities on remaining rangeland (Berger et al., 2013). These changes and disruptions of existing conditions risk intensifying the likelihood of disease transmission (Epstein et al., 2006). Modern livestock management and its interface with wildlife can result in increased cycling of bacterial strains, including those carrying antimicrobial resistance (Vittecoq et al., 2016), which could be acquired and transported by wildlife (Barone et al., 2020).

Rapid urbanization and population growth are a reality across large areas of the temperate Asian rangelands (e.g. Tiwari et al., 2018). The local economies and production systems are increasingly integrated with national and regional economies. This facilitates a high movement of people and goods. For instance, a large part of the Kazakh steppe is seeing a commercial push for wheat cultivation that is aimed to be sold both nationally and internationally (Fehér et al., 2017).

Lastly, across large proportions of temperate Asian rangelands, national public services – including public and animal health (veterinary) – are not specifically adapted to the local conditions, nor always at a technologically advanced level. Inadequate investment in healthcare services and disease surveillance in this region limits the ability to predict and prepare for potential disease events across various management scales, eg. regional and national.

External factors

Temperate Asian rangelands are currently experiencing rapid changes linked to globalization and climate change. These changes have critical implications for increasing the disease risk through various mechanism, including introduction of new pathogens and vectors, habitat fragmentation, and human migration (Patz et al., 2004).

These rangelands are amongst the world’s most vulnerable areas when considering climate change, validated by the fact that in places they are warming at over twice the average rate of the northern hemisphere (eg. Li et al., 2016). Climate change will affect parasite-host assemblages, and likely result in increased frequency and intensification of disease outbreaks (Brooks & Hoberg, 2007). In 2015, there was a Mass Mortality Event (MME) of 200,000 saiga *Saiga tatarica* (65% of the global population) due to hemorrhagic septicemia caused by the bacterium *Pasteurella multocida*. Kock et al., (2018) concluded that this was linked to humidity and temperature anomalies, that are likely to become more common due to climate change.

The once remote landscapes of the Asian steppes and mountains are now under considerable flux of economic and infrastructure development, with remote habitats opening up and integrating with mainstream economies (eg. the Belt and Road initiative; Farhadinia et al., 2020). These infrastructure developments are manifold, with predominant inclusions being mining, gas and oil pipelines, new roads and railways, and large dams (Pomfret, 2005; Grumbine & Pandit, 2013). Such large development projects are often linked with pollution and immigration of workers, opening up new markets for livestock and wildlife trade, and introducing foreign pathogens and vectors (Kilpatrick & Randolph, 2012). There are also unprecedented levels of long-distance movement of people and goods between the Asian mountains and steppe and the rest of the world, creating strong pathways for the spread of disease both into and out of the region (e.g. Berger et al., 2013).

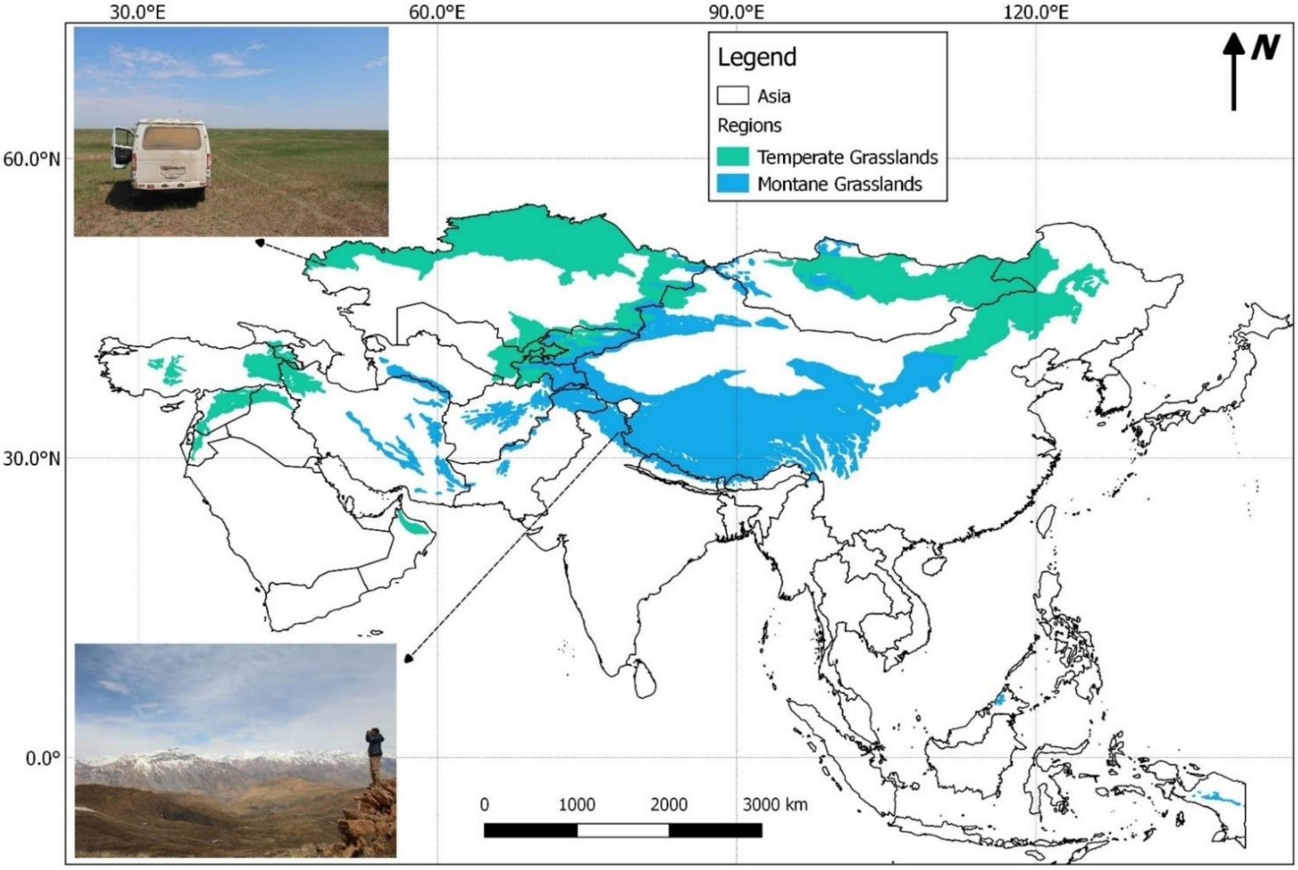


Figure 1.3. Map displaying the temperate Asian rangelands split into temperate grasslands (green; picture on top left) and montane grasslands (blue; picture on bottom left). The two images depict the areas of the Kazakh rangelands (top left) and the trans-Himalayan rangelands (bottom left) in which I worked.

1.4.2 Case study sites for the thesis

In order to address my study aim, throughout this thesis, I worked in two field sites, i) the Indian trans-Himalayas (Pin and Kibber in the Asian montane rangelands) and ii) the Kazakh Steppe (Ural and Betpak-Dala rangelands in Asian temperate rangelands) (Fig. 1.3 and 1.4). In order to address the aims, we needed sites with certain characteristics. Firstly, it was crucial that the sites had multiple hosts, both domestic and wild, as then the questions of disease transmission are relevant. Then, the sites needed to be spatio-temporally dynamic, hence the dimensions of movement influencing parasite transmission could be investigated. Lastly, the sites needed to be part of multi-use rangelands where both the social and ecological factors are likely to play a part in determining disease transmission dynamics. The reasons for working in these specific sites are provided in Table 1.2.

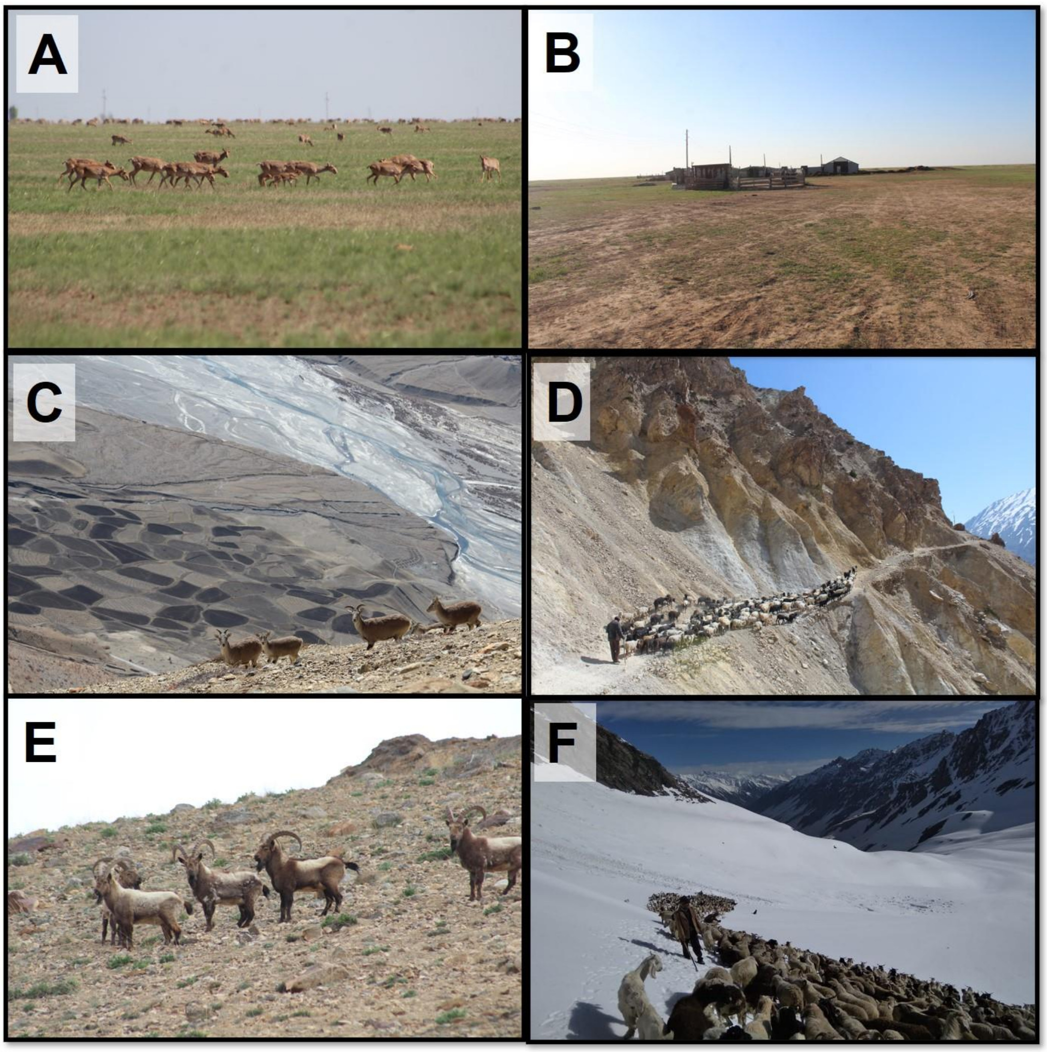


Figure 1.4. Photos of the study sites **A)** and **B)** are from the Ural rangelands within Kazakhstan of the saigas and a steppe-based livestock farm, respectively. **C)** and **D)** are from Kibber in trans-Himalayan India of a mixed Blue-sheep herd (with pea fields in the background) and a local herder, respectively. **E)** and **F)** are from Pin valley in trans-Himalayan India of Asiatic ibex (males) and a migratory livestock herd crossing into Pin valley from their spring home in the lower Himalayas, respectively.

Table 1.2 Reasons for working across the two study regions.

Reasons for working in these sites	**Why is this important?**
Primary land-use is small bodied livestock grazing (sheep and goat) (Kerven et al., 2016; Mishra et al., 2001)	This system is relatively simple in social and ecological terms while still being multi-host systems.
Home to one wild ungulate species: i) Asiatic Ibex, *Capra sibirica* in Pin. ii) Blue Sheep/Bharal, *Pseudois nayaur* in Kibber. iii) Saiga, *Saiga tatarica* in Kazakhstan. (Bekenov et al., 1998; Ghoshal, 2017)	These species are known to have exploitative competition with livestock and to share parasites. But the transmission system is tractable to analysis due to the limited number of species (eg. Morgan et al., 2006)
Spatio-temporally dynamic. i) In Pin: the livestock migrate from the plains to the trans-Himalayas (in the summer) and then back down, while the ibex are sedentary (Ghoshal, 2017). ii) In Kibber: livestock and bharal are sedentary (Mishra et al., 2001). iii) In Kazakhstan: the saiga migrate north in summer and south in the winter, while the livestock are largely sedentary (CMS, 2019).	Results in seasonal movement of hosts, and spatio-temporally varying contact patterns. Environmental heterogeneity interacts with host movement to generate a shifting mosaic of transmission within and between hosts Also, Pin and Kazakhstan are comparable, with one host migrating and another sedentary, while both are in contrast to the sedentary Kibber system.
Similar seasonality with extreme climate: i) Spring/summers are warm with occasional rain. ii) Winters are cold and often dry or witness high snowfall (Mishra et al., 2001; Bekenov et al., 1998)	We would expect GINs to have similar strategies in these environments, making these systems comparable in terms of parasite dynamics (Rose et al., 2015).
Collaborators: i) In Indian trans-Himalaya: Nature Conservation Foundation (NCF) has been working in this landscape for >20 years towards conservation. ii) In Kazakhstan, the Association for Biodiversity Conservation (ACBK) has been working for over a decade on saiga research and conservation. Both organizations collaborate with their country's governments and I have been working with both for five years.	They have reliable on-ground field teams and scientific expertise in their offices to make sure our project goes through well. They provided logistical, technical, and scientific expertise. There also had relevant historical datasets that we accessed through engaging with them.

In summary, owing to the comparability of the three field sites and all having committed collaborating organizations, it was both valuable and feasible to work across them. Understanding gained from one site was applied to the other sites, and rather than having a single case study understanding of GIN dynamics, I therefore could achieve a transferable understanding across several spatio-temporally dynamic sites.

1.5 Chapter summaries

The thesis is divided into six data chapters in order to address the aim.

To begin the thesis, in ***chapter two***, I argue that to align agricultural livelihoods with wildlife conservation in rangelands, a multipronged and interdisciplinary approach for disease management is needed, particularly in data-limited situations with migratory hosts – characteristics that are common across the temperate Asian rangelands as in many other ecosystems globally. Therefore, I developed an iterative three-step framework to assess cross-species disease transmission risk between domestic and wild hosts. I applied the framework to characterize disease transmission between livestock and saigas. This chapter directly addressed objective one, with our iterative framework having wide applicability in assessing and predicting disease spill-over at management-relevant temporal and spatial scales in areas where livestock share space with wildlife, particularly migratory species. Our case study demonstrated the value of combining ecological and social information to inform management of targeted interventions to reduce disease risk, which can be used to plan disease surveillance and vaccination programmes.

Moving forward from this, I wanted to delve deeper into GINs, their transmission dynamics, and attenuation as a means to align agricultural livelihoods with wildlife conservation. GINs are chosen for the reasons already specified, especially because they are omnipresent and impose pernicious effects on host health and performance, which can nevertheless be attenuated by careful management. Therefore, in ***chapter three,*** I suggest that to understand wildlife and livestock health and manage disease transmission in rangelands, particularly GINs, requires an integration of social and ecological knowledge. Using the example of Western Kazakhstan, home to critically-endangered saigas and livestock, I investigated relationships between ecological, social, economic, political and climatic factors acting at multiple scales and affecting host health.

After setting the broad context of the multi-scale factors that affect GIN transmission, I delve a bit deeper into investigating the social factors that can determine host health across different rangelands, in ***chapter four***. I worked with two pastoral communities in the Western Indian Himalaya: the migratory *Kinnaura*s that travel to the trans-Himalayan Pin valley in summer and the resident herders of Pin valley. Asiatic ibex is the predominant wild herbivore in Pin. The pastures in Pin are grazed by both livestock (migratory and resident) and ibex, with the potential for disease transmission. I investigated the effects of herding practices on livestock health and disease transmission, while focusing on GINs due to their interactions with nutrition, climate and observed health of the host.

Therefore, ***chapters three*** and ***four*** illustrate that GIN dynamics within rangelands are affected by various factors, requiring us to incorporate an interdisciplinary approach. Subsequently, in ***chapter five,*** I explored GIN infections in the North India trans-Himalaya through a socio-ecological lens, integrating parasite transmission modelling with field surveys and local knowledge, and evaluated the likely effectiveness of potential interventions. This study is focused in a landscape where both the domestic and wild hosts are sedentary and provides a transferable multi-pronged approach to investigating disease transmission, in order to support herders' livelihoods and conserve wild ungulates.

Building up from the case study in chapter five, ***chapters six*** and ***seven*** investigate GIN transmission dynamics in the Pin and Kazakh rangelands respectively. Both sites have one migratory (livestock in Pin and saigas in Kazakhstan) and one sedentary host (ibex in Pin and livestock in Kazakhstan). Host movement results in an additional layers of complexity in these chapters compared to ***chapter five***. In both ***chapters six*** and ***seven*** I used the same parasite transmission model as in chapter five, but extensively modified to permit investigation of parasite transmission dynamics between hosts in situations of complex movement. These chapters also used sensitivity analysis to virtually evaluate likely interventions to attenuate infection pressure for livestock and wild ungulates. ***Chapter six*** builds on the understanding of the study system laid by ***chapter four***, whereas ***chapter seven*** builds on the understanding of the study system laid by ***chapter three***. ***Chapter six*** is primarily concerned with reducing impact of GINs in migrating livestock to not only ameliorate livelihoods (through health of domestic livestock host) but also have a knock-on positive impact on the health of ibex (wild host) by reducing GIN transmission. By contrast, ***chapter seven*** is primarily concerned with ensuring the health and conservation of saigas (wild host) with potential knock-on positive impacts on livestock (domestic host) health. In ***chapter seven***, we also take GIN parasite transmission dynamics modelling one step further, by assessing how GIN parasitism might change for wild hosts into the future given the anticipated changes in their habitat, using a scenario analysis approach.

Lastly, I synthesize the results from all the chapters in the light of the overall research aim articulated above, and discuss future avenues of work, and current pitfalls, in the discussion, i.e. ***chapter eight***.

1.6 Position statement and ethical considerations

My positionality impacted the research I did for this thesis and the interpretations I made based on my results.

I was born in Kashmir, a region in northern India Himalayas to an upper middle income family. The privilege of being born into an economically stable family in a politically hostile area meant I had the luxury of shifting to Mumbai, a metropolitan city in India. This is where I got educated in a private school, eventually doing my undergraduate degree at an “elite” institution, McGill University in Canada, on Wildlife Biology. This was before starting my PhD at another “elite” institution, the University of Bristol, UK. My entire academic journey has been in an English language dominated context.

All throughout my time as a schoolboy and even whilst I was doing my undergraduate degree, I kept visiting my home in Kashmir. This is where for me “nature” existed in its splendour, an escape from the concrete confines of my city homes. Often my parents and I would go on treks through the mountains searching for wildlife, particularly mountain ungulates - species that not only came to symbolize the mountains, but also home for me. However, finding wildlife in the Kashmiri Himalayas was always a task, as wildlife is predominantly at relatively low densities here. Also, almost all valleys within the

Kashmiri Himalayas are visited by herders (many of them migratory) and their livestock (predominantly sheep and goat). Growing up, to me, these herders came to symbol disturbance, encroachment and the "unnatural" – especially as from my perspective they stood where the "wildlife" should have been.

After my undergraduate degree and just before I was about to start my PhD, I was fortunate to get a job with Nature Conservation Foundation (NCF, a wildlife conservation NGO in India). For over two decades now, NCF has been working in the trans-Himalayan region of India, towards building positive human-nature relations, attempting to work towards coexistence between people and wildlife. Through my time working with them, I came to realize that livestock herders in the Himalaya, much like most other rangelands of the globe (particularly in so-called "developing countries") are found across these areas almost ubiquitously. Not only are these people at the centre of human-wildlife interactions – often ones that negatively affect herders' emotional and economic wellbeing - they are also (often) disproportionately affected by conservation action and policy. I quickly came to realize the mountains I grew up thinking of as "pristine" and "untouched" landscapes, were for millennia, systems where human and wildlife have been inextricably linked – albeit rapidly changing in our contemporary world. This made me aware of the fact that domestic animals and people should be recognized as integral components in contemporary ecosystems.

Therefore, throughout the thesis I have tried to address my research questions at each study site whilst trying to be inclusive of the pluralistic value systems that may exist there. This is particularly important as not only do I come with a background of training in and love for ecology, in the places I worked I am inevitably an outsider to some degree. Kazakhstan is a country I had visited once before the start of my PhD and I don't speak the language, nor did (or indeed still do) I know much about its cultural and ecological context. The Indian trans-Himalayan sites, even though so close to my place of birth, have contextual layers of socio-cultural and ecological subtleties that are far more nuanced that the realities that I knew of while growing up. Beyond the noteworthy ethical considerations of working with wild and domestic species, and their owners/caretakers, throughout the PhD I have tried to conduct my research as a step towards achieving the panacea of human-wildlife coexistence. My work is not independent of the love that I have for the wild species that call many of the globe's rangelands their home, nor is it independent of the admiration and respect I have for the many people that call it home as well.

More formally, I applied for and obtained ethical clearances for each of my chapters through the University of Bristol formal ethics procedure. This included several discussions about ethical implications of our work with my supervisors. Following that, we submitted our proposal along with the official application documents for consideration to the Ethics committees. The committee aims to work collegially, drawing on the diverse research experience of its members, to support the development of ethical mindfulness. The ethics committee's aim is to i) facilitate shared discussion, reflection and learning, and ii) contribute to sensitive, supportive ethical procedures. This committee scrutinized each proposal and raised concerns where needed. Upon addressing these concerns, I was given ethical clearance. Besides this, in both Kazakhstan and India, before starting the work, we had several discussions and submitted proposal to obtain research permits from the appropriate government and local (non-governmental) authorities. Work was only started when we had the legally required paperwork and consent from all the relevant authorities.

Finally, arguably one of the major ethical issues I faced during my PhD was to ensure that I didn’t provide false expectation to the herders I worked with. As my research was applied, there were instances several herders I worked with felt that I might bring about changes that would ameliorate their livestock’s health and their own socio-economics. While my hope is that lessons from my PhD could be applied, with the herders' input, to co-benefit them and the wildlife they share space with; managing herder expectation whilst I did my research was a major ethical challenge. I tried to deal with this by having repeated honest conversations with the herders and explaining to them the process of research - which first forms the knowledge base upon which action can be taken.

1.7 Additional research during my PhD

Below are a set of research outputs that I managed to be a part of during the life of my PhD. These are not directly focussed on my thesis's research aims, but are related work that I was able to do in collaborations with my research partners NCF and colleagues in Oxford university.

Suryawanshi, K. R., **Khanyari, M.**, Sharma, K., Lkhagvajav, P., & Mishra, C. (2019). Sampling bias in snow leopard population estimation studies. *Population Ecology*, *61*(3), 268-276.

Mishra, C., **Khanyari, M.**, Prins, H. H., & Suryawanshi, K. R. (2019). Community Dynamics of Browsing and Grazing Ungulates. In *The Ecology of Browsing and Grazing II* (pp. 181-196). Springer, Cham.

Booth, H., Arias, M., Brittain, S., Challender, D. W., **Khanyari, M.**, Kuiper, T., ... & Milner-Gulland, E. J. (2021). "Saving lives, protecting livelihoods, and safeguarding nature": risk-based wildlife trade policy for sustainable development outcomes post-COVID-19. *Frontiers in Ecology and Evolution*, *9*, 99.

Khanyari, M., Luecke, S., Mishra, C., & Suryawanshi, K. R. (2021). Understanding population baselines: status of mountain ungulate populations in the Central Tien Shan Mountains, Kyrgyzstan. *Mammalia*, *85*(1), 16-23.

Suryawanshi, K. R., Mudappa, D., **Khanyari, M.**, Raman, T. S., Rathore, D., Kumar, M. A., & Patel, J. (2021). Population assessment of the Endangered Nilgiri tahr *Nilgiritragus hylocrius* in the Anamalai Tiger Reserve, using the double-observer survey method. *Oryx*, *55*(1), 66-72.

Khara, A., **Khanyari, M.**, Ghoshal, A., Rathore, D., Pawar, U. R., Bhatnagar, Y. V., & Suryawanshi, K. R. (2021). The forgotten mountain monarch? Understanding conservation status of the Vulnerable Ladakh urial in India. *European Journal of Wildlife Research*, *67*(4), 1-10.

Mishra, C., Samelius, G., **Khanyari, M.,** Srinivas, P.N., Low, M., Esson, C., Venkatachalam, S., & Johansson, O. (2021). Increasing risks for emerging infectious diseases within a rapidly changing High Asia. *Ambio*. DOI: https://doi.org/10.1007/s13280-021-01599-7

Pienkowski, T., Keane, A., Tickell, S. C. Y., Hazenbosch, M., Arlidge, W. N., Baranyi, G., Brittian, S., de Lange, E., **Khanyari, M.,** Papworth, S., & Milner-Gulland, E. J. (2021). Balancing making a difference with making a living in the conservation sector. *Conservation biology*. DOI: https://doi.org/10.1111/cobi.13846.

- Chapter 2 -

Building an ecologically-founded disease risk prioritisation framework for migratory wildlife species based on contact with livestock

Published as **Khanyari, M.**, Robinson, S., Morgan, E.R., Brown, T., Singh, N.J., Salengareyev, A., Zuther, S., Kock, R., & Milner-Gulland, E.J. (2021). Building an ecologically-founded disease risk prioritization framework for migratory wildlife species based on contact with livestock. Journal of Applied Ecology. DOI: https://doi.org/10.1111/1365-2664.13937

Authors' contributions

EJMG and I conceptualised the framework which was further refined by her, SR, EM and NS. We also led the writing of the manuscript. I, SR, EM, RK and SZ conducted the on-ground surveys. TB and I analysed the data. I led the writing and all authors provided critical inputs.

A new born saiga calf

Abstract

Shared use of rangelands by livestock and wildlife can lead to disease transmission. To align agricultural livelihoods with wildlife conservation, a multi-pronged and interdisciplinary approach for disease management is needed, particularly in data-limited situations with migratory hosts. Migratory wildlife and livestock can range over vast areas, and opportunities for disease control interventions are limited. Predictive frameworks are needed which can allow for identification of potential sites and timings of interventions. We developed an iterative three-step framework to assess cross-species disease transmission risk between migrating wildlife and livestock in data-limited circumstances and across social-ecological scales. The framework first assesses risk of transmission for potentially important diseases for hosts in a multi-use landscape. Following this, it uses an epidemiological risk function to represent transmission-relevant contact patterns, using density and distribution of the host to map locations and periods of disease risk. Finally, it takes fine-scale data on livestock management and observed wildlife-livestock interactions to provide locally-relevant insights on disease risk. We applied the framework to characterize disease transmission between livestock and saiga antelopes *Saiga tatarica* in Central Kazakhstan. At step 1, we identified peste-des-petits-ruminants as posing a high risk of transmission from livestock to saigas, foot-and-mouth disease as low risk, lumpy skin disease as unknown and pasteurellosis as uncertain risk. At step 2 we identified regions of high disease transmission risk at different times of year, indicating where disease management should be focussed. At step 3, we synthesized field surveys, government data and literature review to assess the role of livestock in the 2015 saiga mass mortality event from pasteurellosis, concluding that it was minimal. Our iterative framework has wide applicability in assessing and predicting disease spill-over at management-relevant temporal and spatial scales in areas where livestock share space with migratory species. Our case study demonstrated the value of combining ecological and social information to inform management of targeted interventions to reduce disease risk, which can be used to plan disease surveillance and vaccination programmes.

2.1 Introduction

Over one-third of the world's land area is grazed by livestock (Reid et al., 2008). The number of people living on <$2USD per day who also rear livestock is increasing by 1.4% per year, and reached 752 million in 2010 (Otte et al., 2012). On rangelands, the primary resource for domestic and wild ungulates is pasture (Berger et al., 2013). Shared use of rangelands can lead to interspecific disease transmission, which can impact agricultural livelihoods (Reid et al., 2008) and wildlife conservation (Smith et al., 2009).

Although many factors contribute to disease transmission, seasonal distributional overlap between wild and domestic ungulates is particularly significant in the epidemiology of shared pathogens for migratory species. Cross-species disease transmission depends on contact patterns, governed by host distributions and movement (Vosloo et al., 2002), and hence by socio-economic factors and climate-induced changes in resource availability (Robinson & Milner-Gulland, 2003; Weinstein & Lafferty, 2015). Seasonal movements of wild and domestic ungulates, landscape management, and aggregation at various spatial scales, can strongly modify host contact patterns and hence affect disease cross-species transmission risk (Morgan et al., 2006; Pruvot et al., 2020b). However, disease management can have negative consequences like compromised immune responses, altered parasite-mediated apparent competition between hosts, and destabilising the host-parasite arms race (Stringer & Linklater, 2014). Thus, it is important to question what level of contact is detrimental and if control is indeed required, especially in data-poor and logistically challenging systems. Beyond contact patterns, host population size, weather, and the presence, life-histories, and intensity of pathogens also play important roles in disease transmission (e.g. Redfern et al., 2015).

While delineating contact patterns provides a foundational understanding of potential transmission, empirical understanding of disease dynamics in multi-use landscapes faces logistical, technical, economic and political challenges (Wobeser, 2007; Ryser-Degiorgis, 2013). These include constraints of working over large, remote areas; limited tools for disease detection, especially in lesser-studied species; and the hazards of handling wild species (Kosmala et al., 2016). Many multi-use landscapes, defined as areas where livestock use the same space as wildlife (particularly migratory species), are consequently data-poor. Therefore, approaches are needed that support prioritised data collection in such landscapes, to provide preliminary guidance on cross-species transmission risks in data-limited circumstances.

Multiple types of data, across various social and ecological scales, can be collected to understand disease transmission, albeit with methodological challenges in data compilation. Therein, a prioritisation framework can optimise the use of diverse available knowledge to assess risk of disease cross-species transmission based on contact patterns. Empirical approaches can be expensive, particularly if disease prevalence is low (thus requiring extensive sampling), and data collection requires specialized equipment (Lernout et al., 2019). Modelling approaches can be made affordable by accessing publicly-available databases to build models. Additionally, farmers sharing habitats with wildlife can have first-hand experience of wildlife-livestock interactions (Tomaselli et al., 2018) and can provide rich information concerning spatial overlap in different seasons (Huntington, 2000). Capturing this in a systematic and unbiased manner can provide insights on a landscape as a social-ecological system, which cannot be obtained through epidemiological investigations alone (Tomaselli et al., 2018).

While multi-scale disease transmission frameworks exist, most have several limitations. Even though existing frameworks build up from individuals to populations (eg. Garabed et al., 2019; Garira, 2020), often they consider only one definitive host (Morgan et al., 2004), employ resource-intense methodologies (Gaudelet et al., 2020), and fail to incorporate both the social and ecological aspects driving potential disease spill-over risk across various ecological scales. Additionally, Schwartz et al. (2018) caution against using any one framework in isolation as it risks diminishing potential benefits, as no one framework covers the full spectrum of potential conservation planning and decision challenges.

Here, we developed a multi-pronged and interdisciplinary approach for prioritisation of disease risk management, and tested its utility for saiga antelopes *Saiga tatarica* in Kazakhstan. We then explored its potential for wider application. Although many shared pathogens can, in principle, cross between livestock and wildlife in either direction, we regard the implications of disease transmission from livestock to wildlife as particularly concerning, as it might threaten the survival of endangered species' populations. Hence, we decided to focus on only one transmission direction in the development of this framework. Given historical disease events in saigas (Robinson et al., 2019), we expected various diseases to be of concern for saigas. Also, as seasonally migrating saigas range over vast areas, often co-grazed by livestock, we expected differential disease transmission risk across space and time based on contact patterns.

2.2 Material and Methods

2.2.1 A disease risk prioritisation framework

The framework aims to help researchers identify and reduce risk of spill-over from livestock to migratory wild ungulates in resource-limited and logistically challenging landscapes. The outputs can be communicated to decision makers to prioritize further data collection and draft interventions. To do so requires risk assessment of spill-over at various scales. The framework has three steps, each at progressively finer spatial, ecological and institutional scales (Fig. 2.1).

Step one: Identifying disease risks

Step one identifies livestock-wildlife spill-over disease risks at the broadest ecological scale (annual distribution). Firstly, potentially important diseases are identified, based on a literature review. Subsequently, relevant disease-risk information is synthesized into a qualitative risk assessment table, based on: a) likelihood of occurrence in wild ungulates, b) likelihood of transmission from livestock, c) severity (morbidity and mortality once transmitted), d) existing mitigation strategies in livestock. These criteria are synthesized into one risk indicator; high, low, unknown or uncertain. A disease is categorized as high risk when the likelihood of transmission from livestock to wild ungulate is high; disease severity (morbidity and mortality) is high; and mitigation strategies are currently inadequate or unavailable. A disease is low risk when the likelihood of transmission from livestock to wild ungulates is low; the severity is low; or adequate mitigation strategies are already in place. A disease is of unknown risk when the available information about presence in wild ungulates, probability of transmission, mortality rates and mitigation strategies are not adequate for qualitative risk assessment.

For a given disease, if there is a mix of high and low, risk for different criteria, the disease is classified as having uncertain risk.

Step two: Identify locations and times of disease risk

Step two identifies locations and periods of risk for the diseases attributed high, unknown or uncertain risk in step one, at the intermediate ecological scale (seasonal distribution). This step involves designing an epidemiological risk function to represent transmission-relevant contact patterns, combining key host (density and distribution) and pathogen traits (transmission pathway, life history). Accessible datasets on host numbers and locations are used as function inputs. The output is seasonal disease risk maps at a resolution determined by the datasets. These maps can be used to focus local surveillance and prioritize disease mitigation strategies at appropriate administrative levels.

Depending on available information, more or less complex and data-informed functions can represent this risk. We propose the following basic equation (2.1) that can be refined with improved data:

$$R = \left[\frac{n_l}{m}\right] \times n_w \quad (2.1)$$

Where R = disease risk score, n_l = livestock number in a given area, n_w = groups of wild ungulates present in that area at a defined time and m = mean observed distance between wild ungulates and livestock during periods of co-occurrence. Unless the case studies have richer information, and if wild ungulates are herding species, such that group is an appropriate epidemiological unit, we recommend starting with a similar function.

A higher R represents a higher disease risk to wild ungulates based on the density and distribution of livestock and wild ungulates and their proximity. In most countries, disease mitigation (e.g. vaccination) is determined at specific levels of government administration. Hence, calculating risk scores at appropriate administrative levels helps policymakers/practitioners prioritize resource allocation. Regions highlighted as having high disease risk from this step can be prioritized for fine-scale investigation in step three (below).

Step three: Fine-scale disease spill-over risk from livestock to wildlife

Step three identifies fine-scale (within-season distribution) transmission risk from livestock to wild ungulates, with the granularity informed by maps from step two. Participatory research techniques like semi-structured interviews and resource mapping (Huntington, 2000) can be used to gather data on aspects including land access mechanisms (political), livestock distribution (social) and health issues in livestock and their mitigation (veterinary) from a representative sample of local stakeholders. This should focus on diseases of concern delimited by step one, in areas of risk, delimited by step two. Upon synthesizing social and ecological information on the within-season locations and movements of wildlife and livestock, and livestock health issues and disease mitigation strategies, obtained through participatory research techniques with local stakeholders (eg. herders), the output is a disease risk statement. The statement considers the likelihood that i) in case of a disease event, an outbreak originated in livestock and was transmitted to wild ungulates, or ii) in the absence of a disease event, disease will cross-transmit from livestock to wild ungulates.

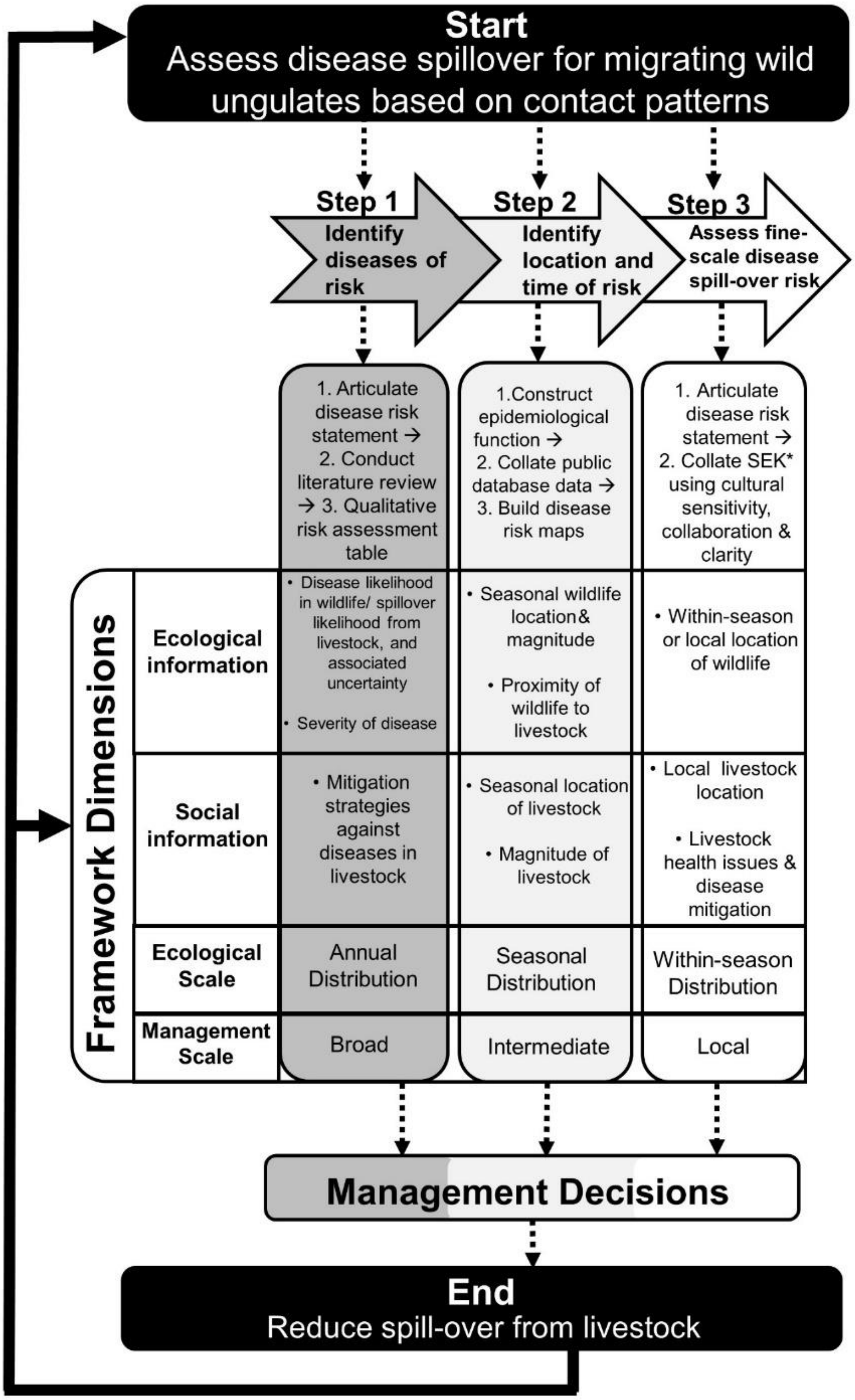


Figure 2.1. A disease risk prioritisation framework based on contact patterns, comprising three steps, with components across four dimensions of information and scale. They collectively inform management decisions across various scales, to reduce potential or actual spill-over. *SEK: socio-ecological knowledge.

2.2.2 Case study of framework application: Saiga antelopes

We explore the potential for disease transmission from livestock to saigas. Saigas are found across the rangelands of Kazakhstan, Russia, Uzbekistan and Mongolia. The so-called Betpak-Dala population, in Central Kazakhstan, undergoes extensive migrations driven by a combination of rainfall and plant phenology (Singh et al., 2010a). They have suffered various disease outbreaks linked to spill-over from livestock, including foot-and-mouth disease (FMD) between 1955 and 1974 (Fadeev & Sludski, 1982). Beyond FMD, pasture-sharing with domestic animals is a source of other diseases which have caused saiga mortality (Lundervold et al., 2001). Mass Mortality Events (MMEs) affecting tens or hundreds of thousands of animals in 1981, 1984 and 1988 were suspected to be various forms of pasteurellosis (Robinson et al., 2019), which also occurs in livestock.

Following the collapse of the Soviet Union in 1991, saigas declined by >90% due to overhunting, leading to them being listed as Critically Endangered on the IUCN Red List (Milner-Gulland et al., 2003). Following a partial recovery, another MME killed >200,000 individuals in Betpak-Dala in May 2015, representing 88% of this population and 62% of the global population (Kock et al., 2018). The proximate cause was haemorrhagic septicaemia caused by a normally commensal bacterium, *Pasteurella multocida* serotype B, possibly linked to heightened humidity and temperature in the 10 previous days (Kock et al., 2018). The role of livestock in the 2015 MME remains understudied. Another MME took place in the Mongolian sub-species *S. t. mongolica* in 2016-17, caused by a livestock-transmitted virus, peste-des-petits-ruminants virus (PPRV), killing a significant proportion of the population (Pruvot et al., 2020aa).

Increasing livestock numbers throughout the saiga range since 2000 (Appendix A, Figure 1) produces both a threat of disease spill-over to saigas, and opportunities to understand shared drivers of disease emergence. We focused our work on the Betpak-Dala saiga population (Fig. 2.2). We defined the "maximum potential range" of the population by pooling seasonal saiga locations from 1970-2008 (Singh et al., 2010a; see step 2 below). Saigas migrate within this range seasonally, with their migration varying annually, based on population size, climatic conditions, pasture condition, availability of surface water, and the amount of disturbance experienced by the animals (Bekenov et al., 1998; Singh et al., 2010a).

Across Betpak-Dala, saigas share the landscape with livestock. Currently, predominant livestock in the area are sheep, goat, cattle and horses. During Soviet times, the steppe contained large state and collective farms, which were provisioned by the state government and housed tens of thousands of livestock (Robinson & Milner-Gulland, 2003). Currently, most households own relatively small numbers of animals, which graze around village centres, typically <3km radius. Some private farms exist away from the village and potentially closer to saigas, which are known to avoid human settlements, especially during the calving period (Singh et al., 2010b).

Step one

We assessed all existing and potential diseases with transmission risk between livestock and Betpak-Dala saigas, to prioritize future investigations. Given the limited literature on saiga disease, we used guided expert opinion to survey all peer-reviewed articles published in English on infectious diseases of saigas and sympatric livestock (Appendix A, Table 1). Due to their extensive contributions to, and engagement with, the saiga literature since the early 1990s, the authors EJMG, ERM, SR and RK were able to point to relevant articles. We also used comprehensive reviews of the relevant information in the Russian literature. For instance, Robinson et al., (2019) reviewed Soviet-era literature on MMEs, Lundervold et al., (2001) reviews historical disease events and prevalence in saigas recorded in English and Russian, and Bekenov et al., (1998) reviews the ecology and management of saigas in Kazakhstan, including disease. This literature was used to understand the presence, transmission risk, and severity of diseases that can infect livestock and saigas. We explored potential mitigation options for these diseases using literature and expert judgement of veterinarians and researchers in Kazakhstan. If there was uncertainty about the host range of a disease and its potential spill-over to saigas, we aided our interpretation by scanning the literature on other wild ungulates, with a particular focus on those co-occurring with livestock across temperate regions, as pathogen range often mirrors host phylogeny (Walker et al., 2017). Diseases known to infect both domestic and wild ungulates in other regions, therefore, were considered likely to cross from livestock to saigas. We conducted the search in Google

Scholar, and used a snowballing approach until we had gathered relevant information or satisfied ourselves that there was no information available. Hence, the assessment was indicative rather than exhaustive.

Step two

At step two we aimed to highlight areas of Betpak-Dala where surveillance could be particularly focussed, due to the spatio-temporal overlap of saigas and livestock. There is limited information on actual disease transmission between livestock and saiga. We therefore used equation (2.1) plugging in number of saiga group for wild ungulates ($n_w = n_s$):

$$R = \left[\frac{n_l}{m}\right] \times n_s \quad (2.2)$$

where R = disease risk score, n_l = livestock number in a given area, n_s = number of saiga groups present in that area at a defined time, m = mean observed distance between groups of saigas and livestock farming settlements during periods of co-occurrence. Table 2.1 gives the data sources for parameter estimation.

As saigas are migratory, estimates of R were generated for spring (1 March-30 April), summer (1 June-30 September), autumn/winter (1 October-28 February) and calving seasons (1-31 May). Calving is separated from spring, because it is a crucial life history stage for saigas when females aggregate in large numbers in relatively small areas to give birth to calves over a short *c.* 7-10 day period, before migrating northward for the rest ofspring and summer (Bekenov et al., 1998). Epidemiologically, a high number and density of hosts is expected to promote disease transmission, assuming presence of transmissible pathogens. The literature frequently highlights calving as a high-risk time for disease (Morgan et al., 2006; Robinson et al., 2019).

Kazakh vaccination plans are primarily executed by *raions* (districts). Target numbers and resource provision for vaccination are set at the next level up; the *oblast* (province). We calculated the risk scores at the *raion* scale.

Step three

In our case study, step three involved gathering fine-scale information to assess the likelihood that disease transmission from livestock had contributed to the 2015 MME. Given that no pathogens except *Pasteurella multocida* serotype B were identified in the dead saigas, Kock et al., (2018) had identified pasteurellosis as the cause of death, consistent with the symptoms of haemorrhagic septicaemia (step one). The 2015 MME occurred across the calving range over the same short time period (Figure 2.2). Most animals observed at the die-off sites died within a few hours of onset of clinical signs (Kock et al., 2018). Incubation periods for haemorrhagic septicaemia range from 12 hours to a few days (Bastianello et al., 1994), suggesting that if transmission from livestock contributed to the pasteurellosis MME, it would have occurred locally – during, or immediately prior to, calving (step one). This does not exclude the possibility of prior transmission of a predisposing pathogen earlier in the saiga migration, but no such pathogen was found (Kock et al., 2018; Fereidouni et al., 2019). Therefore, we focussed step three of our investigations in areas where die-offs were reported, rather than first using step two to identify areas of potential risk. As it happens, these areas are also areas identified at step two as of higher-than average risk. Hence our framework is also useful to potentially traceback places of spill-over.

Semi-structured interviews and resource mapping (Huntington, 2000) were conducted between 6-24 May 2016. Interview topics included land access mechanisms, livestock distribution and health issues in livestock and their mitigation, focussing on pasteurellosis. The team visited the central “Torgai” cluster of die-off sites in Zhangeldi and Amalgeldi *raions* of Kostanai *oblast* (Figure 2.3). We aimed to survey a representative selection of herders, Protected Area rangers and State wildlife rangers; the latter two are mandated to protect saigas. Within each of our five focal study regions (i.e. sub-districts), we first interviewed the mayor and veterinarians and then conducted 19 in-depth interviews using a snowballing approach with livestock owners, as key informants. The selection criterion for interviewees was that they were grazing livestock near areas of observed saiga mortality.

We also visited the land committee and veterinary departments at the administrative centres of Amangeldi and Zhangeldi *raions*. In Zhangeldi, we photographed cadastral maps from 2014, showing village grazing land and parcels leased by registered farms and companies and obtained land statistics

(Appendix A, Table 2,3,4 and Figure 2.3). In Amangeldi, it was not possible to photograph cadastral maps. Instead, committee staff drew the borders of those land parcels located in saiga areas on the topographic maps. The identity and size of those parcels could be inferred based on the land statistics.

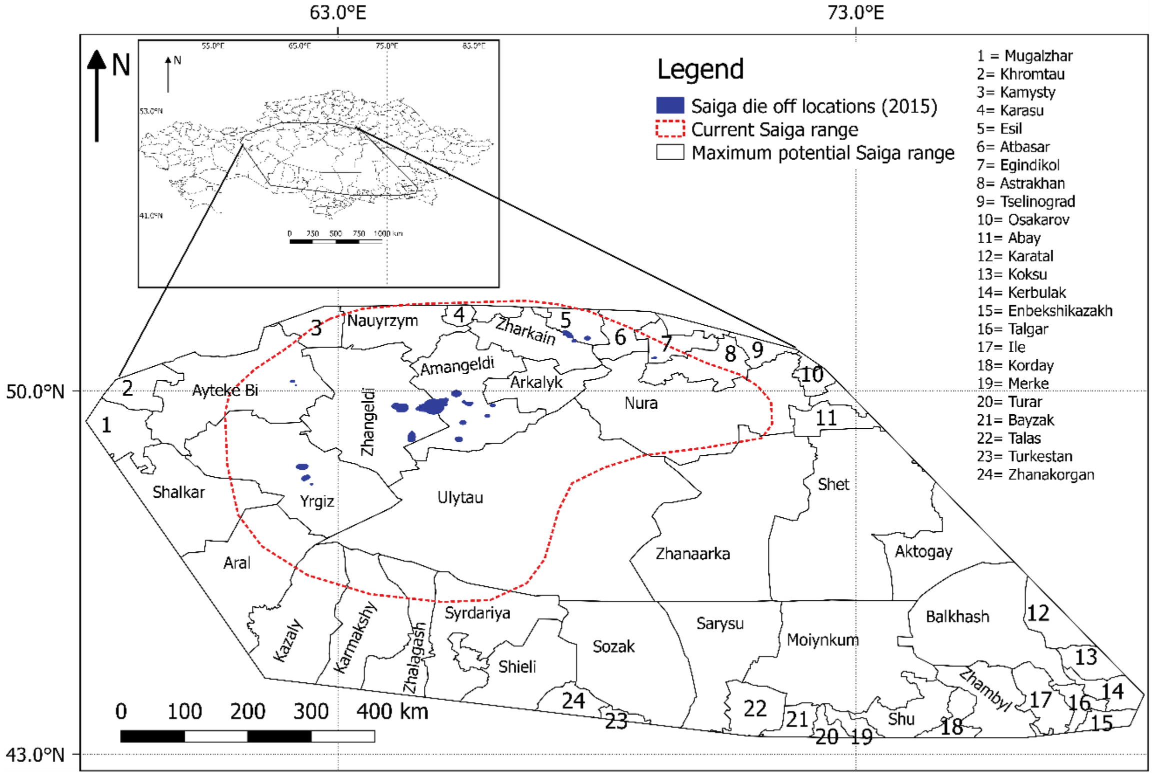


Figure 2.2 Inset: Historic range of the Betpak-Dala saiga population within Kazakhstan. **Main map**: The individual raions (districts) within the maximum potential Betpak-Dala saiga range. Also mapped is the Betpak-Dala population extent during the MME and the 2015 die-off site

Table 2.1. Variables included in the disease risk score, Equation 2.1.

Symbol	What it represents	Database	Reliability of data	Further comments
n_l	Number of livestock in *raion* (district)	Kazakhstan government online livestock identification database (Kazakhstan Government Online Livestock Identification Database, 2018).	Livestock must be registered within 3 months of birth in Kazakhstan. Government collated this information and data are increasingly available as Kazakhstan aims to modernize its veterinary system. Finest scale of comprehensive online data was at the settlement level, but these needed on-ground reconciling of settlement names with GPS locations so aggregated *raion*-level data were used.	For further analyses, livestock was split into three categories, "sheep/goat", "cattle", and "combined" (sheep/goat and cattle). Depending on disease type, transmission threat could be from only sheep/goat, only cattle, or both.
n_s	Number of saiga groups in *raion* for each season	A database of point location of saiga groups, each with a season attribute, was obtained by contacting the lead author of Singh et al., (2010a), which pooled saiga locations from 1970-2008. These were spring, summer,	Singh et al., (2010a) used group locations from historical field reports to generate historical seasonal ranges by migrating saigas. They collated information from books, published articles and other Russian	Saiga population range has changed considerably over the past 5-6 decades and the contemporary saiga range during the die-off (2015) was more restricted than it was in the 1970s (Singh et al., 2011).

		winter and calving. We defined this as the “maximum potential range”. We used this rather than the contemporary range, as we lacked saiga group location data for this area.	language sources. The maximum potential range polygon was generated by drawing a Minimum Convex Polygon (MCP) around the plotted locations of saiga groups retrieved from Singh et al., (2010a), in QGIS. Contemporary saiga distribution (i.e. distribution in 2015) was obtained from the Convention on Migratory species report for saigas (CMS, 2019).	As saigas are a herding species, the group was the appropriate unit of analysis.

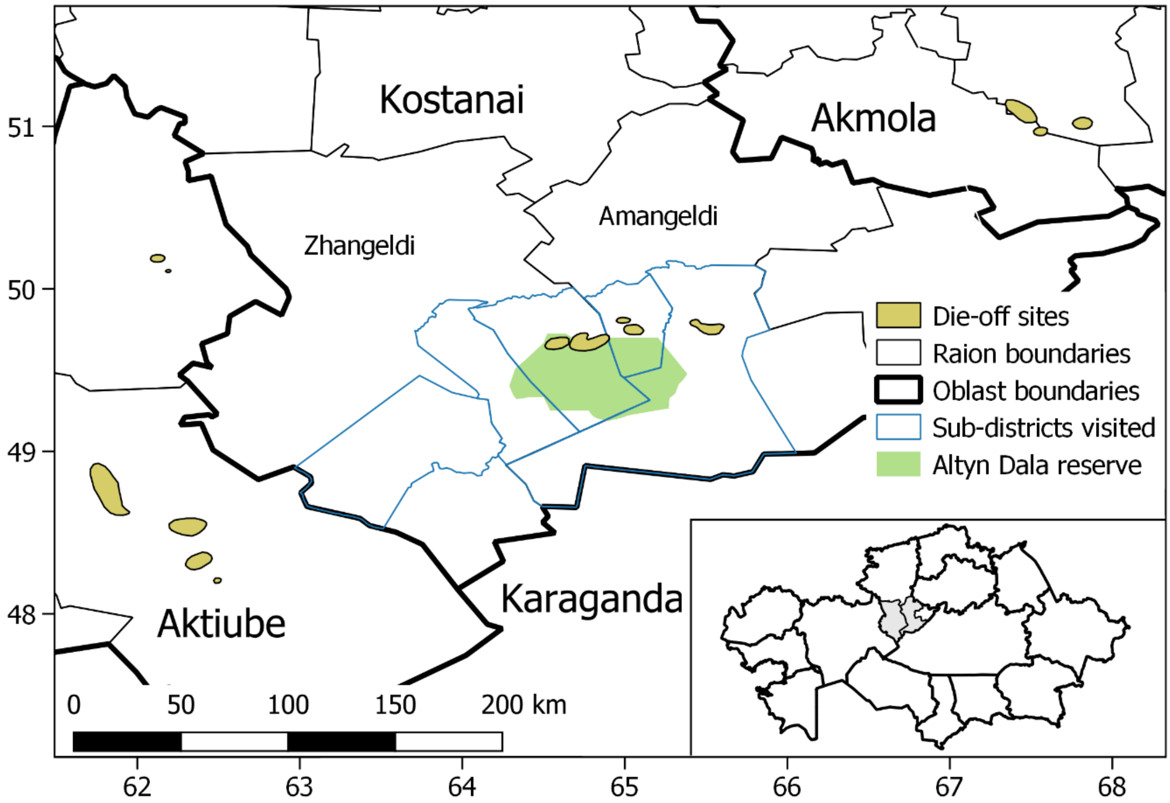


Figure 2.3. Location of 2015 saiga die-off sites including those visited during fieldwork. ***Note:*** *Source of die-off location data: Association for the Conservation of Biodiversity of Kazakhstan / Committee for Forestry and Wildlife of the Ministry of Ecology, Geology and Natural Resources of Kazakhstan.*

2.3 Results

2.3.1 Step one: Identifying disease risks

Table 2.2 is the qualitative integrated assessment of potential risks of disease spill-over from livestock to saigas. Four illustrative diseases are represented here, covering low, high, unknown and uncertain risk. We include pasteurellosis due to its importance for step three. The remaining diseases are listed in Appendix A, Table 1.

Table 2.2. A qualitative integrated risk assessment for potential risk of disease spill-over from livestock to saigas, with a focus on the Betpak-Dala population in Kazakhstan (four exemplar diseases). Green = low risk, red = high risk, dark grey = unknown and grey = uncertain risk.

Disease **(key references)**	**Likelihood**	**Severity**	**Current Mitigation**	**Uncertainty**
Foot and Mouth Disease (FMD) *Bekenov et al., 1998;* Fadeev & Sludskii, 1982; *Morgan et al., 2016*	Cattle, sheep and goats are known to be carriers and transmit to saigas. Cattle are more readily infected by airborne virus.	Historically, spill-over caused MMEs, especially affecting saiga calves .	Kazakhstan is FMD-free due to past livestock vaccination; could be re-instituted if FMD arrives again. Saigas seem to need re-infection from livestock to be affected.	Kazakhstan retains capacity to ensure that FMD remains eliminated. Especially, prevention of re-introduction of FMDV through cross border livestock movement.
Petit Peste des Ruminants (PPR) *Kock et al., 2015; Pruvot et al., 2020a*	Sheep and goats are known to suffer epidemics and can vector virus to wildlife (including saigas) through environment. Novel disease in Kazakhstan, but occurs in neighbouring countries. Unless mitigation is proactive, saigas will remain defenceless.	Caused a devastating MME in Mongolian saiga sub-species in 2016.	Nearly all susceptible animals are vaccinated in oblasts along the southern border region of Kazakhstan. Coverage in other regions is likely low or non-existent.	Lack of knowledge and expertise to deal with PPR. Vaccination coverage limited to preventing disease entering from Kyrgyzstan, but PPR has also been recorded in China and Mongolia and there does not seem to be vaccination in the areas bordering these two countries. PPR outbreaks in Kazakh saigas (the nominate sub-species) not recorded yet, though seroprevalence has been determined.

Lumpy Skin Disease EFSA, 2020; Taylor et al., 2019	Outbreak in cattle in Kazakhstan has been recorded. No published outbreaks in saigas, but there is published evidence of spill-over to wildlife in other regions of Eurasia.	c. 10% of infections resulted in mortality in cattle.	Nearly all susceptible animals are vaccinated in oblasts along the Russian border. Coverage in other region is likely low or non-existent.	An emerging disease in Kazakhstan with only one confirmed report from 2016. Current extent and spread in future remains highly uncertain. Efficacy of vaccines remains uncertain. Evidence of susceptibility and severity of infection in saigas needed.
Pasteurellosis* *Kock et al., 2018; Robinson et al., 2019*	Livestock and saiga are both known to be affected, and transmission between domestic and wild ungulates was known to occur (eg. exposure to Chamois *Rupicapra rupicapra* and Alpine Ibex *Capra ibex* in France, Richomme et al., 2006).	Lives as a harmless commensal in saigas but can cause MMEs on occasions. Saiga MMEs have been linked to temperature and humidity anomalies, suggesting potential climatic drivers.	Livestock is partially vaccinated in parts of Kazakhstan.	Transmission from livestock to saigas has not been demonstrated but there is evidence of cross-transmission from livestock to other wild ungulate species, especially when livestock herds aren't guarded or enclosed. Additionally, coverage of vaccination was unclear. Lack of local capacity for diagnosis.

Note: *Pasteurellosis covers several syndromes and pathogens. The information in this table refers to haemorrhagic septicaemia as that was what caused the death of saigas in the 2015 and 1988 MMEs (Kock et al., 2018). But other MMEs may have involved different syndromes caused by related pathogens, as in the Russian literature all syndromes were described as 'pasteurellosis' without specification of the disease or pathogens (Robinson et al., 2019). See Appendix A, Table 1, for the list of remaining diseases.

2.3.2 Step two: Identifying locations and times of disease risk

Estimated values for R were calculated and mapped to highlight the *raions* with highest risk of saiga-livestock contact. We generated separate R estimates for saiga using numbers of sheep and goats (Figure 2.4), cattle, and combined ruminants (Appendix A, Table 5 & Figure 3) because cross-species transmission risk for various diseases was predominantly from cattle (e.g. lumpy skin disease) or sheep and goats (e.g. PPR), or both (e.g. FMD; Table 2.1).

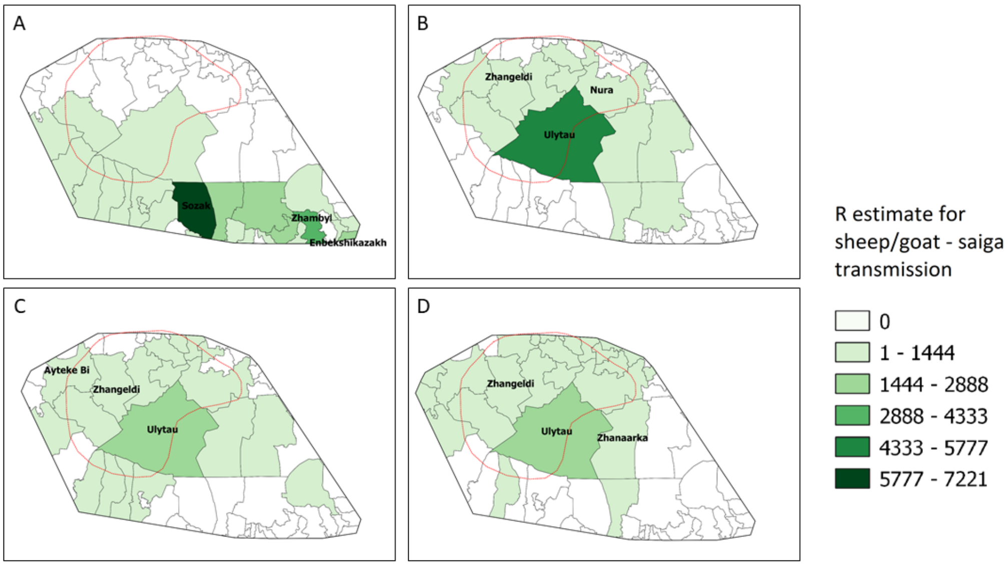


Figure 2.4. Maps showing the disease risk score across the maximum potential saiga range using only sheep/goat distribution data. ***Notes:*** *Darkness of shading represents magnitude of risk. White regions = saigas absent, hence no risk. Saiga ranges: A = winter; B= spring; C= calving; D= summer. For each season the three raions with the highest scores are labelled. Actual values are given in Appendix A, Table 5).*

Depending on diseases of concern highlighted in step one, the assessment of spatio-temporal contact in step two could be used to refine priorities for data gathering and intervention. For example, for a disease to which saigas were especially vulnerable during calving, and for which sheep and goats were the main hosts, it would be logical to prioritize Ulytau, Zhangeldi and Ayteke Bi *raions* (Figure 2.4, C.), for further risk investigation in step three, and for resource allocation like vaccines.

2.3.3 Step three: Assess the actual disease spill-over from livestock to wildlife

In the five regions where pasteurellosis was found in saigas in 2015, *c*.40% of pasture land was leased parcels away from the village, containing 60% of the livestock. The remaining grazing was village land, which represented just 2% of pasture (Appendix A, Figure 2). Most livestock was located along the Torgai and Kabyrga rivers, distant from the saiga calving areas (Figure 2.5). However, a number of large holdings were located further south, some reportedly having over 1000 small stock and many hundreds of cows and horses. The sites closest to the die-off areas were summer camps used for short periods. Horses were not herded, even if owned by village-based farmers, ranged farther than other livestock (c.25 km from farms), and were therefore likely to share grazing with saigas.

Veterinary authorities and the majority of farmers reported that health problems in livestock were rare or absent. Some grasses reportedly caused sporadic problems in sheep turned out after being housed for shearing, leading to gorging and bloat, and sometimes killing 3-8% of the stock. There was no intervention for this. Often unhealthy animals were killed for meat rather than being treated. Vaccines were given in spring and autumn (just autumn for young-of-year). Table 2.3 lists diseases against which vaccination and testing were practised in the five study regions. No FMD vaccine was given, as Kazakhstan was a FMD-free zone at the time of the study. Vaccination across regions varies with disease prevalence, distance from international borders, and other factors (FAO, 2020).

Interviewees agreed that due to the remoteness of the villages, veterinary facilities were limited and focused on vaccinations and brucellosis diagnosis in *raion* veterinary laboratories.

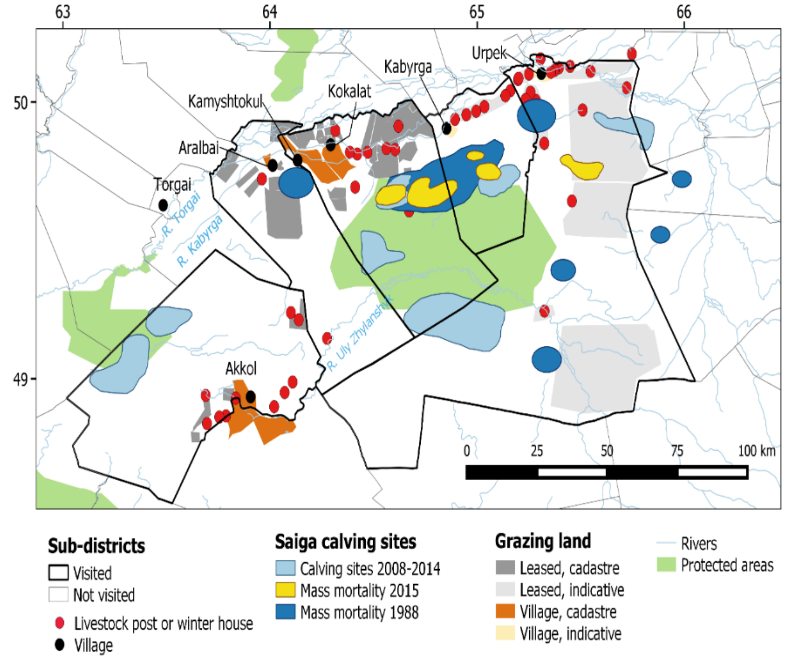
Table 2.3. Diseases of main concern, for which vaccination and testing is reported in our *raions* of interest. Diseases in red are of transmission concern for saigas from livestock (Table 2.1).

***Raion* (year)**	**Species (heads)**	**Vaccine**	**Vaccine planned**	**Vaccine Coverage (%)**	**Test**	**Test planned**	**Test Conducted(%)**
Zhangeldi (2016)	Cattle (27,314)	Rabies	7,800	-	TB	45,420	15,800 (57.8%)
		Pasteurellosis	10,500	9,300 (34.0%)	Brucellosis	33,156	13,275 (48.6%)
		Anthrax	35,000	35,000 (89.3%)			
	Sheep/Goat (60,296)	Rabies	4,600	-	Brucellosis	162,248	26,801 (44.4%)*
		Pasteurellosis	11,200	7,900 (13.1%)*			
		Anthrax	53,300	32,600 (54.1%)			
Amangeldi (2016)	Cattle (13,313)	Rabies	8,000	-	TB	40,140	20,200 (151.7%)
		Pasteurellosis	10,500	10,655 (80.0%)	Brucellosis	38,451	17,546 (131.8%)
		Anthrax	30,900	24,100 (181.0%)			
	Sheep/Goat (34,714)	Rabies	4,700	-	Brucellosis	134,369	50,919 (146.7%)
		Pasteurellosis	12,200	12,670 (36.5%)*			
		Anthrax	41,800	29,000 (83.5%)			
	Cattle (-)	Rabies	-	-	TB	39,700	-
		Pasteurellosis	9,100	-**	Brucellosis	-	-
		Anthrax	24,600	-			
	Sheep/Goat	Rabies	-	-	Brucellosis	-	-

Amangeldi (2015)	(-)	Pasteurellosis	12,100	-**	
		Anthrax	41,600	-	
Urpek & Kabyrga S.O.*** (2015)	Cattle (6,006)	Pasteurellosis	1,400	-**	
	Sheep/Goat (2,774)	Pasteurellosis	2,000	-**	

Notes: ** = Portion of the planned vaccination was to be carried out in the coming weeks from when we got this data. ** = Veterinary officials suggested actual coverage was close to the planned coverage. *** = Two of the five sub-districts within Amangeldi where we conducted field work. Pasteurellosis = We didn't get information to confirm if this covered Pasteurella multocida serotype B. The veterinary official suggested it did. "-" indicates presence but numbers weren't known.*

Very few farmers reported grazing livestock on the steppe in spring 2015. Those who did reported negligible livestock mortalities (Appendix A, table 8), and none related to pasteurellosis. Veterinary teams concurred and indicated no notable increase in any disease or diagnosis in livestock throughout 2015 in the area. In 2015 and 2016, most vets agreed that livestock pasteurellosis vaccine coverage was partial (Table 2.3). Respondents stated that emergency pasteurellosis vaccination was conducted for livestock in the steppe after the MME. Respondents also suggested that planned 2016 coverage for pasteurellosis was directed preferentially towards livestock grazing in steppe areas, rather than those more accessible in the villages as previously, citing the 2015 MME. Pasteurellosis vaccination of horses appeared to increase substantially in 2016 (Appendix A, Table 6 & 7). This could be in response to the MME as horses are free-ranging; despite lack of evidence for cross-species transmission of pasteurellosis between saigas and horses (Table 2.1). No cases of pasteurellosis in livestock had been reported in the area for c.10-15 years, although this is a long-standing endemic infection with some level of ongoing vaccination (Robinson et al., 2019).



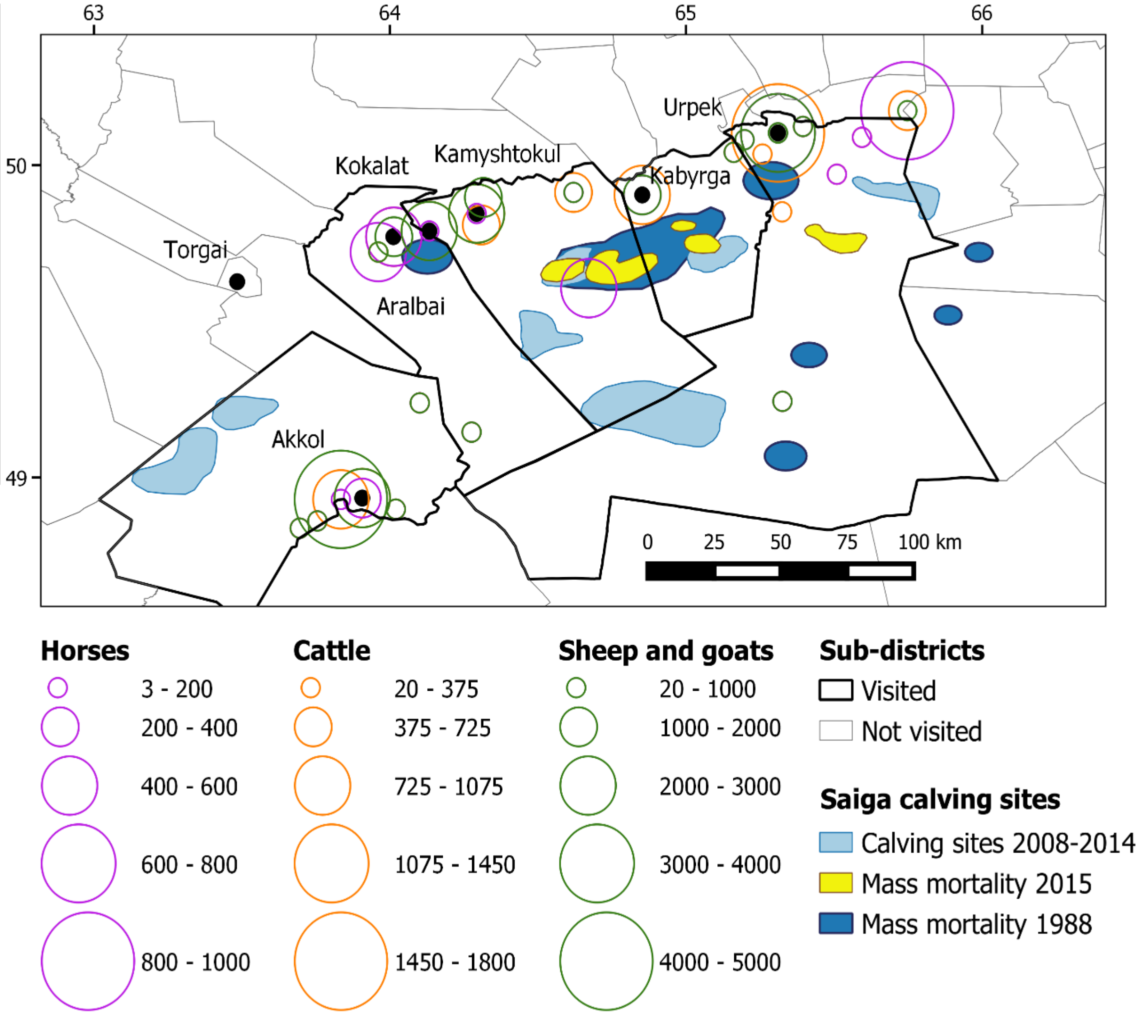


Figure 2.5. Left: Study area, livestock locations, protected areas and designated common and leased grazing areas. **Right**: Livestock locations and numbers in May 2015 ***Notes***: *circle sizes represent numbers of animals only, and not the distances they travel. In reality sheep and goats are likely to travel up to 6km from a central point; cattle move similar distances but may go further if not herded. Horses are not herded [source sub-district boundaries: Lenk (2008)]*

2.4 Discussion

The framework highlights the importance of coordination between stakeholders (e.g. conservationists, veterinarians and land managers) to co-manage potential spill-over from livestock to saigas (Figure 2.6) Several diseases present a risk of cross-transmission to saigas from livestock. These need mitigating, additionally to threats like poaching, to ensure populations remain large enough to survive potential future MMEs (Kock et al., 2018). Uncertainties remain around aspects of cross-species transmission and mitigation, which require careful examination to determine effective solutions (step one). For a given disease (identified from step one), practitioners can use the disease risk maps to identify *raions* and seasons of highest risk depending on the livestock species most likely to be an infection source (step two). This can inform targeted interventions and prioritize detailed field data collection. For saigas, step two identified Zhangeldi *raion*, a site which saw die-offs within the 2015 MME, as high risk for cross-species transmission from sheep and goats to saigas in spring, along with two other *raions*. If our investigation at step three had not been post-hoc, these *raions* would anyhow have been prioritized for further attention.

Finally, we found no evidence that livestock in the die-off region was a source of infection for the 2015 saiga MME. It is possible that disease incidence could be under-reported as sick livestock are often consumed. Also, livestock were protected by partial vaccination, but we lack data to determine if coverage was adequate for effective protection. However, we would expect even the limited veterinary services in the area, or the herders themselves, to detect and document outbreaks of pasteurellosis as this region has a history of this disease (Robinson et al., 2019; table 2.3).Moreover, how contact with livestock in the weeks preceding the die-off (not in the die-off areas) might have affected any cross-species transmission needs investigation. Separation of saigas and livestock at fine scales might not persist in future, as across Kazakhstan livestock are recolonizing the steppe (Dara et al., 2020). Farm locations, size, movement patterns and livestock holdings will all interact to determine future risk.

The applicability of our framework was dependent on the amount and quality of data available. Knowledge gaps exist for all diseases of concern ("uncertainty" in Table 2.1). Our epidemiological function was highly simplified (step two). For instance, it did not capture diseases like helminthoses, where indirect contact through contamination of the environment facilitates transmission (Morgan et al., 2006). Nor did it capture diseases transmitted through non-livestock alternative hosts or long-lived vectors, enabling persistence of infection in the environment. The function for calculating the disease risk score also has caveats.

Firstly, it assumed risk had a linear relationship with livestock number and saiga group number. As saigas are known to avoid livestock (Singh et al., 2010a), the relationship between saiga density, seasonality and group number/size is likely to be non-linear, resulting in disproportionately higher risk when many saigas are concentrated in small areas (eg. calving). Susceptibility of saigas to cross-transmitted pathogens could also vary spatially and seasonally due to nutritional limitations, stress and other factors, and be amplified through disturbance and habitat degradation, introducing additional non-linearities. Currently the criteria for categorizing risk (low, medium or high) are crude and best interpreted qualitatively. Secondly, we assumed the risk score was transferable spatially (eg. from a *raion* to a particular pasture), but livestock husbandry and saiga grouping patterns at the local scale are likely to be important drivers of cross-species transmission (Craft et al., 2015). Hence, step three is important. Thirdly, with increasing infrastructural barriers, poaching, and climate change, saiga migration is being constrained. This may in future increase livestock-saiga contact, and hence risk of disease transmission. Fourthly, due to data limitations, saiga locations were historical. To identify actual priority *raions,* updated saiga distribution data isneeded. Lastly, we assume that *raion* livestock numbers (n_l) adequately reflect potential sources of livestock disease for saigas.

For step three, we were limited by the knowledge local stakeholders held and were willing to share. Inadequate archiving of data (e.g. 2015 records from Amangeldi, Table 2.3) was a hindrance in understanding changes in pasteurellosis vaccination between 2015 and 2016. A major constraint on prioritisation in general is the lack of epidemiological studies and knowledge of infection in wild populations.

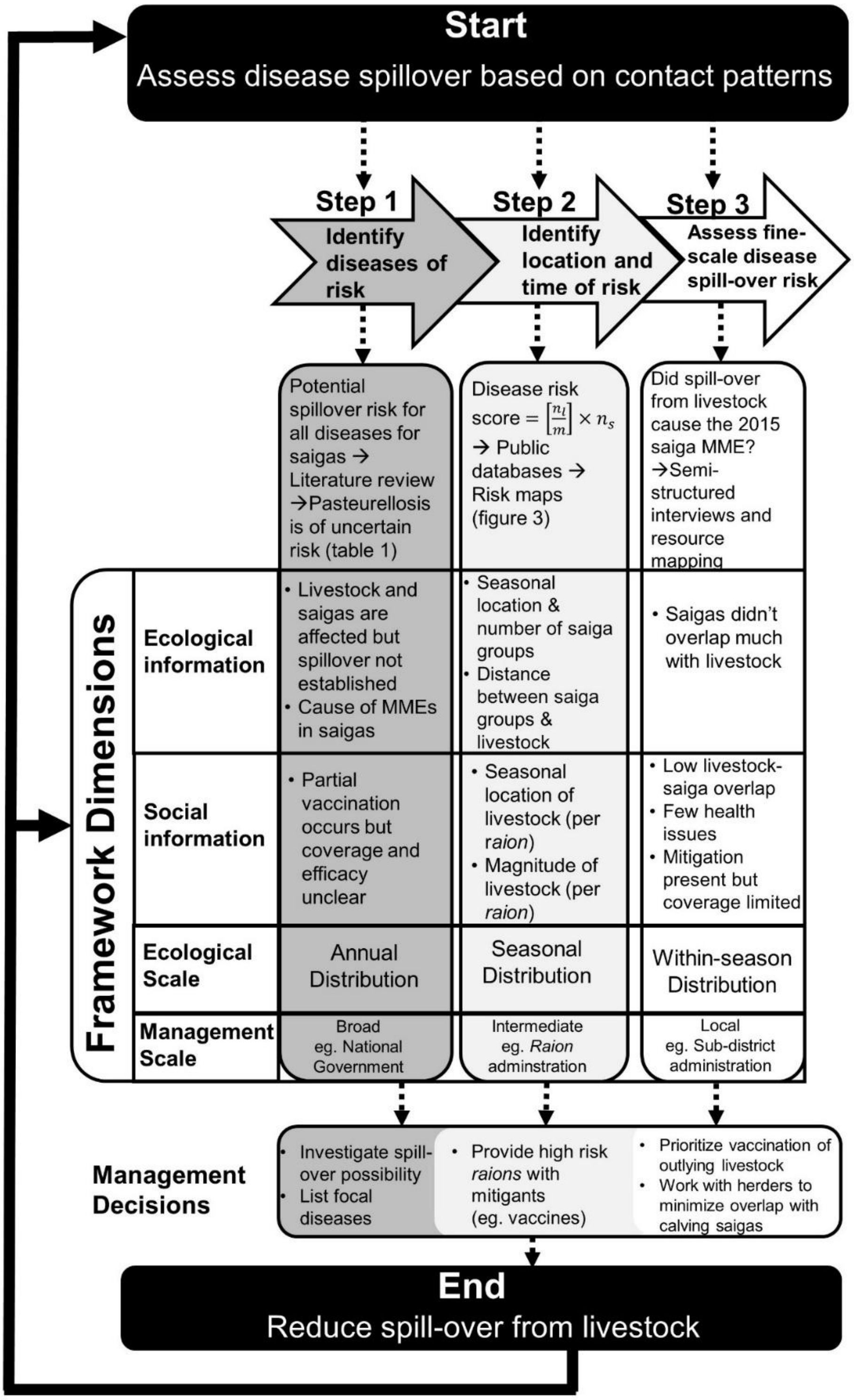


Figure 2.6. Lessons from the application of our disease risk prioritization framework to disease risks from livestock spill-over related to pasteurellosis in the Betpak-Dala saiga population. Information presented here is not exhaustive; see text for more details.

Going beyond saigas, stakeholders can use the framework to inform disease management at relevant scales. Step one could be used by national governments to identify diseases to prioritise mitigation at subsequent steps. Step two could be used by regional governments to prioritise locations and times to implement the mitigation. Step three could be used to plan local-scale livestock management like restricting pasture use at certain times or reactive vaccination. Although developed for Betpak-Dala saigas, our framework is widely applicable, with some adjustments:

Firstly, epidemiologically-relevant species can be linked in ecologically meaningful ways. For instance, in Makgadikgadi Pans, Bostwana, disease transmission could occur from different livestock species to two migratory ungulates, wildebeest and zebra (Walker et al., 2018). For a coarse cross-species transmission assessment, species can be aggregated into two categories "wild ungulates" and "livestock", while for a finer assessment, each species and their interactions can be assessed as a network. The framework can be used to asses risk of cross-transmission in migratory taxa other than ungulates, for example contact-based transmission of avian influenza in migratory birds (Li et al., 2017). Secondly, the framework could be used to consider and manage disease transmission risk from wildlife to livestock. For example, in Africa, FMD is known to spill over from buffaloes (*Syncerus caffer*), to livestock (Vosloo et al., 2002) and impacts on disease control policy and practice, including through biosecurity fencing. Thirdly, our framework could be applied to non-migratory species exhibiting seasonal variation in contact rates driven by movements or behaviour. For instance, white-tailed deer *Odocoileus virginianus* usually have home range of less than one square mile and often share landscapes with sedentary livestock (Barone et al., 2020). Seasonal variation in the number and locations of water and feed sources on a farm, especially in leaner winter months, could nonetheless affect deer and livestock overlap (Berentsen et al., 2014). Hence, the spatial and temporal variation in this sedentary system could, in principle, be considered using our framework.

A strength of our framework is its iterative nature (Figure 2, thick black lines). With new information, the risk assessments, predictions and consequent management actions are updated across all dimensions and components. Our knowledge of biological systems is often inadequate and costly field surveys are generally required to generate the data necessary to inform management (Margules & Pressey, 2000).

Hence, indirect methods of characterising ecological patterns are of value for decision-making. Despite efforts to deal with imperfect datasets, little is known about how data uncertainty translates into management errors (Hermoso et al., 2013). Being explicit about uncertainties allows future work to account for them. Our iterative framework encourages the use of new information to update aims, assessments and predictions.

Schwartz et al., (2018) describe five common types of decision-support framework, like ours, that can be useful for conservation planning and management. However, no one framework covers the spectrum of decision challenges. Our framework addresses three of their five elements: i) strategic foresight, i.e. critical future possibilities and uncertainties of disease risk, ii) systematic planning, i.e. critical locations for action, and iii) open standards for the practice of conservation, i.e. best use of limited time and funding to achieve desired outcomes.

2.5 Conclusion

We have developed an iterative framework to assess cross-species disease transmission risk between migrating wildlife and livestock in data-limited circumstances and across social-ecological scales. We applied the framework to characterize livestock and saiga disease transmission in Central Kazakhstan. The value of our framework lies in assessing and predicting disease spill-over over space and time and across management scales. We also show the strength of combining ecological and social information which is particularly valuable for management of targeted interventions.

We hope our multi-faceted framework will be of use for practitioners globally, in better understanding disease cross-species transmission risks based on contact patterns and their dependencies on wider socio-ecological considerations. Further application of the framework in different contexts will provide opportunities for its improvement, and support the alignment of livestock health with wildlife conservation across multi-use landscapes.

- Chapter 3 -

Identifying relationships between multi-scale social-ecological factors to explore ungulate health in a Western Kazakhstan rangeland

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Authors' contribution

I, EJMG and ERM conceived the idea of this work and designed the study. SR provided critical inputs on the study design. I and AS conducted the field work. I led the data analysis and writing. All authors provided critical inputs on various drafts of the chapter.

Aggregating saiga females with their new born calves in Ural

Abstract

Rangelands are multi-use landscapes which are socially and ecologically important in different ways. Among other interactions, shared use of rangelands by wildlife and livestock can lead to disease transmission. Understanding wildlife and livestock health and managing disease transmission in rangelands requires an integration of social and ecological knowledge. Using the example of Western Kazakhstan, home to two types of ungulate hosts, the critically-endangered saiga antelopes, *Saiga tatarica*, and livestock, we conducted a cross-scale analysis of social-economic, ecological and climatic factors that contribute to transmission of diseases We focused on Gastro-intestinal Nematodes (GINs) because they are transmitted between hosts that share pasture and they affect ungulate fitness. We used an interdisciplinary social-ecological methods approach which included conducting fecal egg counts of GINs in saigas and livestock, semi-structured interviews and focus group discussions with livestock owners and herders in the region, and triangulation of information through secondary sources. Livestock rearing was done in two ways a) village-based livestock and b) outlying farms. The latter overlapped more with saigas. Village-based livestock had significantly higher worm burdens than those on outlying farms, which had comparable burdens to saigas. Various factors exacerbate GIN prevalence and transmission: Veterinary services are minimal; both saiga and livestock numbers are increasing; and changing climate is increasing farmers' dependence on shared pastures for hay production. It will be crucial for saiga conservationists to engage in multi-pronged conservation interventions, which are evaluated and adapted through the lens of rural livelihoods and the livestock health on which they depend. *Synthesis and Application:* Our work provides researchers and practitioners with an avenue to better understand complex inter-relationships and plan interventions within rangelands, while viewing host health from an interdisciplinary perspective - ultimately working towards wildlife conservation whilst safeguarding livelihoods across the world’s rangelands.

3.1 Introduction

3.1.1 Background

Rangelands, comprising grasslands, shrub-lands, savannas and marshes grazed by livestock and wildlife (Allen et al., 2011), cover *c.*40% of all land, and provide habitats for multiple species (Reid et al., 2008). Rangelands provide ecosystem services like carbon sequestration, contribute to satisfying the growing demand for livestock products and hold important biodiversity (Hobbs et al., 2008; Thornton et al., 2010). Much wildlife, including the critically-endangered Saiga antelopes *Saiga tatarica* and various declining populations of reindeer *Rangifer tarandus,* call rangelands their home. Most of these species live outside Protected Areas, sharing rangelands with millions of people and their livestock (Reid et al., 2008).

Worldwide there are >200 million pastoralists. Their livelihoods depend on livestock raised either on communal or private pastures, with varying mobility (Niamir-Fuller et al., 2012). Around550 million of the world's poor people (living on less than $1.25/day) depend on livestock as one of their few or only assets. *c.*58 million of them live in rangelands (Robinson et al., 2011). Rising global demand for livestock products (Otte et al., 2012) may increase human impact on both wildlife management and pastoralism in rangelands. Alongside, poverty and vulnerability are high in rangelands in developing countries, with climate change set to increase weather volatility and impact already-vulnerable pastoralists (Thornton et al., 2014). While the links between climate change, food security and vulnerability are complex, increased understanding of these interactions can enhance interventions to support adaptive capacity of rangelands (Boone et al., 2018).

The sharing of pasture by multiple species of domestic and wild ungulate can lead to interactions which may be positive, e.g. facilitation (eg. Odadi et al., 2011), neutral, i.e. co-existence with limited interaction (e.g. Mori et al., 2020) or negative, e.g. competition (e.g. Bagchi et al., 2004). Pasture sharing can also lead to disease transmission, which can impact livestock-based economies (Reid et al., 2008) and wild ungulate health (Smith et al., 2009). This is particularly relevant for wild ungulates as pathogen assemblages are associated with host phylogeny (e.g. Walker & Morgan, 2014). Pozo et al., (2021) identified four social-ecological challenges underlying conflict between livestock production and wild herbivore conservation, of which disease transmission is one. The interplay between factors like resource availability, climate, and disease, nestled within complex interactions with livestock in pastoral systems, produce a net effect on wild species (Sæther, 1997). For instance, climate change influences forage availability for ungulate hosts parasite-host assemblages and also interactions between the two through host nutritional status (Brooks & Hoberg, 2007).

From this point of view, endo-parasites, particularly Gastro-intestinal nematodes (GINs), are of particular interest in rangelands as they are determinants of fitness for wild and domestic ungulates (Gulland, 1992; Perry & Randolph, 1999). Indirect contact, particularly via pasture sharing, can enable cross-transmission of trophically-acquired GINs, whose development on pasture generates a lag time between pasture occupation and infectivity (Morgan et al., 2006). Because part of GIN's life history is affected by environmental conditions, changes in climate are likely to impact them profoundly (Brooks & Hoberg, 2007). In rangelands, human intervention to reduce or mitigate the impacts of GINs can strongly influence their presence in livestock and consequently co-transmission with wild ungulates (Weinstein & Lafferty, 2015). To ensure effective GIN management, it is critical to incorporate these social determinants of livestock health in order to fully understand the disease transmission dynamics. For instance, broad-spectrum anthelmintic use in livestock is common, often either strongly suppressing GINs or causing resistant strains to persist (Weinstein & Lafferty, 2015). Van Veen (1997) summarized activities by transhumant livestock owners across Central Asia and Africa to evade disease transmission (including GINs), showcasing local understanding of disease epidemiology. Yet, understanding of disease mechanisms and management at the livestock-wildlife interface remains limited, particularly with respect to GINs (Rhyan & Spraker, 2010).

Moreover, while many studies consider a number of ecological and social factors influencing rangelands, advances in integrating these components to reconcile potentially competing goals (e.g. livelihood and wildlife conservation) have been limited (Hruska et al., 2017). For instance, ecological research has seen considerable focus on grazing regimes and ecological indicators with limited consideration of the goals of livestock owners. Similarly, social science has provided a lot of information on rangeland users, but has focused less on how social and ecological factors combine to produce ecological outcomes (Brunson et al., 2012). Rangeland research and management, particularly concerning host health, cannot overlook the human dimension if it aims to be applied.

Given the intricate interconnections between people, their livestock, wildlife and the collective social, political and ecological surroundings of wildlife and livestock, it is clear that rangelands are intertwined social-ecological systems (Reid et al., 2014; Hruska et al., 2017). Consequently, host health and disease management in rangelands is also a social-ecological concern (Valente et al., 2020).

3.1.2 Research questions and aims

We aimed to understand the inter-relationships between ecological, social, economic (market-related), political and climatic factors affecting host health in rangelands (Fig. 3.1). We look for evidence of links between different factors by mapping their directionality and strength, while considering uncertainties and discuss the likelihood that these links might change in the future. We illustrate this approach using a case study from the Western Kazakh rangelands, where saiga antelope, *Saiga tatarica,* shares pastures with livestock.

While various pathogens of concern exist, we focused our work on GINs (hereafter "health" and "disease" is in reference to GINs unless stated otherwise) because indirect contact, particularly via pasture sharing, can facilitate cross-transmission of trophically-acquired GINs. We restricted our work to wild ungulates (saigas) and small-bodied domestic ungulates (sheep and goats) for two main reasons: 1) these are the main grazers in this system and, 2) because phylogenetic relatedness is a good predictor of resource competition and disease transmission. Saigas in Kazakhstan are known to share the majority of their GIN species with sheep and goats (Morgan et al., 2005a; Appendix B – Figure 1 and 2).

Research questions used to explore each type of inter-relationship are illustrated in Figure 1 and defined in Table 3.1, which also highlights key uncertainties based on literature. Our overarching research question was to investigate how ecological, social, economic, political and climatic factors interact with each other across spatial scales to affect host health in a multi-use rangeland system. Given the social-ecological complexities of rangelands, we expected that various factors would interact to affect disease prevalence and transmission. To investigate this, we used mixed methods within a social-ecological approach. This included conducting faecal egg counts of GINs in wild and domestic hosts, semi-structured interviews and focus group discussions with livestock owners and herders in our study area and triangulation of information through secondary sources.

Inter-relationships between different factors affecting host health within rangelands are scale-dependent (Cash et al., 2006). Each scale may have different social and ecological patterns and processes at different hierarchical levels (Hruska et al., 2017). For instance, in the case of rangeland sustainability, the grazing distribution of wild and domestic animals may be critical at the level of a rangeland ecological site. This is driven by ecological processes determining resource availability and social management systems that determine livestock location (Western et al., 2011). However, at the regional level, market prices and legislation governing land access and use may be important (Hruska et al., 2017). Due to financial and logistical constraints, it is most feasible to concentrate analysis at one or few spatial scales. Therefore, for simplicity and applicability to real-world management decisions, we distinguish in our work between two scales: i) the “local” scale, which refers to factors affecting host health at a pre-defined location, in our case the calving and summer range of saigas in 2019 in Ural (see 3.2.1 below); and ii) the “-regional” scale, which refers to broader factors that affect host health.

Thus, at the local scale, we aim to compare spatial distributions of livestock and saiga in order to determine whether these result in contact patterns enabling disease transmission. We also compare the abundance and diversity of GINs across species and investigate local disease control efforts amongst livestock owners. More broadly, we look at the mandate and coverage of veterinary services in our study area, investigate the impact of land access arrangements and market access on livestock grazing, and the implications of climate change for the study system.

Given the complexities involved in these systems, our approach is primarily descriptive, at least initially. Through our work, we hope to highlight and map the interdisciplinary and cross-scale nature of the research required in order to better understand and manage livestock-wildlife interactions through GIN disease and shared resource use.

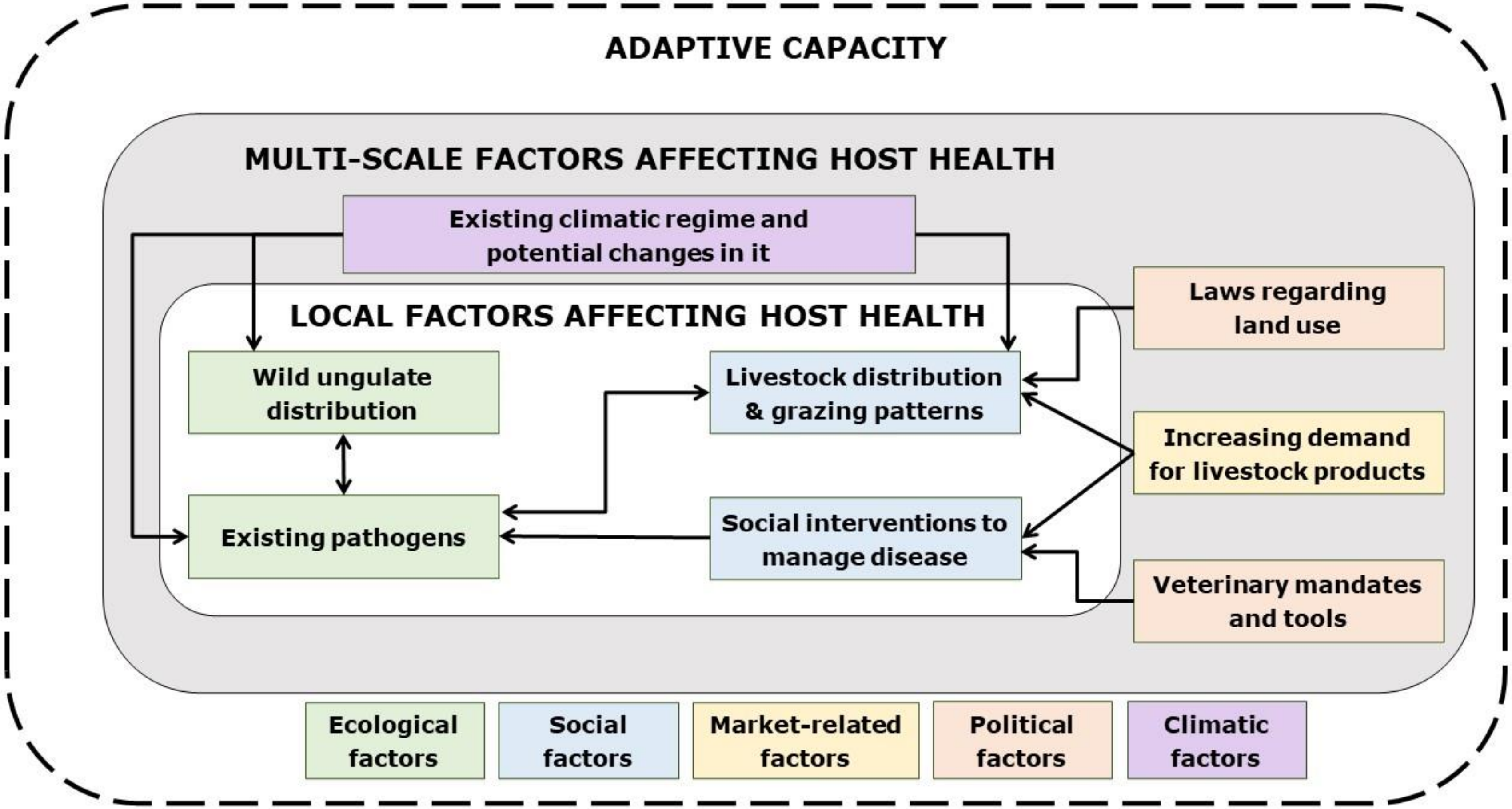

Figure 3.1. A schematic representation of the various factors affecting host health within a rangeland system. Each box represents a component in Table 3.1). Adapted from Reid et al., 2014 & Hruska et al., 2017.

Table 3.1. Components of the conceptual model in Figure 3.1, that aims to map factors and their interactions affecting host health in multi-use systems. Although shared pathogens can, in principle, impact both livestock and wildlife, we are most concerned with the conservation implications of transmission from livestock to wild ungulates. GIN = Gastro-intestinal nematode.

Component*	**Potential interactions with and implication for host health**	**Key uncertainties when considering impact of factors on host health**	***Research Question***
Wild ungulate distribution	Cross-species disease transmission depends on contact patterns, governed by host distribution and movement (Vosloo et al., 2002).	Distributions may cover vast areas and be highly dynamic in a changing environment (e.g. Singh & Milner-Gulland, 2011)	*Does saiga distribution result in contact patterns which can enable disease transmission from livestock?*
Existing prevalence and diversity of pathogens	Depending on species and abundance, GINs may cross-transmit and are determinants of fitness in wild and domestic ungulates (Gulland, 1992; Perry & Randolph, 1999).	Identification of pathogens can be resource intensive (Avramenko et al., 2019). GIN eggs are deposited in the environment in faeces, where they develop to infective larvae, which then move onto herbage. Larvae are ingested by hosts during grazing. Climate / weather and availability of forage impact this process and if not accounted for, leads to uncertainty (Rose et al., 2015).	*What is the abundance and diversity of GINs, and how do helminth burdens compare between saiga and livestock (across different livestock grazing practices)?*
Livestock distribution and grazing patterns	Cross-species disease transmission depends on contact patterns, governed by host distribution and movement (Vosloo et al., 2002).	Micro-scale grazing patterns/ movement can facilitate transmission (Wilcox et al., 2005). Stocking densities and livestock herd composition can determine magnitude of impact on livestock health and transmission to wildlife (Macpherson, 1995).	*Do livestock distributions and grazing patterns result in pasture sharing with saiga? How does this differ between different livestock grazing practices?*

Human interventions to manage disease	Human (herder/owner) interventions can improve livestock health by reducing pathogen burdens – but interventions may lead to adverse effects, e.g. drug resistance (Charlier et al., 2014).	Changes in diseases targeted by treatment may in fact, reflect net-effects of other factors (Brock et al., 2014). Human interventions, especially in resource poor environments, tend to be dynamic and erratic (Van Veen, 1997).	*Are there prevalent anti-parasite interventions that can influence GIN burdens in livestock and potentially in saigas?*
Veterinary mandates and tools	In many countries, disease mitigation programmes (e.g. vaccination/use of anthelmintics) are determined at specific levels of government. Their implementation, and alternative private provision of health care, can directly alter livestock health, with the potential to affect wild host health.	Veterinary services are set at varying levels of government (eg. national), but can differ between spatial scales within a country (eg. states/provinces) Additionally, sometimes this information is not always publicly disclosed.	*What is the state of veterinary services in our area of interest? Are there services that can deal with suppression of GINs?*
Legislation and institutions governing land access and use	Can directly or indirectly influence contact patterns between wild and domestic hosts (Robinson & Milner-Gulland, 2003; Weinstein & Lafferty, 2015).	Whilst property rights legislation is determined at the national level, implementation can differ considerably between regions and other spatial scales within a country (e.g. states/provinces and districts). Presence of a law does not guarantee its enforcement, whilst many informal arrangements may exist. In many cases economic factors may be more important in determining land use decisions (Robinson et al., 2016)	*What are the laws regarding land-use in our area of interest, and what are their implications for host health?*
Increasing demand for livestock products	This can alter livestock herding and health management practices, in turn potentially altering livestock and wild ungulate health in multi-use systems (Thornton, 2010).	Market drivers operate at various scales, with manifold impacts on livestock management practices. It is difficult to tease these apart (Thornton, 2010).	*What is the demand for livestock produce from our study area? How does this impact livestock*

			management strategies with implications for host health?
Existing climatic regime and potential future changes	Climate contributes to host contact patterns and availability of pathogens of concern (Vosloo et al., 2002; Rose et al., 2015).	It is difficult to decouple the impact of climate from the many confounding variables and interactions determining host health in rangelands (Pruvot et al., 2020b). There is uncertainty in understanding future trajectories of climate and hence its implications for host-parasite assemblages - particularly in remote data poor regions (Rose et al., 2015).	*What impact is climate having on the interactions between the rangelands and hosts, and what is the implication of this for host health in our study area?*

*Colours of the column correspond to the legend represented in Figure 3.1.

3.2 Methods and Material

3.2.1 Study Area

Kazakhstan's rangelands are home to >80%of the global population of critically endangered saiga antelope (CMS Saiga MoU, 2015). Saiga habitat is a predominantly flat, treeless landscape characterized by hot, dry summers and severe winters. Annual rainfall is low, varying from an average *c*.300mm in the steppe to *c*.250 mm in semi-desert and *c*.<250 mm in desert zones. Migrating saigas use all these zones seasonally, spending summer in the north and winter in the south (Bekenov et al., 1998). Saigas congregate in dense aggregations in early to mid-May. Calving grounds usually cover around 150–900 km^2 (Bekenov et al., 1998) with site selection increasingly driven by human disturbance (Singh et al.. 2010b). Calving is a critical life-history period for saiga (Singh et al., 2010); for example a recent mass mortality event during calving, though driven by a temperature and humidity anomaly, was probably exacerbated by calving-related stresses (Kock et al., 2018).

We focused on the calving and summer distribution of the Ural population in Western Kazakhstan Province (Fig. 3.2). We chose to work in this area as livestock and saiga population densities and overlap are particularly high, both seasonally and annually, compared to other saiga populations (Dara et al. 2020). Hunting following the collapse of the Soviet Union caused major declines in saiga numbers range-wide and remains a threat (CMS Saiga MoU, 2015). However, although the Ural saiga population fell from 236,000 in 1991 to 26,400 in 2013, it had recovered to around 217,000 by 2019 (Zuther, 2020). Livestock numbers across Kazakhstan are also currently recovering from their post-Soviet Union decline (Kerven et al., 2016), providing a renewed threat of disease transmission to saigas. There is even a perception that in Ural, exploitative resource competition between saigas and livestock might be occurring (Satke, 2020). Given this background and that livestock densities are currently low in the other populations (Dara et al., 2020, Khanyari et al., 2021; Chapter 2), saigas are more likely to come in contact with livestock in this population than the others, making it a relevant case study site.

Historically, Kazakh pastoralists followed long-distance seasonal migratory routes. This remained so during the Soviet period as a result of support for State Farms. However, after the Soviet collapse, State Farms were broken up and herds fragmented amongst thousands of small private households and farms.

Many people were constrained to graze their animals around villages, as they could not afford seasonal migration (Kerven et al., 2016; 2021). Nonetheless, those with larger livestock holdings increasingly leased pasture further from villages, out in the steppe (Kerven et al., 2021). Therefore, we divide livestock holdings into two types: village-based and outlying. Most village-based livestock are held by private households which are not registered as farmers and cannot lease land. Their animals thus usually graze on village lands (usually up to a 3km radius around the village) physically demarcated and legally designated for common use, although some types of livestock (e.g. horses) may roam much further. Outlying holdings belong to registered farms and utilise land parcels leased privately, beyond the village lands. Villages employ the *khyzyk* system, where all the sheep and goats owned in the village are grazed together as one herd, with herding duties rotating amongst owner households daily. Animals at outlying stations are grazed in single-owner herds.

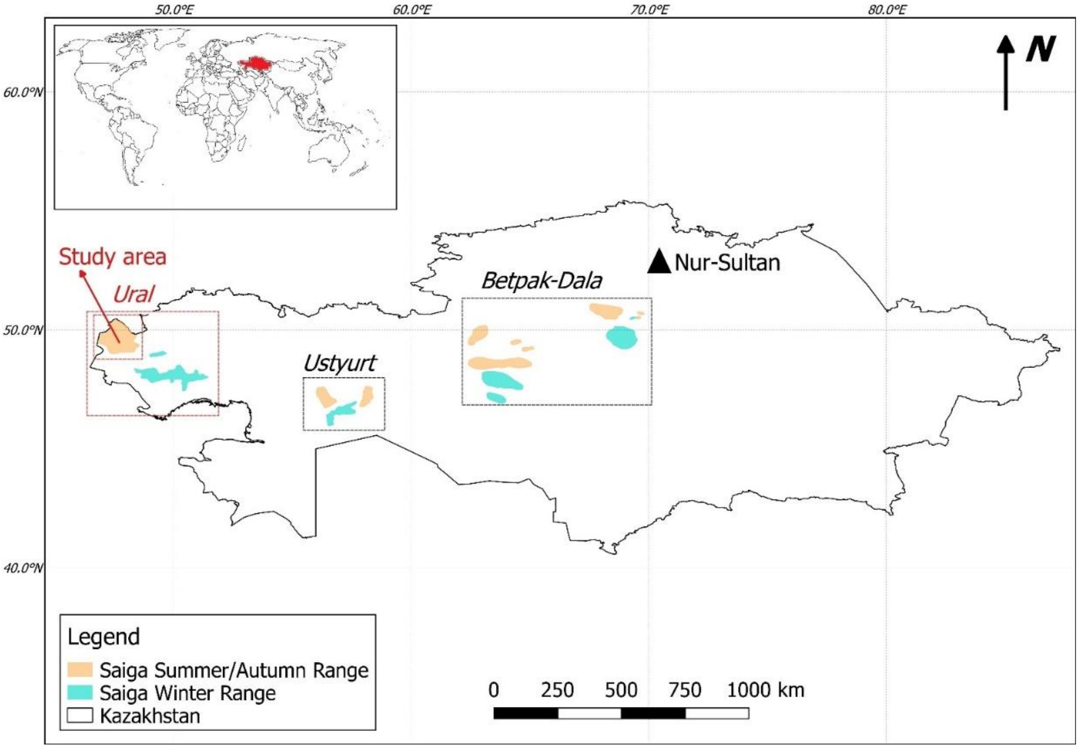

Figure 3.2. Map displaying the three populations of Saigas in Kazakhstan. We worked in the summer/autumn range (smaller red square) of the Ural population (larger red square). Spring calving areas are found within the summer/autumn range. Inset map shows the location of Kazakhstan

3.2.2 Data collection and analysis

Social factors affecting host health

Given the logistical issue of covering all farms in vast and remote areas, we used a snowball sampling strategy (Noy, 2008) to obtain a representative sample of outlying farm owners to interview, as well as one key informant per village. We considered our sample to be adequate when all additional respondents provided similar responses to previous ones.

We conducted 46 semi-structured interviews with livestock owners and professional shepherds; 11 in villages and 35 on outlying farms. Answers for village-based-livestock were obtained at the level of each *khyzyk* (as these animals are managed as single flocks), while answers for outlying livestock were obtained at the level of each outlying farm. From each village, we interviewed a member of the *khyzyk* who served as the key-informant for the village – all villages we visited had one *khyzyk*. These informants were identified by the *khyzyk* members and chosen based on their knowledge about livestock management.

We also conducted key-informant interviews with veterinary officials where possible, particularly to validate livestock health information (n=5). The aim was to understand livestock rangeland use, livestock composition and distribution and livestock health and its management (Table 3.1). We also collected information on livestock numbers at each village and outlying farm, and calculated stocking densities by dividing the number of animals (individual stocks of sheep and goat) by the area grazed (demarcated by interviewees and key-informants as circles, with radius equal to the furthest distance routinely grazed from the central point). Quantitative and semi-quantitative answers to these questions were analysed using descriptive statistics and bootstrapped with replacement (10,000 iterations) to estimate means and 95% confidence intervals. Where applicable, bootstrapped t-tests were used to compare significance. The questionnaire can be found in Appendix B - Questionnaire. The survey was approved by the University of Bristol's Ethical committee; consent was established orally before the surveys, all the responses were coded, and respondents' names or other identifying features were not used or shared to ensure anonymity.

Local ecological factors affecting host health

The Association for Conservation of Biodiversity of Kazakhstan (ACBK, an NGO) have been monitoring saigas for several years. They record exact GPS locations of saiga calving sites, rough maps of saiga locations in other seasons, and a saiga population count. These include historic saiga locations (Singh et al. 2010a), and updated locations since. We delimited the calving and summer distributions of the Ural saiga population through a combination of field surveys and expert opinion of researchers within ACBK. As fine-scale calving location can change annually (Singh et al., 2010b), we identified specific calving locations in 2019 (the year of the study) from aerial and ground surveys conducted by ACBK (see Singh et al. 2010a for survey methods).

Within the calving and summer areas, fresh faecal samples were collected from sheep, goats and saigas. At least one pooled faecal sample was collected from each village and outlying farm interviewed. Because sheep and goats are herded together and kept in enclosures at night, these samples were collected from the ground of enclosures or pasture, and comprised faeces from multiple individuals (i.e. pooled samples of at least 15 individuals), which could include sheep and/or goats. Results are therefore presented for small ruminants in aggregate, and it was not possible to separate parasitological results by livestock species. Between 5th May and 2nd June 2019, we collected and analysed 155 pooled faecal samples: 79 from saigas and 76 from livestock (split equally between outlying farms and village-based livestock). Livestock samples were pooled for each village or outlying farm and saiga samples were pooled at the level of the study population (following Morgan et al., 2005b).

Faecal samples were analysed for helminths using the mini-FLOTAC technique (Cringoli et al., 2017), which uses flotation-dilution to quantify parasite egg density, expressed as Faecal Egg Counts (FEC). FEC in an aliquot of pooled faecal sample should be a good reflection of the average individual FEC (Morgan et al., 2005b). While FEC do not correspond precisely to counts of adult helminth worms within the animal, there is a correlation between the two, including in ungulates in this system (Morgan et al., 2005a). FEC provide a direct measure of the relative contribution of different hosts to pasture contamination. Given their adverse impact on wild and domestic ungulate health and fitness, we were particularly keen to investigate existence of strongyle helminths in both hosts.

Following the protocol described in Cringoli et al., (2017), 5g of faeces were analysed per sample in 45 ml of saturated salt solution. The number of eggs found for each parasite was recorded for each sample and multiplied by a factor of 5 to obtain the total faecal egg count (FEC) in eggs per gram (EPG) of faeces. Thus, the sensitivity of the mini-FLOTAC technique is 5 EPG. Parasites were identified to morphologically distinguishable egg types, since overlap in egg appearance limits species level identification.

As our sample sizes were small, we bootstrapped our data with replacement 10,000 times to obtain means and 95% confidence intervals (0.025 and 0.975 quantiles) of faecal egg counts for livestock and saigas. We used the bootstrap t-test to compare mean abundance of endoparasites between saigas and livestock.

To supplement the livestock FEC data, we developed impact scores to assess the effect of endoparasites on livestock health. This was done by direct questioning of the livestock caretakers, who adjudged the impact of endoparasites (particularly GINs) on a scale of 0-5 (5 animal dies – 4 alive but useless, in term of what they define productivity to be – 3 severely impacted – 2 impacted but not so severely – 1 little impact – 0 barely noticeable). A Mann-Whitney U-test and a frequency analysis using Fisher’s exact test was used to assess differences in impact scores across village-based and outlying livestock.

Regional factors affecting host health

The same interviewees and key-informants described in section 2.3.1 were used to gain information on the market, policy and climate-related factors affecting host health. The questions revolved around the components affecting livestock production (Fig. 1.1): market demand, land tenure laws, veterinary regimes and the impact of climate and climate change on host health (see Appendix B- Questionnaire). Where possible, information from interviews was cross-validated with information in published literature and public datasets: We cross-verified claims about changes in livestock numbers by looking at livestock data from the Kazakh Bureau of National Statistics (stat.gov.kz, 2020). Livestock numbers were available by province and district from 2014-2020. Our study falls primarily in the Zhanybek district of Western Kazakhstan province, hence we extracted data for both and analysed the trend in numbers of sheep and goats, which are recorded in aggregate as small ruminants, and all livestock (sheep/goats, cattle, and horses) over time using Pearson's correlation against year. We cross-verified claims about climate change by referring to literature and online climate data. Daily temperatures and precipitation were obtained from the POWER Data Access Viewer (DAV) (POWER, 2020). We used the POWER Single Point Data Access widget which provides access to near real-time 0.5 x 0.5 degree datasets, obtained for the years 2000-2019 and averaged across the calving and summer saiga range. We generated a scatter-plot of the time series data and checked for trends over time using Pearson's correlation, after plotting the residuals of the original data to rule out auto-correlation.

To better contextualize the information from the semi-structured interviews, we conducted 15 focus group discussions (FGDs; Nyumba et al., 2018). Group size was 3-11 people (average = 6). As grazing is mostly managed by men, most participants were males (32-68 years old) and included farmers and government employees. However, where possible, we tried to include female respondents in our discussions . To compare change over time, a reference point of the period just after the collapse of the Soviet Union in 1991 was used. This time brought sudden and remarkable social and economic change and was readily identified by participants.

3.3 Results

3.3.1 General overview of results

At the local level, we found that livestock rearing was done in two ways a) village-based livestock and b) outlying farms. The latter overlapped more with saigas. Village-based livestock had significantly higher worm burdens than those on outlying farms, which had comparable burdens to saigas. Treatment against worms was limited and spatially variable. Village-based livestock were primarily treated with anthelmintics, while outlying farms predominantly did nothing or consumed individuals showing signs of disease.

Zooming out to the regional scale, we found that increasing demand for livestock products is driving increases in livestock numbers. We also found that the traditional seasonal movement of livestock seldom occurs now, as most outlying farms are single sedentary entities leased by single owners (usually a family) and used throughout the year. Reasons for this may include costs of movement and high transaction costs of obtaining a 49-year land lease, currently allocated by auction. Lastly, climatic alterations in the summer and winter are negatively affecting the quantity and quality of forage. This in turn is affecting livestock health, resulting in compromised productivity and even death. Moreover, climatic alterations are also resulting in pastoralists not being able to collect enough hay as there is less growth. Additionally, saiga numbers are growing rapidly and they are eating the grass that farmers normally harvest for hay.

Results are explained in detail in the following sub-sections. Overall, it is evident that various factors are exacerbating GIN prevalence and transmission: both saigas and livestock host GINs and both are increasing in number; veterinary services are minimal; livestock movements are now limited; and a changing climate is increasing farmers' dependence on hay pastures, which are shared with saigas.

3.3.2 Livestock distribution and grazing patterns

Using available district land committee (cadastre) maps covering the saiga’s spring and summer range, we were able to identify and visit 11 villages and 68 outlying farms. This included more than *c.*70% of outlying farms within the saiga summer and calving distribution. A few of the outlying farms were abandoned or had absentee owners. Saigas and livestock share large areas of pastures throughout the saiga's summer and calving extent (Fig. 3.3).

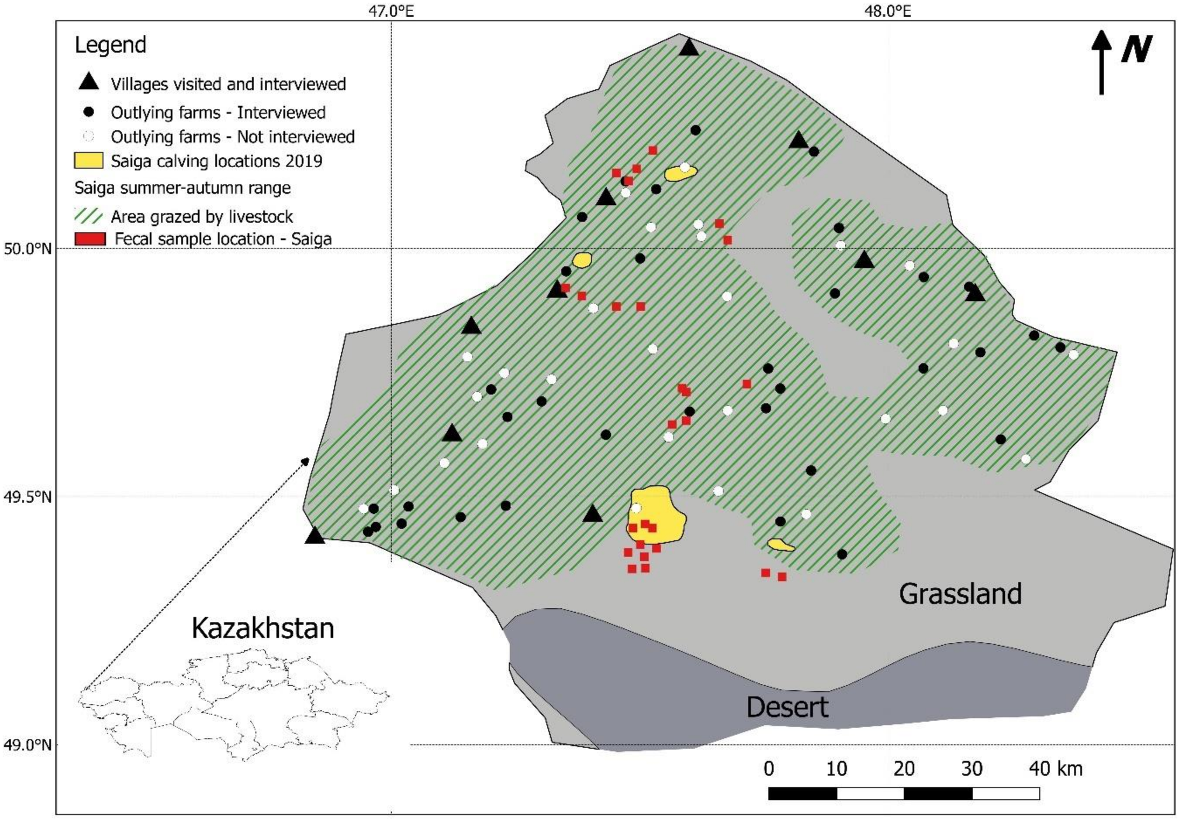

Figure 3.3. Map displaying saiga distribution along with locations of outlying and village- based farms visited. Outlying farms not interviewed (white circles), were visited with the intention of conducting interviews, but owners/caretakers were reluctant or too busy to participate. Grazing areas are exact for interviewed outlying farms and villages, while they are an estimate for non-interviewed farms as identified by our five veterinary key-informants who visit them occasionally. The inset map shows the map of Kazakhstan divided by districts. The arrow in the inset situates the study areas within the Western Kazakhstan district. The grassland and desert eco-regions are delimited on the map based on Olson et al., 2001.

Livestock rearing was done in two ways a) village-based livestock and b) outlying farms. In both management systems, livestock were present in a given area throughout the year. Outlying farms are located on owned or leased land parcels away from the village (>3km). They usually have infrastructure like housing, watering wells and a fixed area (not fenced) where livestock are housed and grazed. Outlying livestock herds were all too isolated to interact with other herds. Sheep/goats on these farms are taken out to pasture by the farm owners, or paid workers. After a day of grazing, they are collected and bought back to a corral (fenced livestock pens) for the night. Most flocks are stall-fed in winter due to the cold and lack of forage. For this, hay is collected from the farmland or purchased from other farms, in late summer/early autumn. If the winter is mild, then the flocks graze outside as during other months. Animals are taken to water points to drink, usually supplied from man-made wells or boreholes.

All village-based key-informants (n=11) confirmed that villages used *khyzyks* to herd small ruminant livestock. Village-based sheep and goats roam within *c.*2-3 km of the village, however cattle and horses may go beyond the cadastral boundaries of 'village lands' and tend to be free-ranging. No significant difference was found in stocking densities of small ruminants between the villages and outlying farms (*p*=0.16), while there was a significant difference in mean small ruminant numbers (*p*=0.01). Thus, total and mean per-location livestock numbers are higher on outlying farms than in *Khyzyks*, while both graze up to similar distances from their night-time locations, thus using similar pasture area. Table 3.2 presents information regarding livestock numbers and stocking densities for outlying farms and village-based livestock (per *khyzyk*).

Table 3.2. Data on livestock abundance and stocking densities for outlying farms and village-based livestock, from key informant interviews supplemented with direct observations and literature. District numbers used official statistical bureau data.

	Outlying Livestock	**Village Livestock**
Sample size (number of farms surveyed) *of which supplied stock numbers*	35 28	11 11
Total small ruminant numbers surveyed *Total numbers in Zhanybek district*	7,725 40,868	1,120 27,143
Mean small ruminant numbers per farm	276 (172- 397)	102 (63-150)

Range small ruminant numbers per farm/Khyzyk	0 – 1300	30-250
Mean stocking density (head per km^2)	13.8 (4.6 - 27.1)	5.1 (3.2 – 7.1)
Range stocking density (head per km^2)	0 - 153	1.5 – 12.5

3.3.3 Endoparasites in livestock and saigas

Outlying livestock had worm burdens comparable to those of saigas, as indicated by FEC data, while village-based livestock had significantly higher burdens compared to both of them (bootstrap $p<0.05$, table 3.3). Strongyle nematodes and *Nematodirus* sp. GINs, along with the tapeworm *Moniezia* sp., were found in both saigas and livestock (table 3.3).

Table 3.3. Endoparasite prevalence, range (eggs per gram) and mean (± standard error) (eggs per gram, EPG) across outlying livestock, village livestock and saigas. Sample sizes are number of pooled faecal samples, each representing a group (livestock) or sample location (saigas), and 15-20 individual faecal samples. Prevalence is expressed at the level of the pooled sample and not the individual animal. Livestock comprise mixed groups of sheep and goats. Strongyles include eggs morphologically characteristic of the Trichostrongylidae (see text).

		Strongyles*	*Nematodirus**	*Trichuris**	*Moniezia*	*Dicrocoelium*
Outlying Livestock (n=38)	**Prevalence (%)**	34	32	16	37	13
	Range (EPG)	5-35	5-25	5	5-110	5-10
	Mean (± SE) EPG	4.6 (± 1.3)	3.2 (± 0.9)	0.8 (± 0.3)	11.2 (± 3.6)	0.8 (± 0.4)
Village Livestock (n=38)	**Prevalence (%)**	74	45	47	82	18
	Range	5-45	5-25	5-20	1-155	5-25

	Mean (± SE) EPG	12.8 (± 2.0)	5.4 (±1.2)	4.9 (± 1.0)	34.6 (± 6.0)	1.8 (± 0.8)
Saiga Antelope (n=79)	**Prevalence (%)**	42	33	0	29	0
	Range	5-45	5-25	-	5-30	-
	Mean (± SE) EPG	4.7 (± 0.9)	3.2 (± 0.6)	-	3.8 (± 0.8)	-

*Gastro-intestinal nematodes, GINs; others are platyhelminths. All hosts also had oocysts of coccidia (*Eimeria* sp.) present. *Marshallagia* were present solely in outlying livestock and were included in strongyles (prevalence = 29%, mean (± SE) = 3.5 (±0.8))

As our focus is on GINs, information from 46 respondents (n=35 outlying and n = 11 village-based), on prevalent livestock health issues, their potential causes, impact on animal productivity, and treatments is summarized in Appendix B, Table 1. Respondents recognized GIN presence through symptoms like diarrhoea, weight loss, pale ocular mucous membranes, liquid discharge from nose, loss of appetite and visible worms in faeces. While the Mann-Whitney U-test showed that overall perceived health impact is similar between outlying and village-based livestock (w= 148.5, *p*=0.89) (Fig. 3.4b), the Fisher's exact test using proportions for each category (1-5) revealed that a larger proportion of village-based herders considered there to be some impact of GINs on health – albeit mild (*p* = 0.0006) (eg. 55% respondents in villages suggested "2 – impacted but not severely" as an impact score, while only 29% suggested so for outlying livestock; Fig.3.4a). See also the individual Five-point Check scores in Appendix B, Figure 5.

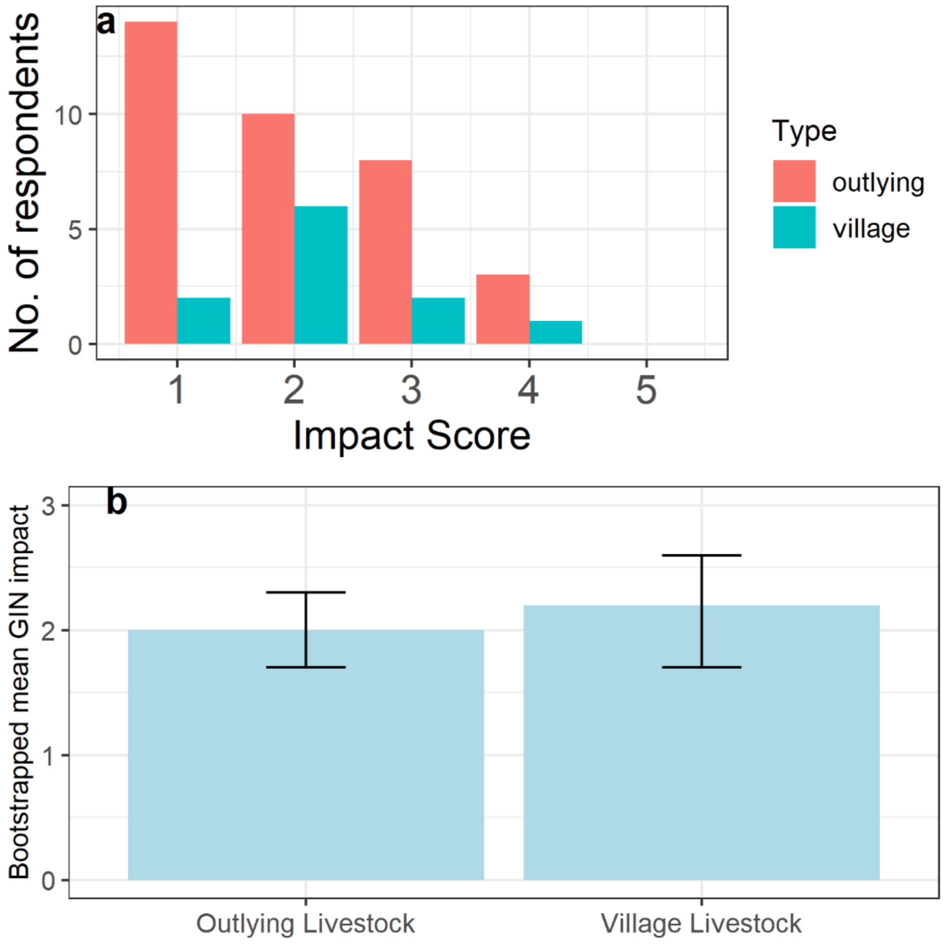

Figure 3.4. Graphs displaying a) impact scores of endoparasites (particularly gastro-intestinal nematodes, GINs) on livestock health; and b) bootstrapped mean and 95% CI of impact scores as related to herder perceptions of level of damage to health, for outlying and village-based livestock. 5 animal dies – 4 alive but useless (in term of what they define productivity to be) – 3 severely impacted – 2 impacted but not so severely – 1 little impact – 0 barely noticeable.

3.3.4 Treatment against endoparasites in livestock and saigas

We found that treatments against endoparasites (particularly GINs) depended on livestock location (Fig. 3.5). For instance, village-based livestock predominantly used anthelmintics as they could be bought from Uralsk (nearest town), which was easier to travel to from villages given road access, while outlying farms mostly did nothing or consumed the affected individual before health further deteriorated. Plant-based treatments were mentioned by herders on outlying farms but not in villages.

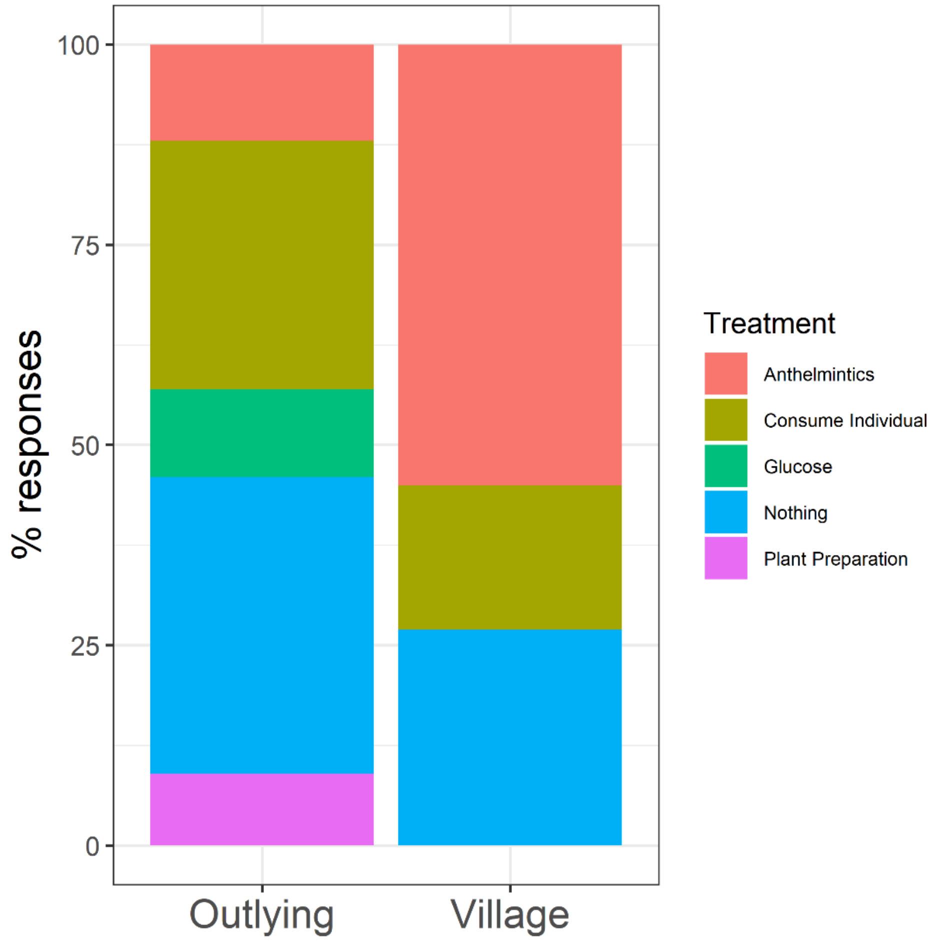

Figure 3.5. Stacked bar graph displaying the % responses of key informants for different treatment types against gastro-intestinal nematodes. n=35 outlying and n=11 village-based key-informants.

Sheep and goats are reported to be vaccinated against rabies, pasteurellosis, anthrax, pox and glanders in our study area (official Kazakh vaccination plan, 2019). We did not find any official treatment mandate for GINs from the state, which was confirmed by the five veterinary key informants. Hence it appears that GIN treatment was opportunistic, spatially variable and managed by livestock owners/shepherds. Livestock owners thus needed to source anthelmintic drugs themselves, which often came with a high expense as it involved travelling to nearest town/city, which could be up to a day's drive away.

3.3.5 Regional factors influencing disease transmission

Increasing demand for livestock products

Participants in 14 of the 15 FDGs arrived at the consensus that livestock numbers have increased in the region since the immediate post-Soviet period (1990s). Survey respondents (n=41) associated this change with government subsidies aiming to increase sale of livestock products (meat and dairy). Official data from the statistics bureau of Kazakhstan confirmed that between 2014-2020, Zhanybek district has seen a significant increase in small ruminants numbers owned by registered farmers (mostly outlying) and a relatively stable population owned by households (mostly in villages) (Fig. 3.6). This is similar to the trends in other livestock in Zhanybek and generally for Western Kazakhstan province (Figures 3 and 4 in Appendix B).

All respondents suggested that markets to sell livestock products (eg. meat) were more accessible now than in the 1990s; before 1991 procurement of livestock and its products were the state's responsibility. Additionally, the number of individual livestock owners was reported to be increasing. This has resulted in increasing occupation of outlying lands.

Furthermore, participants in 12 out of 15 FGDs arrived at a consensus that over time land parcels available to own or lease (as farms) in outlying areas are getting smaller, thus increasing stocking densities. Given pasture sharing, this is leading to potential resource competition with saigas. This possibility was confirmed when 41 out of the 46 key-informants suggested they had negative perceptions towards saigas as these reduce the available forage for livestock, especially during summer and autumn, a time when hay is also being collected for the winter.

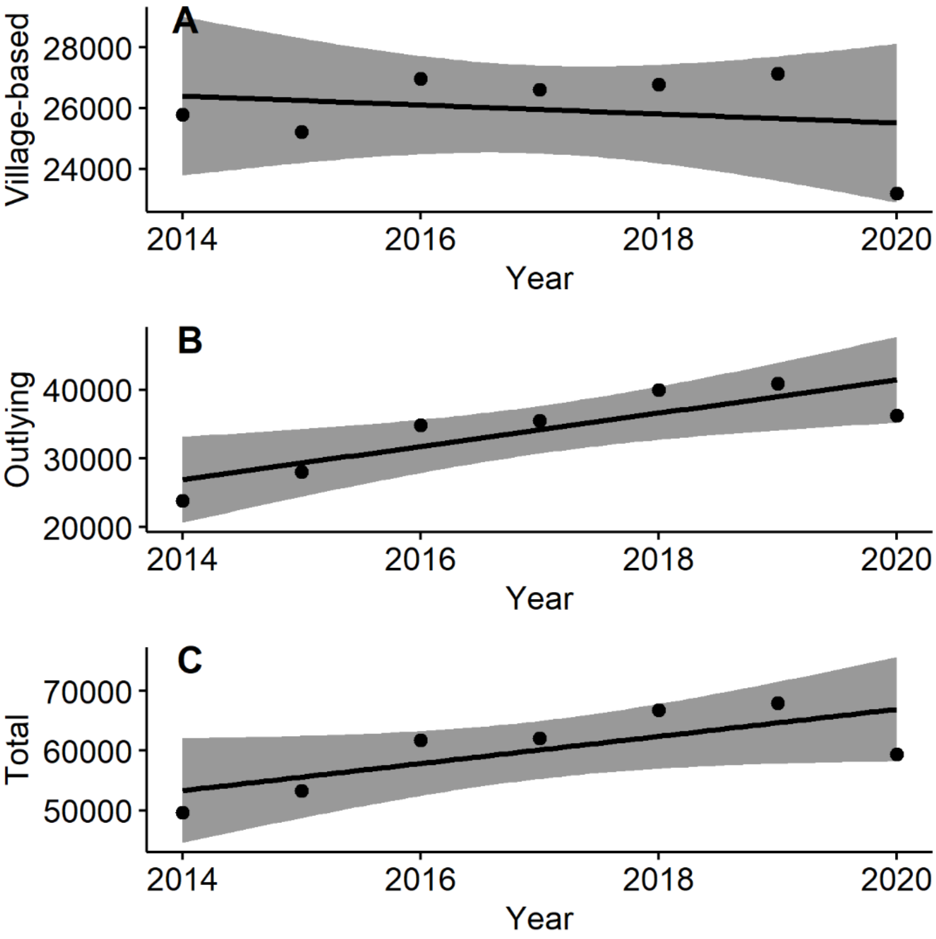

Figure 3.6. A panel graph showing the number of small ruminants (sheep and goats) A) belonging to households (mostly village based) (r = -0.23, *p* = 0.62), B) belonging to registered farms (mostly outlying) (r = 0.85, *p* = 0.016) and C) total holdings (r = 0.73, *p* = 0.061), over time (2014-2020) in Zhanybek district. Data from Kazakh Statistics Bureau. *P* <0.05 is considered significant. Shaded area in the graph is the 95% confidence interval. *Note*: Although the number of livestock have dropped in 2020 compared to previous years, we don't have evidence as to why this has happened.

Laws regarding land-use

FGDs revealed that during Soviet times, livestock herders used two state-owned locations; *zimovka* (winter house) and *letovka* (summer house), and migrated annually between them. In Ural, these movements were short in distance and duration (usually one day in transit), unlike in other parts of Kazakhstan where migrations could last several days or even weeks (Robinson et al., 2016). Today, even the short *zimovka* to *letovka* migrations are seldom occurring as most outlying farms are single sedentary entities leased by single owners (usually as family) and used throughout the year (see 3.3.1). Reasons for the loss of the two-season migration were not established with any certainty but are likely to include the costs of movement, establishment and maintenance of infrastructure at two sites (Kerven et al., 2016), and high transaction costs of obtaining the 49-year land lease, which are now allocated through a complex auction process (Robinson et al., *in press*).

Thirteen FDGs arrived at a consensus that the reasons for non-mobility were interconnected, and involved complications with legal access to land, high capital costs of investment in movement, and the availability of feed during the winters facilitating sedentarisation. The other two FDGs suggested that the reasons for non-mobility were that individual livestock holdings were not large enough for movement to either be necessary or cost-effective. Of the 35 survey respondents based in outlying farms, 29 said they collected hay for winter from their own farms while six suggested they purchased hay for winter from neighboring farms or from markets in nearby towns like Uralsk. All 11 village-based respondents said they purchased hay for winter either from neighboring outlying farms with surplus hay or from nearby towns like Uralsk. All 46 respondents suggested that availability of hay during winter was a key facilitator of non-mobility, as adverse weather during winter, often means they have to stall-feed their livestock.

Current climate and potential changes

Eleven of the 15 FGDs agreed that summers have become hotter and drier since the break-up of the Soviet Union. Since 2000, we found statistically significant evidence of warming summers in Ural as well as indications of decrease in summer precipitation, albeit not statistically significant (Fig. 3.6).

The 11 FGDs also agreed that winters had worsened, i.e. increased snowfall and narrowing *dzud* cycles. *Dzud* describes winter conditions leading to an icy snow surface, and is often associated with mass death of livestock and saigas from lack of food. *Dzud* conditions are associated with low temperatures accompanied by high precipitation. Since 2000, we find evidence for a trend towards lower winter temperature and increasing winter precipitation, albeit non-significant (Fig. 3.7). Temperature and precipitation data alone, however, might not capture the conditions leading to *dzud*. Respondents (n=43) suggested that one consequence of increased perceived *dzud* risk in Ural is that herders need to prepare more hay for the winter. This is challenging as the quality and quantity of grass has declined according to respondents. FGDs agreed that this affects livestock health, resulting in compromised productivity and even death. Forty-one of the 46 key-informants expressed concern at not being able to collect enough hay, as the saigas were eating grass that farmers normally harvest for this purpose. All five veterinary key-informants acknowledged that drier summers and large saiga numbers had minimized the amount of hay being collected by farms to sustain their stocks in winters. They suggested that this adversely affected livestock health and numbers, particularly in *dzud* years.

The remaining four of the 15 FGDs arrived at a consensus that climate has been relatively similar throughout the post-Soviet period, with marginally less rain in spring and summer. These four FDGs did not indicate any discernible impacts of climate on the rangelands (including hay collection) and host health. Nevertheless, they still indicated that saiga numbers were limiting hay collection.

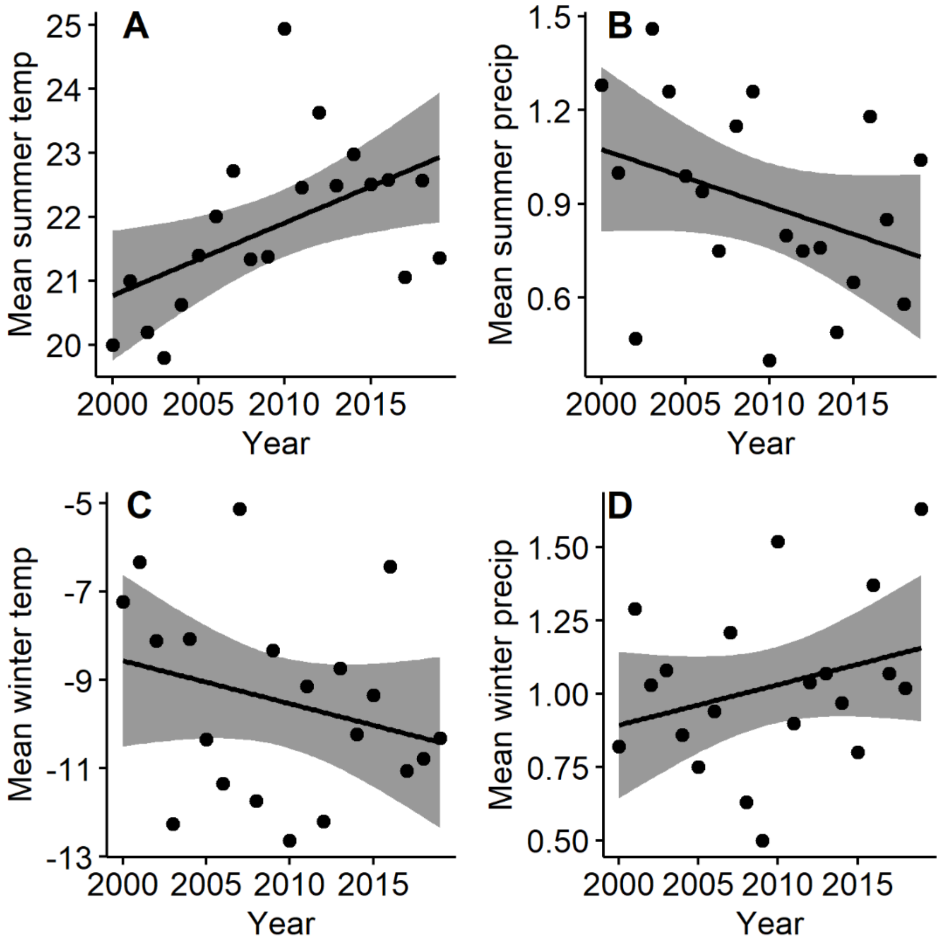

Figure 3.7. Panel graph presenting climate data over time across the calving and summer range of Ural saigas. Temperature in ^{0}C, and precipitation in mm. A = mean summer temperature (r= 0.53, *p* = 0.017), B = mean summer precipitation (r= -0.35, *p* = 0.13), C = mean winter temperature (r= -0.27, *p* = 0.26), D = mean winter precipitation (r= 0.29, *p* = 0.21). Data from POWER Data access viewer (POWER 2020). *P* <0.05 is considered significant. Shaded areas in the graphs are the 95% confidence interval.

3.4 Discussion

Our aim was to understand the inter-relationships between factors affecting ungulate health in the Western Kazakh rangeland, which is home to saigas and livestock. We specifically investigated the evidence for links between different factors, while considering uncertainties, with a focus on GINs. Below we discuss these links and the likelihood and possible consequences of future change.

3.4.1 Local social factors affecting host health

All respondents suggested some – albeit mild - impacts of GINs on livestock health in outlying farms and village-based livestock. Outlying livestock - likely to share pasture with saigas – were less likely to be treated for GINs than village-based animals. Whether this is because GINs are less common or problematic in outlying areas or the logistical difficulty in accessing treatment, needs investigation. As a result, GINs are likely to persist in livestock and transfer to saigas. However, the impact on livestock health and consequently the impact on saiga health of current interventions, if any, also needs investigation. Across Kazakhstan, outlying farms are increasing (Kerven et al., 2020). While vaccination regimes seem to be effectively implemented, delivery of anti-parasite care does not seem to have followed that trend. This could negatively impact both livestock and saiga health.

Given low levels of anthelmintic treatment of livestock on outlying farms, the spread of anthelmintic-resistant parasites to saigas and onward transfer between livestock farms, as observed in other wild ungulates using shared pastures (Chintoan-Uta et al., 2014), seems unlikely. With increasing modernization, more outlying farms will likely become connected by road to nearby towns (Pomfret 2009). This could increase anthelmintic access, which may reduce GIN transmission to saigas. Yet, if done as whole-herd treatments, this risks the development and spread of anthelmintic resistance (Charlier et al., 2014). Some outlying farmers reported using plant-based therapies against GINs. A wide range of plants can have combined antiparasitic and nutritional benefits (Hoste et al., 2012), and such 'nutraceutical' plants could help to support livestock health with less dependencies on external inputs and lower risk of fostering drug resistance (French, 2018). Such plants are presumably also accessible to saigas. Further research could identify likely plant-based interventions using ethno-veterinary and epidemiological studies, to improve prospects for sustainable GIN control.

3.4.2 Local ecological factors affecting host health

We found that saigas are carrying GIN burdens when grazing in their calving and summer range, although it is not known if they are at physiologically detrimental levels. We do have some evidence for this in livestock. The levels of FEC observed here are consistent with negative correlations with body condition in saigas (Morgan et al., 2005a). This is concerning for females as worm burdens may further compromise their immunologically stressed-state during calving; and in other wild ungulates have been associated with decreased fecundity (Albon et al., 2002). In Ural, contact with sympatric livestock is likely to increase in coming years as saiga and livestock numbers are both seeing an increase (Zuther, 2020). The contribution of migration to worm burdens needs investigation. For instance, Morgan et al., (2006; 2007) show that saigas probably contributed to GIN transmission from their winter range, to sheep in their summer range in Betpak-Dala, under prior conditions of high livestock densities and close contact with livestock in the winter range, which likely no longer hold as saigas don't migrate as far south in the winter. Alternatively, migration could inhibit parasite transmission by reducing host availability (Altizer et al., 2011), and could be adaptive in wild ungulates (Folstad et al., 1991).

Saigas are most likely to share pasture with outlying livestock (Khanyari et al., 2021; Chapter 2) which have significantly lower worm burdens than village-based livestock, and comparable burdens to saigas. However, this situation may worsen with further increase in livestock numbers and increased resource competition. Our results and official online digital cadastre records of Kazakhstan indicate that although there are areas of the steppe without farms, large areas are in fact leased indicating possibility of pasture overlap between saigas and outlying livestock (stat.gov.kz, 2020).

3.4.3 Regional factors affecting the system

As state support dwindled following the breakdown of the Soviet Union, the Kazakh rangelands witnessed an abandonment of outlying areas (Dara et al., 2020). For the first decade following the Soviet Union's collapse, the livestock sector received limited state attention – which was predominately concerned with developing oil and gas reserves (Pomfret, 2009). Recently, the Kazakh government has introduced large subsidy programs supporting livestock production (Petrick et al., 2018), but these tend to benefit large-scale livestock owners, while households (livestock owners not registered as farms) are ineligible (Kerven et al., 2021). There is evidence that many larger livestock operations have become much more mobile in recent years as they rebuild economies of scale for movement (Robinson et al.

2016, Kerven et al., 2016, Robinson et al., in review), but smaller farms and household remain more sedentary. Our study showed that in Ural outlying farms were entirely sedentary, in contrast to areas in Central and Southern Kazakhstan where the above-cited studies were conducted. Overall, a general reduction in livestock mobility is a trend observable across temperate Asia and indeed globally (Fratkin, 2005). The end of collectivized agriculture and subsequent reforms in most Central Asian and Caucasian states have tended towards reduction in herd sizes and individualization of pastoral tenure (Robinson et al., 2016). China's Grassland Contract Policy, mandating privatization and fencing of pasture, has affected the ability of herders to exploit rangeland variability and led to environmental deterioration (Næss, 2013).

Concerning the effects of these changes on livestock-wildlife interactions, Western et al., (2009) showed that sedentarisation was a factor in wildlife declines in Southern Kenya, attributed to direct displacement of wildlife and the reduction in grass production following a swap from seasonal to permanent grazing. While, we don't have evidence of this yet in Kazakhstan's rangelands, the literature certainly cautions that it is possible and the availability of subsidies for fencing may yet have negative impacts in this respect. Additionally, sedentarisation can lead to increased opportunities for GIN transmission linked to tighter contact patterns (given saiga presence) and increased stocking densities. Although we have no data on the impact of sedentarisation on livestock parasite loads, modelling suggests that for saigas, migration broadly results in lower overall infection pressure (Khanyari et al. in review; Chapter 7) and such a finding might reasonably be expected for livestock. However, the impacts of reduced livestock mobility on host health might vary across the saiga's range, which need reconciling into more spatially-explicit impacts.

Lastly, we found some evidence of climate change. Climate can affect livestock and saiga health, their numbers and distributions (Bekenov et al., 1998). Salnikov et al., (2015) demonstrated statistically significant decreases in precipitation and increased temperatures, particularly during summer, across Kazakhstan since 1941 . Although there is limited information from Western Kazakhstan, studies have indicated an increasing frequency and severity of *dzud* (harsh winters), coupled with a warming and drying trend across other parts of Central Asia, since the turn of the 21st century (eg. Shinoda, 2017).

Mobility has been cited as being a key reason why pastoralists do relatively well during extreme climatic events and its loss can limit pastoralists' resilience (Næss, 2013). In Central Asia, studies in Turkmenistan have shown that, where transport and capital costs of pasture occupation are low, and formal barriers to land access absent, livestock owners remain highly mobile and responsive to vegetation variability, which is high in that drought-prone state (Behnke et al., 2016). The severe drought of 2021 in Kazakhstan may highlight the importance of policies which promote easier access to pasture, both physically through infrastructure like machinery for hay cutting, and administratively through simplified leasehold allocation and transfer between users, or common property systems.

Climatic factors are contributing to increased need for hay for livestock. Mechanized hay cutting can exacerbate resource competition and tighten contact patterns during the calving and summer periods, with consequent impacts on livestock and saiga health. Other studies show exacerbated grassland degradation and desertification across Kazakhstan, particularly Western Kazakhstan (Hu et al., 2020). This could also lead to interference and exploitative resource conflict across the autumn saiga range. Nevertheless, we need to triangulate interview data which predominantly concerns perceptions, with other sources such as remotely-sensed data, in order to draw firm conclusions.

3.4.4 Implications for saiga health in Ural

It is apparent from our results that saiga health is not only intertwined with sympatric livestock health, but also is affected by a number of factors across varying scales. It is key to consider saiga health in conservation planning, in addition to threats like poaching, to ensure that populations remain large enough to deal with future mass mortality events (Kock et al., 2018). This requires considering the complex inter-connected factors affecting saiga health and their potential future changes, and filling of current knowledge gaps. As conservation is a resource- and time-limited discipline, such interdisciplinary exercises can help shape interventions that take account of such pluralistic interactions, rather than implementing silo solutions (William et al., 2020). For example, in this case, it seems that livestock and wildlife health cannot be disentangled from issues of resource competition (particularly for hay meadows, both in calving/summer and autumn saiga range); both of which are likely to be exacerbated by climate change.

Nevertheless, there are some key caveats to consider about our work. Our results are not an exhaustive representation of inter-connections between factors, as we lacked data on various aspects. For instance, because of limited ability to differentiate between nematode species using egg morphology alone, the extent to which particular species of GIN are shared between saigas and livestock in this population is unknown. Previous studies in the Betpak-Dala population showed that of 38 helminth species found in saigas, 36 were also found in sympatric livestock (Morgan et al., 2005a), but to demonstrate this required post-mortem recovery of adult worms. Genetic sequencing of parasites in host faeces can provide species-level information on parasite presence (Avramenko et al., 2019), on which to base inferences about parasite overlap between hosts.

While uncertainties remain, our study demonstrates the importance of viewing host health in rangelands as a complex adaptive social-ecological system. Such systems have many dynamic components, determining the ability of rangelands and their inhabitants to cope with disturbances and respond to changes, including those affecting disease transmission. Adaptation needs to be a continual and iterative process and is linked to resilience, ensuring that the system adapts to new forces without losing functionality or transforming in fundamental ways (Hruska et al., 2017). These aspects are relevant for saigas in Ural and across their global range, as they are surviving in a dynamic world in which: livestock increasingly use outlying steppe areas (Kerven et al., 2016); climatic changes potentially alter host-pathogen interactions (Kock et al., 2018) and resource acquisition (Pruvot et al., 2020a); and state policies push towards more intensive livestock production systems (Kerven et al. 2021). It will be crucial for saiga conservationists to engage in multi-pronged conservation interventions, which are evaluated and adapted through the lens of rural livelihoods and the livestock health on which they depend.

3.5 Conclusion

In conclusion, multi-use rangelands across the world are socially and ecologically important for a variety of reasons and are characterized by complex interactions between various factors. While there have been some advances in understanding these interactions for the functioning of rangelands themselves (Reid et al., 2014; Hruska et al., 2017), there has been little done on understanding their impact on animal health. Our work provides insights into the social-ecological factors affecting host health in rangelands, as well as the complex interactions among species that share and potentially compete for space and forage. Overall, this work fills an important gap in the rangeland and pastoralism literature, because measuring the impacts – positive and negative – for wild and domestic species of sharing space and resources is one of the biggest challenges for wild herbivore conservation and local livelihoods. We hope our work will provide researchers and practitioners with an avenue to better understand these complex inter-relationships, while viewing host health from an interdisciplinary perspective - ultimately working towards wildlife conservation whilst safeguarding livelihoods across the world's rangelands.

- Chapter 4 -

Pastoralism in the high Himalayas: Understanding changing practices and their implications for parasite transmission between livestock and wildlife.

In review **Khanyari, M.**, Robinson, S., Milner-Gulland, E.J., Morgan, E.R., Rana, R.S., & Suryawanshi, K.R. (no date). *Pastoralism*.

Authors' contribution

I, ERM, EJMG and KRS conceived the study. I and RSR collected the data. I analyzed the data and lead the writing of the manuscript. All authors contributed to revised drafts.

The trans-Himalayan region of Pin Valley

Abstract

Rangelands are increasingly being affected by climatic variations, fragmentation and changes in livestock management practices. Along with resource competition between livestock and wildlife, disease transmission has implications for people and wildlife in these shared landscapes. We worked with two pastoral communities in the Western Indian Himalaya: the migratory *Kinnaura*s that travel to the trans-Himalayan Pin valley in summer and the resident herders of Pin valley. Asiatic ibex (*Capra sibirica*) is the predominant wild herbivore in Pin. The pastures in Pin are grazed by both livestock (migratory and resident) and ibex, with the potential for disease transmission. We investigate the effects of herding practices on livestock health and disease transmission, while focusing on Gastro-intestinal Nematodes (GINs) due to their interactions with nutrition, climate and body condition of the host. We found that the *Kinnaura* flocks share pasture with ibex during their time in Pin, exhibiting significantly higher endoparasite burdens than sedentary livestock, and the *Kinnaura* flocks are increasing in number. This suggests GIN cross-transmission is possible, as GINs have low host specificity and a free-living, environmental stage that is trophically-acquired. As local (sedentary) sheep and goats rarely share pasture with ibex, have low endoparasite burdens and are few in number, they are unlikely to transmit parasites to ibex. However, increasingly large local stock numbers may be contributing to pasture degradation which could cause nutritional stress and resource competition, exacerbating GIN impacts. We also find evidence for transhumance persisting, in spite of signs of pasture degradation that are seemingly affecting livestock productivity and potentially disease transmission. It is critical that proactive measures are taken, like participatory disease management with the *Kinnauras*, to align livelihoods with wildlife and rangeland conservation.

4.1 Introduction

Pastoralism – production systems and livelihoods that predominantly depend on livestock raised either on communal or private pastures, with varying amount of mobility (Niamir-Fuller et al., 2012) – is practiced globally. Forms of pastoralism adapted to high levels of climatic variability are particularly present in the rangelands of Asia and Africa (Goldstein & Beall, 1990), where migratory livestock grazing is widely practiced in areas of high seasonal variation and limited natural resources (Saberwal, 1996; Coppolillo, 2000; Axelby, 2007).

Rangelands are increasingly being impacted by climatic variation, ecosystem fragmentation and changes in livestock management practices, with implications for the people and wildlife that call them home (Mishra, 2001; Galvin et al., 2008; Kerven et al., 2016). Over the past few decades, pastoralism has been particularly influenced by social-political changes affecting pastoralist rangeland use and management (Robinson & Milner-Gulland 2003; Nori & Scoones 2019). Reductions in pasture quality, sedentarization, increased livestock populations and conflict with wildlife are commonly observed impacts of these changes (Singh et al., 2013). Importantly, sharing of rangelands by different ungulate species can lead to resource competition between livestock and wildlife, and potentially disease transmission (Rhyan & Spraker, 2010).

Disease transmission across multi-use rangelands can negatively affect pastoralist livelihoods (Reid et al., 2008) and wildlife conservation (Smith et al., 2009). Among wildlife species, ungulates are most likely to be affected, as they share resources and many pathogens with domestic ungulates (Walker & Morgan, 2014). Endoparasites, such as Gastro-intestinal nematodes (GINs) are particularly important as they are determinants of fitness for wild and domestic ungulates (Gulland, 1992; Perry & Randolph, 1999) and are acquired by feeding on pastures. As they have free-living environmental stages, their transmission is enabled by indirect contact, which in turn is governed by host distributions and movement (Vosloo et al., 2002); and hence by climate-induced changes in resource availability and socio-economic factors (Robinson & Milner-Gulland, 2003; Weinstein & Lafferty, 2015). Seasonal movements of wild and domestic ungulates, landscape management, and aggregation at various spatial scales can strongly modify GIN transmission risk (Pruvot et al., 2020b). In mixed-use systems, human interventions in GIN management can influence GIN presence in livestock and consequently the dynamics of co-transmission to wild ungulates (Weinstein & Lafferty, 2015). Changes in any of these factors may affect the adaptability and resilience of pastoral systems (Hruska et al., 2017). Evaluating host health and disease transmission in pastoral systems therefore requires an interdisciplinary perspective that can cover both the social and biological aspects of transmission risk (Tomaselli et al., 2018).

Migratory livestock grazing is a widespread form of pastoralism in the Himalayas and Trans-Himalaya (Saberwal, 1996; Axelby, 2007). There is increasing evidence of negative impact of livestock grazing manifested through pasture degradation and competition between livestock and wild ungulates (Mishra, 2001; Bagchi et al., 2004). For instance, Bagchi et al. (2004) found interference competition between migratory livestock and Asiatic ibex *Capra sibirica* in Pin valley. Similarly, exploitative competition between blue sheep *Pseudois nayaur* and resident livestock has been shown to reduce juvenile blue sheep survival (Mishra et al., 2004; Suryawanshi et al., 2010). Studies in the Indian Himalayan rangelands have also recorded several livestock diseases and parasitic infestations of relevance to wildlife, including foot-and-mouth-disease (FMD), haemorrhagic septicaemia, Peste-des-petits-ruminants (PPR) and GINs (Dixit et al., 2009; Muthiah et al., 2013). Against this backdrop, understanding disease management and the impact of livestock husbandry practices on key aspects of disease risk, such as contact patterns, in the multi-use Indian Himalayan pastoral systems, has remained relatively unexplored.

We worked with two pastoral communities in the Western Indian Himalaya – the migratory *Kinnaura* herders and local livestock herders of Pin valley – to investigate contemporary herding practices, in order to understand potential impacts on domestic and wild host health and disease transmission to wild ungulates in the Pin valley. We focus on GINs because these are acquired on co-grazed pastures, associated with host nutrition and body condition (with effects exacerbating and exacerbated by under-nutrition), and are strongly affected by season and climate. GINs are thus expected to be particularly affected by changes in the social-ecological system of the Himalayan rangelands. Our secondary focus was on pasture condition and implied (rather than demonstrated) impacts on GIN susceptibility and impact. We specifically assessed host contact patterns, endoparasite worm burdens, livestock holdings and composition for both communities, reasons for and persistence of migratory herding, and state of pasture quality in Pin valley. Where possible, we assessed how these factors have changed since the turn of the 21st century (see Table 4.1). Insights gained from our work can be used to develop effective participatory rangeland management programs to align pastoral livelihoods with wildlife conservation.

4.2 Materials and Methods

4.2.1 Study area

We worked with two communities in Himachal Pradesh, India: the migratory herders of Rupi-Bhaba area, Kinnaur district (*Kinnauras*) and the resident herders of Pin valley, Lahual-Spiti district (Fig. 4.1). The *Kinnaura* herders undertake long-distance migration with their sheep and goats. Traditionally they graze pastures of the trans-Himalayan Pin Valley during summer (June-August), spending winters in the Himalayan foothills of the Sirmaur region (November-March) and a large part of spring and autumn in their native Rupi-Bhabha area (April-May and September-October; Fig. 4.1 and Fig. 4.2). Men are exclusively responsible for the care of migratory livestock herds, whilst their families live in settled villages in the Rupi-Bhabi area, where they grow wheat, millet, pulses (food crops), apple and apricots (cash crops). Agriculture is primarily taken care of by the women. Rupi-Bhabha is located between 2,100 and 3,500 m, with some peaks reaching as high as c. 5,900m. Temperate and alpine conditions predominate, characteristic of the Greater Himalaya (Olson et al., 2001; Fig. 4.1).

The settled residents of Pin valley are predominantly agro-pastoralists (Bagchi et al., 2004). They rear livestock including sheep, goats, horses, donkey, cow, yak and yak-cow hybrids called *Dzo*. Alongside, they grow a few crops during the short summer months including green pea, black pea and barley. Each village within Pin valley holds traditional rights to rangelands in Pin. Annually, the *Kinnaura* herders pay a “tax” to each village committee to use these pastures for the summer months. Pin valley falls within the Trans-Himalayan region, which is in the rain-shadow of the Greater Himalayas and adjacent to the Tibetan plateau. The altitude ranges from around 3,200 m to above 6,000 m, with rangelands located primarily between 3,200 – 4,200 m. Pin valley is a cold desert, characterized by rugged terrain and dry-alpine steppe meadows (Chandra Sekar & Sivastava, 2009). The Asiatic ibex is the predominant wild herbivore in the region, and also the primary prey of the snow leopard *Panthera uncia*, the apex predator of this ecosystem. As the ibex is a caprine, it is most likely to share pasture and GINs with sheep and goats (Bagchi et al., 2004; Walker & Morgan, 2014); hence we concentrated our work on these two species (livestock hereafter refers to sheep and goats, unless stated otherwise). Even though the migratory livestock share pasture with other ungulates to some extent throughout their migratory range, we concentrated our work in the Trans-Himalayan Pin valley as its rangelands are co-grazed by livestock and ibex during the short yet important growth season (Ghoshal, 2017). Additionally, there is evidence that Pin valley is particularly heavily grazed by livestock compared to surrounding rangelands, causing conservation concern for wild ungulates, with calls for integration of social and ecological considerations into management planning for the valley (Bagchi et al., 2004; Ghoshal, 2017)

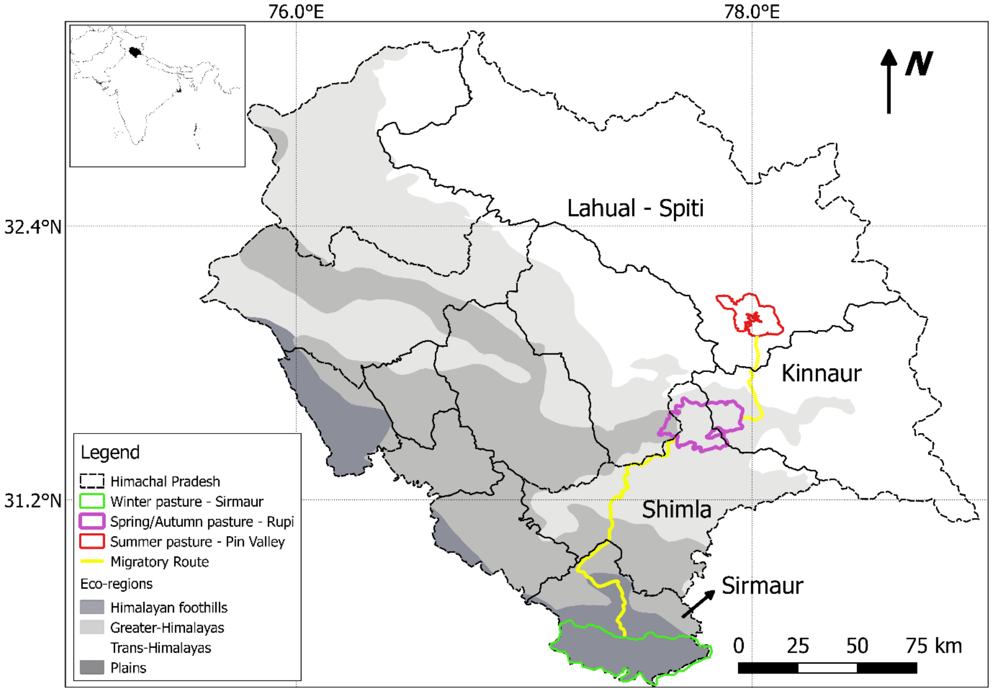

Figure 4.1. Map displaying the migratory route and seasonal pastures of the *Kinnaura* herders. The inset map situates the state of Himachal Pradesh within India. Districts in Himachal Pradesh within which seasonal pasture of the *Kinnaura* herders are found are named on the map. Eco-regions were obtained from Olson et al. 2001. Our study area (Pin valley) is outlined in red.

4.2.2 Data collection and analysis

Survey on livestock movement and management and its consequences

We used qualitative research methods to interview 41 key informants, one from each of 28 migratory livestock herds (called *tols*) and 13 villages in Pin valley between June-August 2019. The village heads in Pin valley and the Rupi-Bhaba area confirmed that these were all the *tols* that undertook the migration that year. Each *tol* is composed of animals belonging to many people, only some of whom actually travel with the animals. The key informants were chosen based on their knowledge of pastoral activities, the rangelands, livestock health and management, and changes in these factors since the start of the 21st century. The interviews with the migratory herders were done in the form of a walking interview (Anderson, 2004; Carpiano, 2009) on their route from Rupi-Bhaba area to Pin valley (Fig. 4.1, Fig. 4.2). The interviews with the resident livestock owners in Pin valley were conducted in their villages. Questions revolved around characterizing pastoral activities (e.g. individual livestock holdings and herd sizes), pasture overlap with ibex, perceptions of pasture quality changes, their livestock's health issues and treatments administered (see Table 4.1 for specific research questions). We also explored interactions between the two types of pastoralism, including their spatial overlap, pastoralists' interactions with Asiatic ibex, impact of livestock grazing on rangelands, the prevalence, impact and transmission of disease in general, and other factors (e.g. climate) contributing to changes in livestock grazing on these rangelands.

Where possible, quantitative and semi-quantitative data were analyzed using descriptive statistics or by bootstrapping answers with replacement (10,000 iterations) to estimate means and 95% confidence intervals. Particularly for the open-ended questions, analysis followed open and axial coding as suggested for grounded theory generation (Creswell, 1998). We performed inductive analysis to facilitate the emergence of patterns, themes and categories out of the data (Patton, 1990). For each of the questions, cross-interview analysis was performed, bringing together responses from different key informants for the same question to illustrate broader patterns and categories under each theme (Patton, 1990). The analysis was conducted in Microsoft Excel and the R statistical and programming environment (R Core Team, 2020). Table 4.1 lists the set of research questions the key-informant interviews aimed to answer, along with their rationale (see Appendix C - Questionnaire). The survey questionnaire was approved by the University of Bristol's Ethical committee. Consent was taken orally before conducting the surveys and all the responses were coded; names or other identities of respondents were not used, in order to ensure anonymity.

Figure 4.2. A *Kinnaura* herder *tol* crossing the Bhaba pass from Rupi-Bhaba into Pin valley. Some livestock do not make it across the pass, as seen by the lone goat-kid left behind the pass.

Table 4.1. Research questions that we addressed in the key-informant interviews, and the rationale behind them.

Research Question	**Rationale****
Are domestic and wild hosts sharing pasture in Pin valley?	The majority of rangelands in the Western Trans-Himalayas, including Pin valley, are co-grazed (Bhatnagar, 1997; Bagchi et al., 2004). This can lead to resource competition and disease transmission. Being restricted to grazing around villages, local livestock are unlikely to share pasture with wild hosts.
*What is the GIN burden and impact on host health?**	Due to increasing herd sizes and limited veterinary care/interventions, we predict that migratory livestock have substantial health issues, in particular that they have high GIN burdens.
How do current livestock holdings compare to those of 20 years ago?	Herd sizes of migratory livestock have been increasing across regions of the Western Trans-Himalayas (Ghoshal, 2017) and we expect to find the same pattern in our study area. Resident livestock have seen major declines in the region due to a number of social and political factors (Singh et al., 2015).
What are the current reasons for undertaking the long-distance migration, is it likely to persist and what governs leasing of pasture?	Long-distance migrations occur for multi-faceted ecological and social reasons, many of which are likely to persist into the future (Ghoshal, 2017). Therefore we expect migration to continue.
What is the current state of the pasture quality in Pin valley and how has it changed over time?	There is evidence of increasing pasture degradation across the Western Trans-Himalayan rangelands (Mishra et al., 2001; Bagchi et al., 2004). Pasture degradation can impact resource competition and disease transmission. Degradation and transmission both have a common cause in high livestock stocking rates. Degradation adds to the problem of disease through nutritional stress and resource competition (Kock, 2004) - which can exacerbate the impacts of GINs.

*This is supplemented by the endoparasite analysis; ** while we are unable to rigorously or systematically test the hypotheses expressed here, we articulate them in order to clarify the rationale behind our research questions.

Endo-parasites in ibex and livestock

Fresh faecal pellet samples were collected from sheep, goats and ibex. Collection was opportunistic and covered the entire period that migratory livestock were in Pin valley (June-August). Livestock samples were pooled at the level of each livestock herd (migratory and sedentary separately) and ibex samples were pooled at the level of the study population (Morgan et al., 2005b). For ibex, samples were collected from all age-sex classes. The date and location for each sample collected were recorded. Provided that the material is well-mixed, the faecal egg count (FEC) in an aliquot of pooled faecal sample is a good reflection of the average individual FEC (Morgan et al., 2005b). FEC provide a direct measure of the relative contribution of different hosts to pasture contamination. Given their adverse impact on wild and domestic ungulate health and fitness, we were particularly keen to investigate existence of strongyle helminths in both hosts.

Infection intensity and contribution to pasture contamination were estimated by FEC on pellet samples, to evaluate endoparasite worm burdens. The mini-FLOTAC technique (Cringoli et al., 2017) was used as a field-friendly method for FECs in remote areas. This method estimates the abundance and diversity of endoparasites, using sedimentation-flotation to separate nematodes and protists eggs from the faecal matter and allow them to be identified and quantified under a microscope. The protocol given in Cringoli et al., (2017) was followed, with 5 ml of faeces analysed per sample in 45 ml of saturated sodium chloride salt solution. The number of eggs found for each parasite was recorded for each sample and multiplied by a factor of 5 to obtain the total FEC in eggs per gram (EPG) of faeces. The sensitivity of the mini-FLOTAC technique at this dilution is 5 EPG. We used the bootstrap t-test to compare the difference in mean abundance of endoparasites between ibex and livestock (Wilcox, 2017).

To supplement the FEC data for local and migratory livestock, we assessed impact scores of endoparasites on livestock health. This was done by direct questioning of the 41 key informants, who judged the impact of endoparasites (particularly GINs) on a scale of 0-5 [5 animal dies – 4 alive but useless (in term of owner-defined measures of productivity) – 3 severely impacted – 2 impacted but not so severely – 1 little impact – 0 barely noticeable].

4.3 Results

4.3.1 Are domestic and wild hosts sharing pasture in Pin valley?

We mapped pasture use by local and migratory livestock (Fig. 4.3). It is clear that pastures are shared between ibex and migratory livestock throughout the summer. Ibex locations were mapped by the 41 key-informants and were also triangulated by the annual population monitoring exercise conducted by the Nature Conservation Foundation (NCF unpublished data). We found no evidence for pasture sharing between local (sedentary) livestock (sheep and goats) and ibex (Fig. 4.3). While Figure 4.3 represents data for the summer months (June-September), all 13 key-informants from the Pin villages confirmed that local livestock distribution is limited to the orange polygon displayed in Figure 4.3, and that they are stall fed in the harshest winter periods (usually December-February). They also confirmed that even though ibex exhibit some degree of vertical movement seasonally, they rarely share pastures with local livestock.

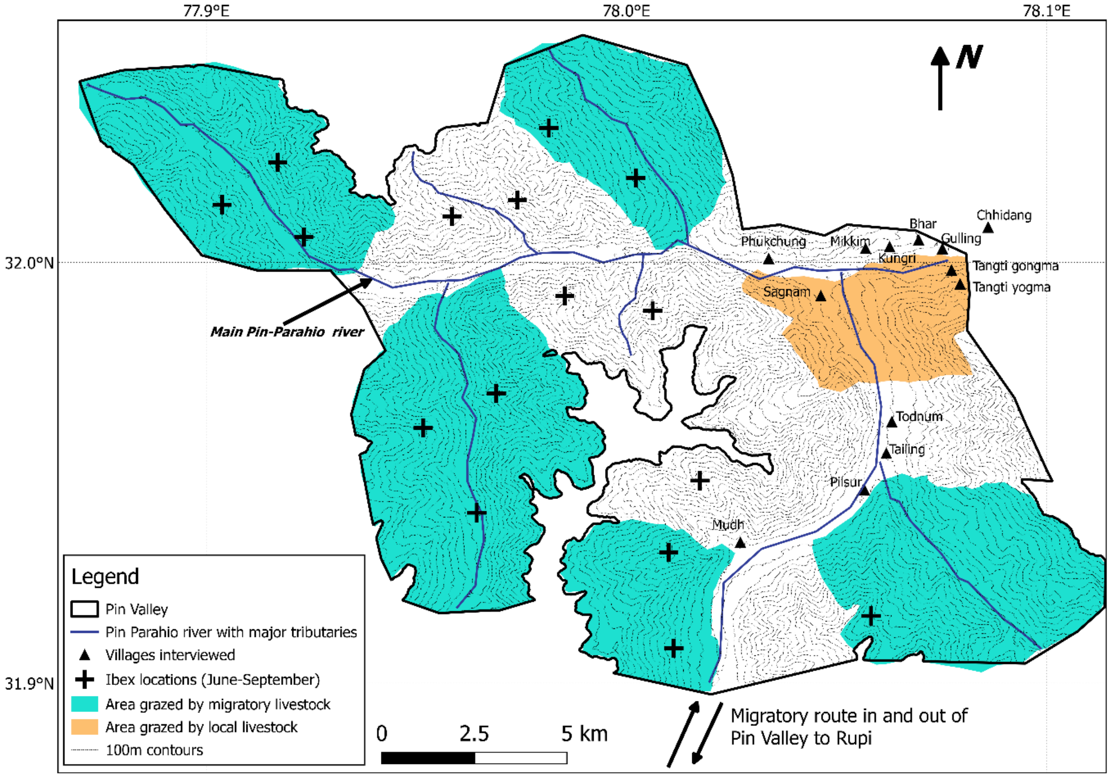

Figure 4.3. Map displaying grazing areas of migratory and local livestock (sheep and goat) within Pin valley, along with locations of ibex and villages, for the months of June-September.

4.3.2 What is the GIN burden and impact on host health?

We analyzed 65 pooled fresh faecal samples from migratory livestock, 86 pooled samples from sedentary livestock and 74 samples from ibex. Table 4.2 presents the endo-parasites present in these samples with their prevalence. Apparently shared GINs between both types of livestock and ibex were *Strongyloides* sp., Strongyle GINs and *Nematodirus* sp. They also shared the platyhelminth, *Moniezia* sp.

Table 4.2. Endoparasite prevalence, range (eggs per gram) and mean (± standard error - eggs per gram) across migratory livestock, local livestock and ibex. Sample sizes are number of pooled faecal samples, each representing a different host category: migratory livestock, local livestock and Asiatic Ibex. Prevalence is expressed at the level of the pooled sample and not the individual animal. Livestock comprise mixed groups of sheep and goats. Strongyles include eggs morphologically characteristic of the Trichostrongyloidea.

		Strongyloides*	**Strongyle GINs***	***Nematodirus****	***Trichuris****	***Moniezia***
Migratory Livestock (n=65)	Prevalence	9%	89%	15%	11%	55%
	Range (EPG)	5-10	5-195	5-10	5-55	5-270
	Mean (± SE) EPG	0.7 (± 0.29)	25.6 (±4.35)	1.1 (± 0.34)	2.2 (± 1.03)	35.8 (± 7.56)
Local Livestock (n=86)	Prevalence	6%	47%	6%	-	34%
	Range	5-10	5-20	5-15	-	5-220
	Mean (± SE) EPG	0.4 (± 0.19)	4.7 (± 0.63)	0.5 (± 0.23)	-	15 (± 4.87)
Asiatic Ibex (n=74)	Prevalence	11%	47%	9%	-	26%
	Range	5-10	5-20	5-15	-	5-185
	Mean (± SE) EPG	0.8 (± 0.29)	4.1 (± 0.66)	0.7 (± 0.28)	-	5.5 (± 2.68)

*GINs. *Moniezia* is a GI platyhelminth. All hosts also had oocysts of coccidia (*Eimeria* sp.) present.

When considering overall endoparasite loads, migratory livestock had significantly higher egg densities than local (sedentary) livestock (t=4.79, df=95.81, *p*= 6.17 e-6) and ibex (t=5.94, df=76.71, *p*=7.79 e-8); whilst sedentary livestock and ibex had similar loads (t=1.47, df=139.89, *p*=0.143) (Fig. 4.4). This was also true when considering strongyle GINs alone (table 4.2). While there was a varying level of reported impact from endoparasites, key-informants revealed significantly worse impacts (t=3.19, df=31.47, *p*=0.0032) in migratory livestock compared to local livestock (Fig. 4.5).

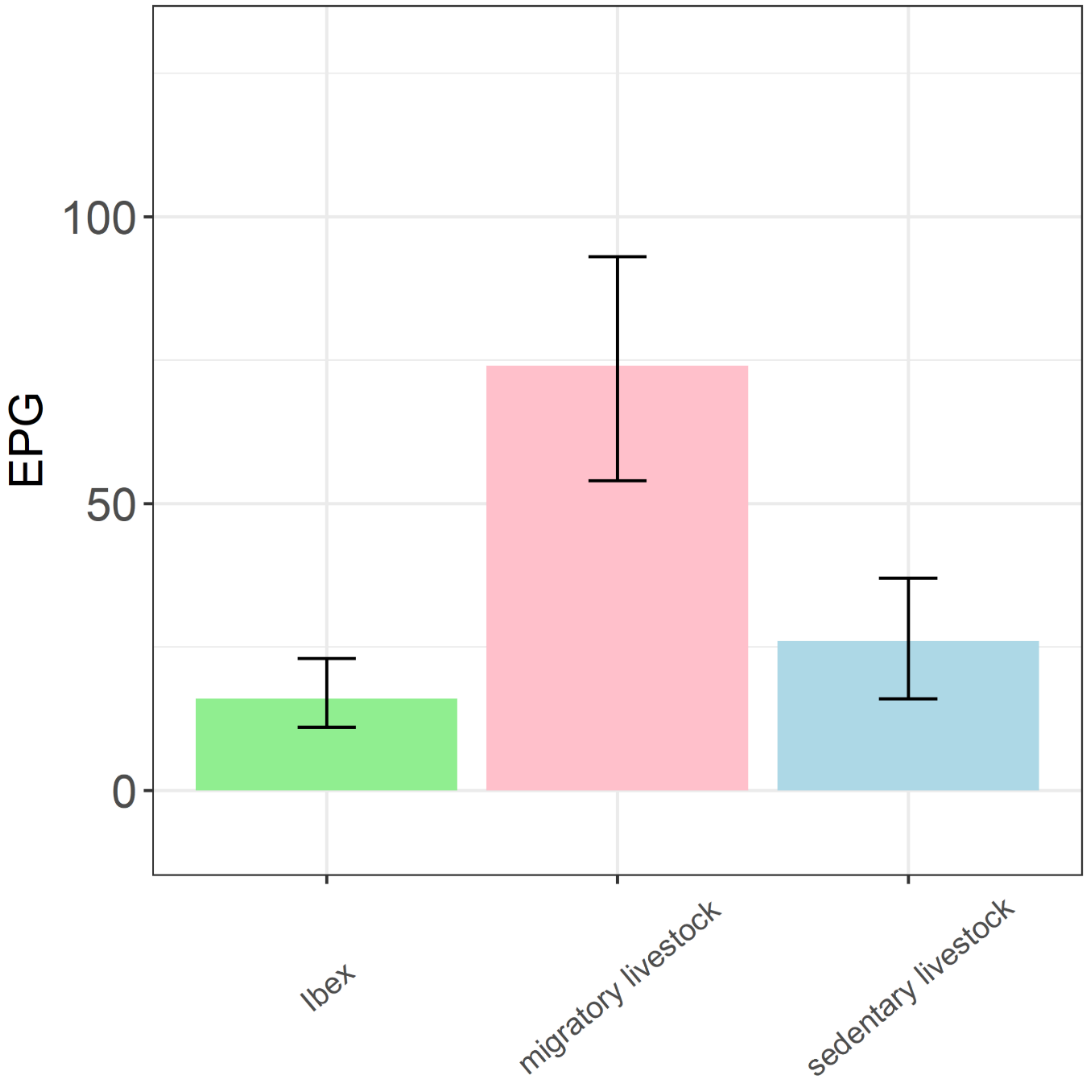

Figure 4.4. Bar-plot displaying bootstrapped mean cumulative Fecal Egg Counts (eggs per gram, EPG) for all endoparasites (except coccidia) across hosts. The bars display the 95% confidence intervals after bootstrapping the data. Sedentary = local livestock.

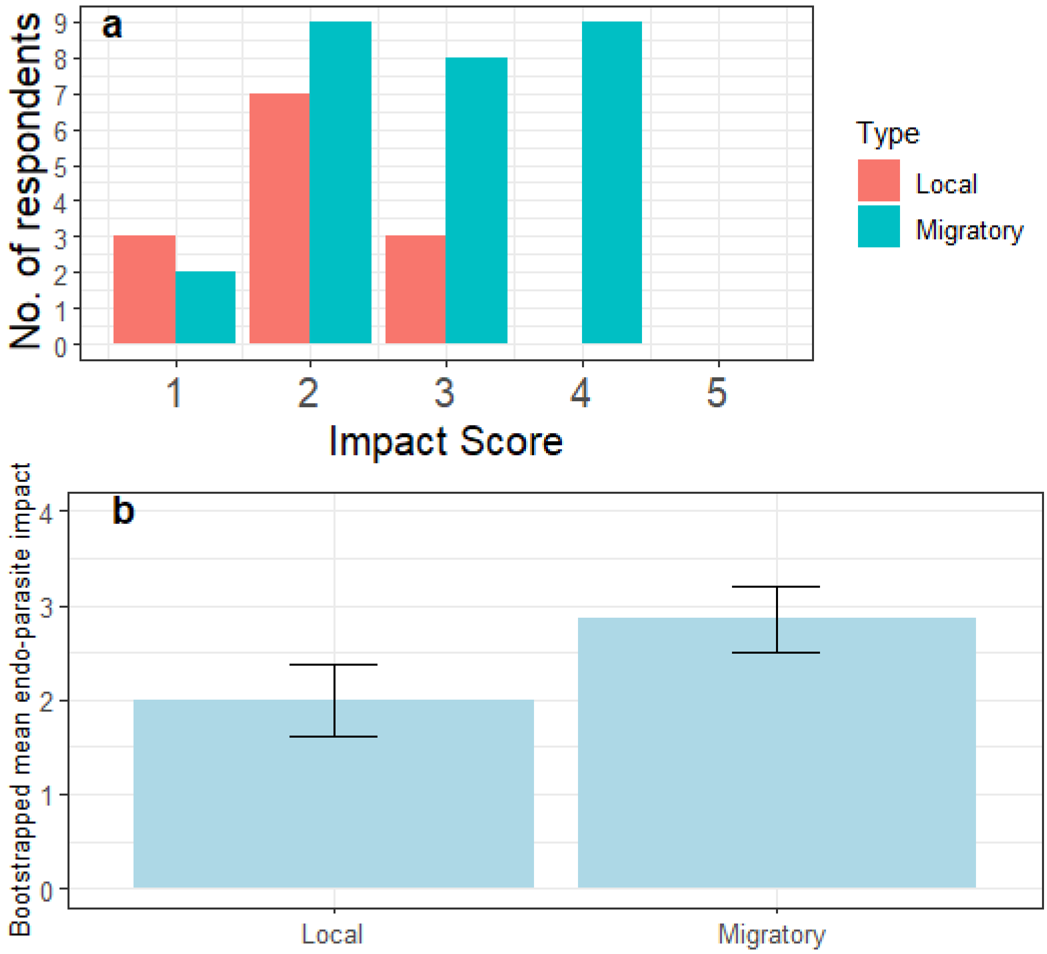

Figure 4.5. Panel graph displaying a) impact scores of endoparasites on livestock health and b) bootstrapped mean and 95% CI endoparasite impact scores for outlying and village based livestock. 5 animal dies – 4 alive but useless (in terms of owner-defined measures of productivity) – 3 severely impacted – 2 impacted but not so severely – 1 little impact – 0 barely noticeable.

Additionally, we found that different treatments against endoparasites were employed depending on the type of livestock (Fig. 4.6). For instance, migratory livestock were mostly reported to be consumed if the effects of endoparasites became a problem. More rarely, herders used plant preparations from local herbs to treat endoparasite infections and in some instances changed the location of livestock grazing to deal with endo-parasitic infestation. No measures were taken by owners of resident (= local = sedentary) livestock to deal with endo-parasitism, including by the local veterinary services.

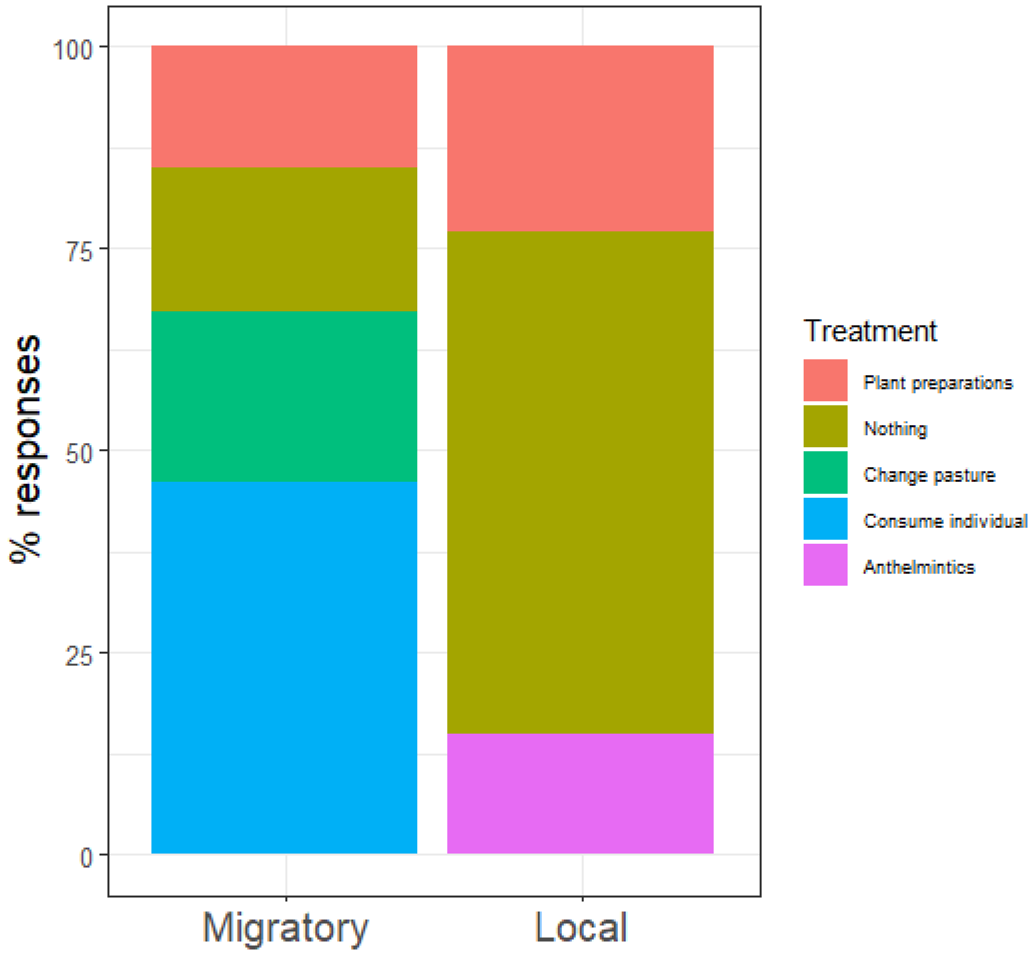

Figure 4.6. Stacked bar graph displaying the bootstrapped mean % responses of different treatment types between migratory (n=28) and local (n=13) livestock.

4.3.3 How do current holdings and flock composition compare to those of 20 years ago?

The respondents were asked for the herd sizes in 2019 and in the early 2000s but also asked to comment verbally on change. Sheep and goat are herded together. In 2019, the average size of the 28 migratory herds was 809 sheep and goat (SE ± 39.2). While respondents mentioned that herd sizes have fluctuated across the years, the survey data suggest an increase in overall herd sizes since the start of the century of 44% (from 560 sheep and goats, SE ± 27.7, in the early 2000s). In 2019 the average number of goats in a herd was 504 (SE ± 24.5) and the average sheep herd size was 305 (SE ± 18), while in early 2000s the average herd size was 260 goats (SE ± 14.7) and 299 sheep (SE ± 12.7). Twenty-five of the 28 key-informants practiced migratory grazing in both the early 2000s and in 2019 and respondents suggested that, since early 2000s, the total number of *tols* had remained relatively stable, albeit with annual fluctuations. Collectively, this suggests not only a definite increase in average herd size, but a likely increase in total head of migratory livestock.

Across the 13 villages in Pin valley, there were a total of 930 sheep and goats in 13 herds (433 sheep and 497 goats) in 2003 (Spiti livestock census, 2003). These numbers have seen a drastic decline to a total of 55 (48 sheep and 7 goats) across 3 herds in the valley in 2019. Key informants were unanimous in confirming this decline, which they attributed to an increase in green-pea cultivation in the past 2 decades, similarly to patterns in certain other areas in Spiti (Singh et al., 2015). Accounting for the increase in migratory stock and decrease in resident small stock, there seems to be a net increase in small stock grazing in Pin valley in 2019 compared to early 2000s. Given the fact that local livestock rarely share pasture with ibex, have low endoparasite burdens and are few in number, we focused our remaining questions on the migratory livestock.

4.3.4 What are the current reasons for undertaking the long-distance migration, is it likely to persist, and what governs leasing of pasture to migratory herders?

Given the consistency of responses, these are presented together rather than individually. Resident villagers hold the rights to lands across the Pin valley. These lands are used to graze local livestock, sow crops and collect natural resources. Pastures have been leased to the migratory herders for decades, for various reasons (Table 4.3). The reasons for undertaking the migration from the migratory herder's perspective include the acquisition of good quantity and quality of forage, tied closely to the lack of pasture land in Rupi (Table 4.3). Illustrating this point, a migratory herder said:

"…. *the high altitude and the harsh climate of Pin results in a short but bountiful growing season for the vegetation. The plants make best use of the short growth season, and hence are full of nutrients. Unlike Rupi or Sirmaur, Pin is a vast region, with very few people. This gives our livestock large areas to roam and graze*." (Key informant, Herder *Tol* 2).

Other reasons cited were weather-related increases in disease incidence and difficulty in finding livestock due to the mist during the rainy summers in Rupi, as well as tradition.

Table 4.3. Frequency (F) of reasons for villagers to lease pasture in Pin to migratory livestock herders (based on 13 interviews with Pin villagers) and frequency (F) of reasons that result in the *Kinnaura* herders undertaking migration, based on 28 interviews.

Reasons for leasing pasture	**F (n=13)**	**Reasons for undertaking the migration**	**F (n=28)**
Spiritual – a local deity in the Rupi-Bhaba area is worshipped by both the people of Pin and the migratory *Kinnaura* herders. It is said that the deity demarcated Pin valley as an important seasonal area for the migratory herders. The local community in Pin valley continues to comply with this.	12	Nutrition - Migration is essential for finding both quality and quantity of forage.	27
Monetary – Migratory herders pay a fee to access the grazing pastures in Pin. Income from this is used for communal activities such as repairing community halls and contributions to religious activities.	11	Space - Rupi-Bhaba pastures aren't large enough to feed the livestock during summers, when they need nutritious forage before being sold in the autumn.	24
Fertilizer – the faeces from the large migratory sheep/goat herds is considered to be an effective manure, particularly for agricultural pea and barley fields. Dung is collected in autumn (after the herds leave Pin) for use in the following spring.	9	Disease - The rains hit Rupi-Bhaba during the time the livestock are in Pin. The wet weather increases prevalence of diseases like endoparasites, ectoparasites and FMDV.	21
Meat – Based on long-standing relationships, migratory herders are known to share meat from their sheep/goats with certain members of the Pin valley community. The latter in turn share the meat with other villagers.	5	Weather - Due to the rains in Rupi-Bhaba, the mountains get extremely misty. This increases the chance of losing livestock	19
		Tradition - It is tradition and thus needs to continue	9

4.3.5 What is the current pasture quality in Pin valley and how has it changed over time?

Interviews with migratory herders revealed three indicators of pasture quality (Table 4.4). The presence of certain herbs and grasses was the main indicator, whilst absence/limited coverage of unpalatable species was also a factor. An elderly herder emphasized this by saying:

"*…. the main reason why we undertake the long and treacherous migration from Rupi to Pin is for the forage it provides our livestock. It is during the summer time (June-September), that the forage in Pin is at its best in terms of nutrition. Back in Rupi, it is so wet and hence the forage is far too lush and unpalatable for our sheep and goats."* (Key informant, Herder *Tol* 4)

Table 4.4. Frequency (F) of indicators of pasture quality based on interviews with 28 migratory herders.

Indicators of pasture quality	**F (n=28)**
Presence of certain herb species (particularly *Cicer* spp., *Aconogonum* spp., *Artemisia* spp.)	26
Presence of certain grass species (particularly *Leymus* spp., *Stipa* spp. and *Elymus* spp.)	24
Absence/limited coverage by unpalatable species (particularly *Caragana* spp. and *Eremurus* spp.)	13
Absence/limited denudation and rock-cover	11

Of the 28 herders, 26 suggested that pasture quality had changed for the worse. The remaining two herders said the pasture quality remained largely similar. Climate-related irregularities were the predominately-cited reasons behind this degradation, although interestingly they were less unanimous about these reasons than they were about the main reasons for migration and indicators of pasture quality (Table 4.5). A village elder from Pin valley summed up the problem:

"The winter never came to Pin Valley in 2018-2019! No wonder there wasn't much for the migratory herds to eat. Many of the villagers also suffered losses for their pea cultivation, as lack of snow in the winter meant very little glacial melt water for their crops in the summer." (Key informant, Villager 2).

Additionally, while the migratory herders visited Pin valley each year, they would try not to graze the same pasture annually, giving it time to regenerate. However, in recent years, the villagers of Pin have increased restrictions to certain pastures, citing their importance for fodder collection for their large-bodied livestock (Yaks, *Dzos*, cows, donkey and horses). Key-informants in Pin suggested this is primarily as large bodied livestock numbers have slightly increased in number, from 1326 in 2003 (Spiti livestock census, 2003) to 1866 in 2019. This is due to their importance for meat (particularly in winter), milk and as a commercial commodity – for instance, horses are often sold to the military as pack animals. This leads to pasture degradation in two ways: i) the migratory herders having to graze similar pasture year after year, and ii) large amounts of fodder being extracted from the pastures for large-bodied livestock. Four major implications of the changes in pasture quality were noted by the migratory herders, with disease, including GINs, being the most-cited implication of the worsening pasture quality (Table 4.6).

Table 4.5. Frequency (F) of reasons for changes in pasture quality, based on interviews with 28 migratory herders.

Reasons for changes in pasture quality	**F (n=28)**
Irregular winter snows result in lack of summer forage	19
Increased temperature and rainfall during the grazing season results in less nutritious forage	18
Restricted access to some traditionally grazed pastures by the local authorities is resulting in repeated grazing on the same pasture by higher number of migratory livestock.	18
Increased soil erosion due to glacial melt	13
Increased intensity of livestock grazing compared to before – driven by increase in migratory livestock numbers, with a relatively stable local livestock numbers	9
Increased fodder collection by locals to sell	7

Table 4.6. Frequency (F) of implications of changes in pasture quality, based on interviews with 28 migratory herders.

Implications of changes in pasture quality	**F (n=28)**
Occurrence of frequent disease events (Foot-and-mouth disease, respiratory diseases and endoparasites outbreaks)	21
Decreasing body-size of livestock	20
Lowered pasture regeneration – herders reported that previously they could use the same pasture year on year, however now pastures need to be changed every three-six years.	18
Reduced milk production in livestock	10

4.4 Discussion

4.4.1 Lessons for our work

We worked with two pastoral communities in Western Indian Himalayas– the migratory *Kinnaura* herders and local livestock herders of Pin valley - to investigate contemporary herding practices and their changes since the beginning of the 21st century. Our aim was to understand potential impacts on host health and disease transmission to Asiatic ibex in Pin valley, with a focus on GINs as a prevalent and important cause of reduced livestock productivity.

We found that the migratory *Kinnaura* flocks share pasture with ibex during their time in Pin, are increasing in both mean herd size and overall numbers, and have higher GIN burdens - hence are likely to make a larger contribution to the shedding of these parasites into the environment - than other hosts. These factors point to their potentially significant role in GIN cross-transmission, as GINs have a free-living, environmental stage that is trophically-acquired due to co-grazing pastures (Anderson, 2000). Although it is not known if worm burdens for each hosts are at physiologically detrimental levels. However, even subclinical GIN infection can reduce growth rates in ungulates (Forbes et al., 2000).

Theoretically, migration can reduce infection pressure through escape from contaminated habitats, however, recent work has shown that migratory hosts have higher parasite species richness and little support for migratory escape of infection pressure (Teitelbaum et al., 2018). Interestingly, the migratory livestock had one endoparasite (*Trichuris*) that was not found in sedentary livestock or ibex (table 4.2). Whether this is acquired through migration needs further investigation. Our sampling strategy for endoparasites did not enable us to identify various other potential helminths, including those found in the Indian Himalayas in previous studies (eg. *Fasciola*) (Muthiah et al., 2013). The seasonal migration of the *Kinnauras* could result in their livestock carrying novel infection of endoparasites, than those present in Pin valley – from the lower regions, into Pin. As local small-bodied livestock rarely share pasture with ibex, have low endoparasite burdens and are few in number, they are likely to have minimal interactions with, or impacts on, either ibex or the Pin valley's rangelands.

The high and increasing number of migratory livestock sharing limited pasture areas with low numbers of ibex (*c.*200-250 ibex; NCF, unpublished data), suggests that an increasing level of cross-transmission of GINs from migratory livestock to ibex may be taking place. This is likely to be exacerbated by an increased number and proportion of goats in the migratory flocks, as goats are more closely related to ibex than sheep, hence use similar environments (i.e. rugged areas) - whilst sheep prefer more undulating areas. This possibility could be further explored and validated by modelling the transmission loop incorporating the life histories of the endoparasites concerned, relevant climatic factors and the spatial dynamics of the migratory herds (Rose et al., 2015). The extent of cross-transmission, however, cannot be properly evaluated without further taxonomic investigation of the parasite species present, since eggs are morphologically similar between GIN taxa in particular. Additionally, more research is needed to understand the impact of treatment and mitigation actions by herders on endoparasite burdens, and how these might be improved in future.

The *Kinnaura* herders' home district, Kinnaur, experienced growth in the cash-based and market-oriented cultivation of apples in the 1980s (Sharma, 2005; Basannagari & Kala, 2013). Around the same time, across Spiti valley (in which Pin is located), the same trend was observed with green pea cultivation (Mishra, 2001). A key consequence of this for the *Kinnauras* was that large singular family units broke down into several smaller nuclear families, predominantly cultivating apples. This shift seems to have played a major role in the decline of traditional polyandry and increase in monogamy in the area (Gautam & Kshatriya, 2011). However even predominantly apple-cultivating households own a few livestock as an additional economic safety-net. Therefore, more people now own at least some livestock – albeit usually in smaller numbers - than before. Today, these smaller livestock holdings are clubbed together into large livestock groups – *tols*. These are herded by people owning limited land and large livestock holdings (hence with no or limited dependence on apple cultivation), who practice migratory pastoralism. This is the reason why migratory livestock herd sizes have increased while individual livestock herd sizes is decreasing (Ghoshal, 2017). A similar trend of increasing contracting among herders can be observed in the Gaddi community of migratory herders from other districts of Himachal Pradesh (Axelby, 2007), as well as in Tibetan herder communities (Yeh et al., 2017).

While we restrict our work to sheep and goats, some larger-bodied livestock like donkeys, horses and yaks from Pin villages also co-graze pastures with ibex (Bagchi et al., 2004; Ghoshal, 2017) and appear to have contributed to recent restrictions in grazing by migratory livestock. How and if these local large-bodied livestock interact with ibex with respect to disease transmission needs research. For instance, we know large-bodied livestock can contribute to competition with ibex in Pin valley (Bagchi et al., 2004). Increasing numbers of large stock are likely to eat more forage from the shared pasture and require increased fodder collection for their winter stall feed, particularly if climatic factors are lowering pasture productivity (Murthy & Bagchi, 2018). Such practices have caused pasture degradation in Spiti (Mishra et al., 2001; Bagchi et al., 2014). Degradation could add to the problem of disease through nutritional stress and resource competition, in turn exacerbating GIN impacts (Kock, 2004).

The slight increase in large-bodied livestock numbers, and hence the requirement for increased fodder in Pin, has several reasons. The increase in the dependence on green peas as a cash crop, which requires demanding work in the field, has resulted in many households ceasing to keep livestock that need daily care - sheep and goats. Large-stock like yaks and horses are free-ranging for large parts of the year (Singh et al., 2015). Economic gains from green peas have also enabled locals to purchase more large-stock from neighboring regions as additional economic safety-nets. The market value of livestock may also be important. For instance, the local *Chumurti* breed of horse is bred for sale in Ladakh, while some yaks are sold to tourism operators from lower Himachal (eg. Manali). Yaks and *Dzos* remain important for meat (particularly in the winter) and milk, while donkeys are important beasts of burden used for transporting drinking water and dung collected from pastures (Bagchi et al., 2004). More research into the role of large-stock in driving changes in pasture use and condition, and the knock-on impacts on small-stock and ibex, is required.

Lastly, we find evidence that the long distance migrations are likely to persist, even though there are worrying signs of pasture degradation contributed to by increased migratory livestock numbers and cutting of fodder for large-bodied local livestock. We also find that pasture degradation can result in a perceived increase endoparasite outbreaks. There is a link between livestock density and GIN transmission, wherein more livestock using the same areas can contribute to both increased degradation related to resource competition and GIN transmission (Grenfell, 1992). The respondents perceived this to be a major issue. However, perception of respondents, albeit extremely valuable for understanding the dynamics of traditional systems where data are limited (Tomselli et al., 2018), can still have biases. Most perceptions expressed in our interviews are not triangulated with primary data. In our parasitological investigation, levels of endoparasites in general and GIN in particular were higher in the migratory herds, suggesting that sedentary management did not constrain livestock to highly infected pastures. Nonetheless there is evidence of extensive livestock grazing and climate change contributing to degradation in our study area (Mishra, 2001; Mishra et al., 2004; Bagchi et al., 2004; Murthy & Bagchi, 2018). Moreover, parasites were held by migratory herders to impact their animals more severely than for sedentary livestock, while they were more likely to intervene through grazing management, plant-based medicines, and culling and consumption of weakened individuals. It is possible that the arduous migration and need to survive the outward and return journeys both increases the consequences of moderate parasite burdens, and motivates herders to reduce their impacts. If successful co-existence is to be maintained into the future, ensuring viable ibex populations persist along with livestock that support people's livelihoods, it will be critical for managers to proactively tackle interconnected issues such as resource competition, disease transmission and pasture degradation, rather than just looking at them as singular issues – the latter may have unintended consequences. For instance, community-based livestock grazing free reserves are often used in the Indian Trans-Himalayas to limit resource competition from livestock to wild ungulates (Mishra et al., 2016). However, in Pin valley this could result in increased stocking densities of migratory livestock in certain areas, accelerating its degradation while also potentially compromising their health through increased GIN transmission.

4.4.2 Steps into the future

Given this understanding, it is critical that proactive measures are taken to align people's livelihoods with wildlife conservation. It will be crucial for conservationists to work with both the migratory *Kinnaura* herders and the resident livestock owners to better understand and limit pasture use in Pin valley, so that the pasture is not further degraded in the face of accelerating climate change. Participatory approaches to explore climate change scenarios and how they would impact pasture quality of Pin and its hosts' health (migratory livestock, local livestock and the ibex) can help guide potential ways forward for co-existence. Given that herders felt that disease was a potentially important implication of reduced pasture quality, innovative approaches such as herder-run livestock insurance schemes to offset losses through diseases (GIN or otherwise) might be of interest to them. Building herder capacity to identify early signs of parasitism in livestock, combined with selective treatment using anthelmintics, could help to develop resilient and healthy livestock herds that are less likely to transmit disease to ibex. Anthelmintics if used non-selectively are known to cause GIN resistance in both livestock and wildlife (Barone et al., 2020).

Collectively, these interventions would not only help address the ecological and economic interests of the migratory livestock herders, but can also contribute to the conservation of the high Himalayan rangelands and the wildlife that call it home.

- Chapter 5 -

Predicting parasite dynamics in mixed-use trans-Himalayan pastures to underpin management of cross-transmission between livestock and bharal

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Authors’ contribution

I, EJMG, KS and EM conceived the idea of the project. I, AK and RS conducted the field work. I led the analysis with support from ED and HRV. I and EM wrote the first draft of the manuscript and all authors commented on and refined subsequent drafts.

A herd of male blue sheep foraging in the Kibber pastures

Abstract

The complexities of multi-use landscapes require sophisticated approaches to addressing disease transmission risks. We explored gastro-intestinal nematode (GINs) infections in the North India Trans-Himalayas through a socio-ecological lens, integrating parasite transmission modelling with field surveys and local knowledge, and evaluated the likely effectiveness of potential interventions. Bharal (blue sheep; *Pseudois nayaur*), a native wild herbivore, and livestock share pasture year-round and livestock commonly show signs of GINs infection. While both wild and domestic ungulates had GINs infections, egg counts indicated significantly higher parasite burdens in bharal than livestock. However, due to higher livestock densities, they contributed more to the total count of eggs and infective larvae on pasture. Herders also reported health issues in their sheep and goats consistent with parasite infections. Model simulations suggested that pasture infectivity in this system is governed by historical pasture use and gradually accumulated larval development during the summer, with no distinct short-term flashpoints for transmission. The most effective intervention was consequently predicted to be early-season parasite suppression in livestock using temperature in spring as a cue. A one-month pause in egg output from livestock could lead to a reduction in total annual availability of infective larvae on pasture of 76%, potentially benefitting the health of both livestock and bharal. Modelling suggested that climate change over the past 33 years has led to no overall change in GINs transmission potential, but an increase in the relative influence of temperature over precipitation in driving pasture infectivity. Our study provides a transferable multi-pronged approach to investigating disease transmission, in order to support herders' livelihoods and conserve wild ungulates.

5.1 Introduction

Globally, land conversion and intensification of land use means that wildlife habitats and livestock pastures increasingly overlap, creating more intensive, multi-use landscapes (Daszak et al., 2001). A factor driving this intensification of contact is the increasing demand for livestock products. Although much of this global demand is met by intensive livestock farming, there are c.752 million low-income livestock herders (earning <$2/day) who carry out extensive herding on rangelands where wildlife is also present (Thornton, 2010; Otte et al., 2012). This leads to the potential for disease cross-transmission, which can impact the incomes of resource-poor herders (Reid et al., 2008) and wildlife conservation (Walker et al., 2018).

Amongst a diverse set of disease-causing agents, endoparasites (particularly gastro-intestinal nematodes, GINs) are important determinants of fitness in wild ungulates (Gulland, 1992; Albon et al., 2002). They also impact milk production, growth rates, fertility, and susceptibility to other diseases in livestock (Thumbi et al., 2013), and are economically costly to farmers in both monetised and informal economies (Perry & Randolph, 1999). Transmission is through indirect contact by sharing pasture and water points (Morgan et al., 2004), leading to ingestion of free-living infective stages in the environment (Zajac, 2006; Fig. 5.1). Often GINs get overlooked in assessments of disease risks, as their impact can be subtle and clinical signs hard to detect, even though they can cause large aggregate impacts on health and productivity. Importantly, since part of GINs life history is driven by environmental conditions, climate change could alter their transmission in ways that are difficult to predict but which may have substantial impacts on both wildlife and livestock health (Brooks & Hoberg, 2007).

Understanding impacts and transmission of GINs is especially difficult, yet pertinent, in remote and harsh multi-use landscapes, home to both wildlife and livestock-dependent herders. These landscapes often offer little access to veterinary facilities and advice (Chatterjee et al., 2016), meaning knowledge of GIN impacts and implementation of control measures may be very limited. Most studies of these systems are limited to short time-scales, providing only a snapshot of current conditions, which may vary between years. This means that measuring important variables for understanding GINs transmission, such as infective larval density, is challenging (Morgan et al., 2005b). Given the difficulties and hazards of disease control interventions directed at wild species, GINs management is often focussed on livestock. Yet, crucially, trialling control options in practice is difficult, expensive (Learmount et al., 2018) and can be damaging to the animals concerned (e.g. where treatment is withheld). Therefore, models can be useful to explore potential interventions in a virtual environment before attempting them in practice (Walker et al., 2018). While most GINs models are species-specific (Rose et al., 2015), the main GINs species in wildlife and livestock broadly share climatic envelopes and parameter values. Therefore, general livestock GINs models can be used to understand GINs transmission in multi-use landscapes (Rose et al., 2015). Additionally, people who share habitats with wildlife have first-hand experience of wildlife-livestock interactions (Huntington, 2000). They too can provide rich information concerning the health of both livestock and wild ungulates (Tomaselli et al., 2018).

The Indian Trans-Himalaya region is symbolic of remote multi-use landscapes. Most of the area is inhabited by agro-pastoral societies. This region also harbours a unique assemblage of mountain ungulates, which maintain vegetation structure and serve as the main prey for rare predators such as the Snow Leopard, *Panthera uncia*, and Tibetan wolf, *Canis lupus* (Bagchie & Ritchie, 2010; Suryawanshi et al., 2017). Whilst there is significant literature examining the competition for resources between domestic and wild ungulates in these areas (e.g. Bagchi et al., 2004), disease dynamics has been subject to less research. Disease cross-transmission between wild and domestic ungulates is particularly likely in these settings because parasite host range often mirrors host phylogeny (Walker et al., 2017). These regions are particularly sensitive to changes in climate (Li et al., 2016), which can have numerical, functional and micro-evolutionary impacts on parasite-host assemblages (Brooks & Hoberg, 2007).

Despite the importance of GINs for livestock productivity and wildlife conservation, understanding of transmission risk, assessment of the potential effects of climate and climate change, and recommendations for appropriate interventions at the livestock-wildlife interface across multi-use landscapes are all still limited (Rhyan & Spraker, 2010). More case studies are needed to understand these issues, particularly from temperate multi-use landscapes, as they remain understudied with respect to disease dynamics (Mishra et al., 2021). High mountain areas can also serve as model systems to understand dynamics across other temperate areas with comparable land use and climatic patterns (Olson et al., 2001); and to understand shifts in species distribution under climate change in vertical as well as horizontal planes (e.g. Chhetri et al., 2021).

Due to the socio-ecological complexities of multi-use landscapes, a multi-pronged interdisciplinary approach is needed. With this in mind, we explored disease transmission risk between wildlife and livestock in the Kibber area of the Indian Trans-Himalaya through a socio-ecological lens and, based upon that, evaluated the likely outcomes of potential interventions. Specifically, we aimed to investigate the general dynamics of the multi-use system with respect to GINs parasite transmission and, by investigating climate cues to trigger interventions, explored what actions taken in livestock herds might limit cross-transmission to wild ungulates. We did so by collating existing datasets and collecting additional data to parameterise a GINs transmission model and then building on and contextualising the model using Traditional Ecological Knowledge (TEK) (Huntington, 2000). We modelled bharal (blue sheep; *Pseudois nayaur*) because it is the only wild ungulate in the study area, and sheep and goats because they are most likely to share GINs with bharal (Fig. 5.1). Our integrated approach could form a basis for discussions with local stakeholders on introducing locally-applicable and socially-relevant interventions to better align people's socio-economic priorities with wildlife conservation.

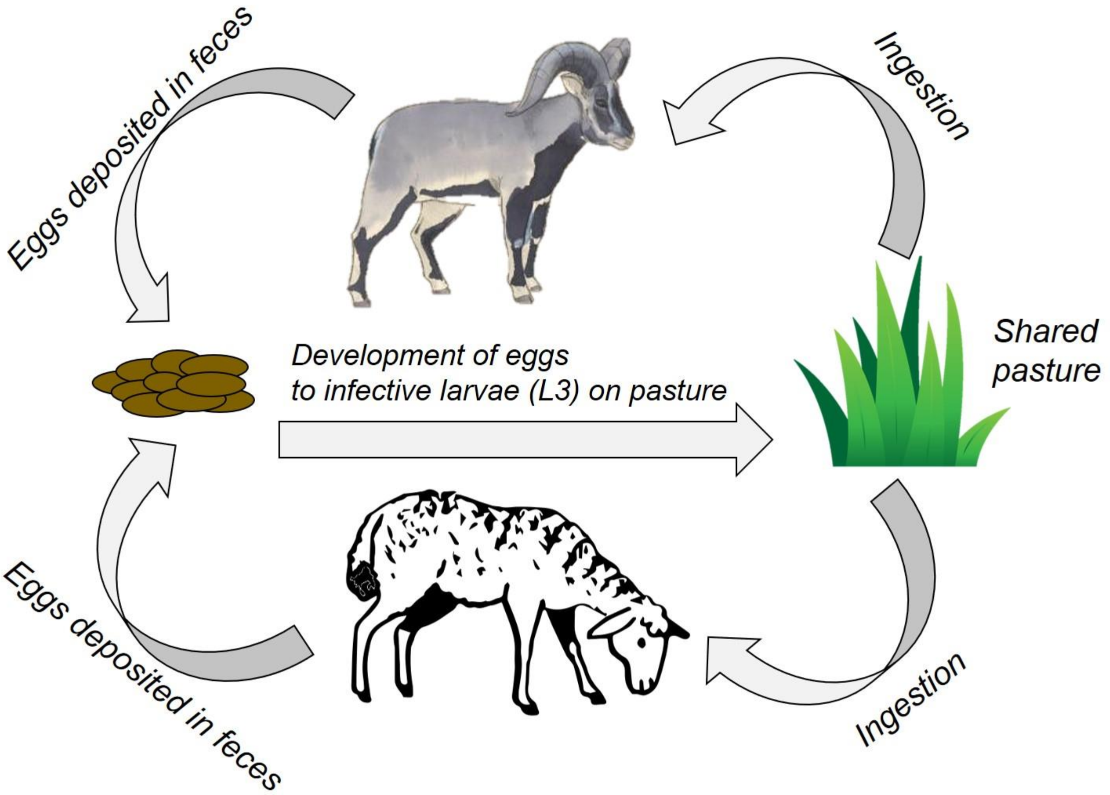

Figure 5.1. A schematic for GIN transmission in our case study site. Above: Bharal, Below: Livestock (sheep/goat). Sheep icon courtesy Francesco Cesqo Stefanini (noun project) and bharal courtesy Sartaj Ghuman.

5.2 Materials and Methods

5.2.1 Study Area

The 186,000 km^2 of the Indian Trans-Himalaya, includes parts of the Tibetan Plateau and its marginal mountains (Mishra et al., 2001). Our study area included Kibber village and its surrounding livestock pasture, which is within Lahaul-Spiti district, Himachal Pradesh. The region is characterized by low precipitation (<500 mm annually, with most precipitation in the form of winter snow), a short growing season, low primary productivity, and high livestock densities (Mishra et al., 2001). This high-altitude (3500m-6700m) region experiences extreme climatic conditions, with winter temperatures ranging from -35°C to 3°C, and summer temperatures ranging from 1°C to 28°C. Our field study period was the entire year of 2018 (1st January-31st December).

The vegetation is classified as “Alpine scrub” or “dry Alpine steppe” (Champion & Seth, 1968). The large mammalian fauna includes bharal and their predators the snow leopard and the wolf. This region is also home to one herd of Asiatic Ibex *Capra sibirica* but they are spatially separate from the pasture shared by bharal and livestock, by a deep gorge. Agro-pastoralist communities, have inhabited this region for 2–3 millennia. The livestock assemblage includes sheep, goats, cattle, cattle-yak hybrids, yaks, donkeys and horses. Cattle, donkeys, cow-yak hybrids, goats, and sheep are herded to pasture (herded stock), while yaks and horses are free ranging. Herded stock are shepherded to the pastures every morning and brought back to stocking pens inside the village in the evening. Families take turn shepherding the entire village’s herded stock alongside a designated village shepherd. Most families own small land holdings (c.1.5 ha) for cultivation, mainly of barley, *Hordeum vulgare,* for subsistence, and green pea, *Pisum sativum*, as a cash crop.

5.2.2 Data Collection

Data collection aimed to assess the relationship between wild and domestic ungulates based on spatial overlap and potential GINs parasite cross-transmission. Further data on levels of nematode eggs in faeces over time were collected and used to calibrate a parasite transmission model (based on Rose et al., 2015), which enabled evaluation of cross-transmission risk under different scenarios, including alternative management strategies. Figure 5.2 and Table 5.1 articulate how different forms of evidence were combined to investigate the dynamics of this GINs system in order to inform management.

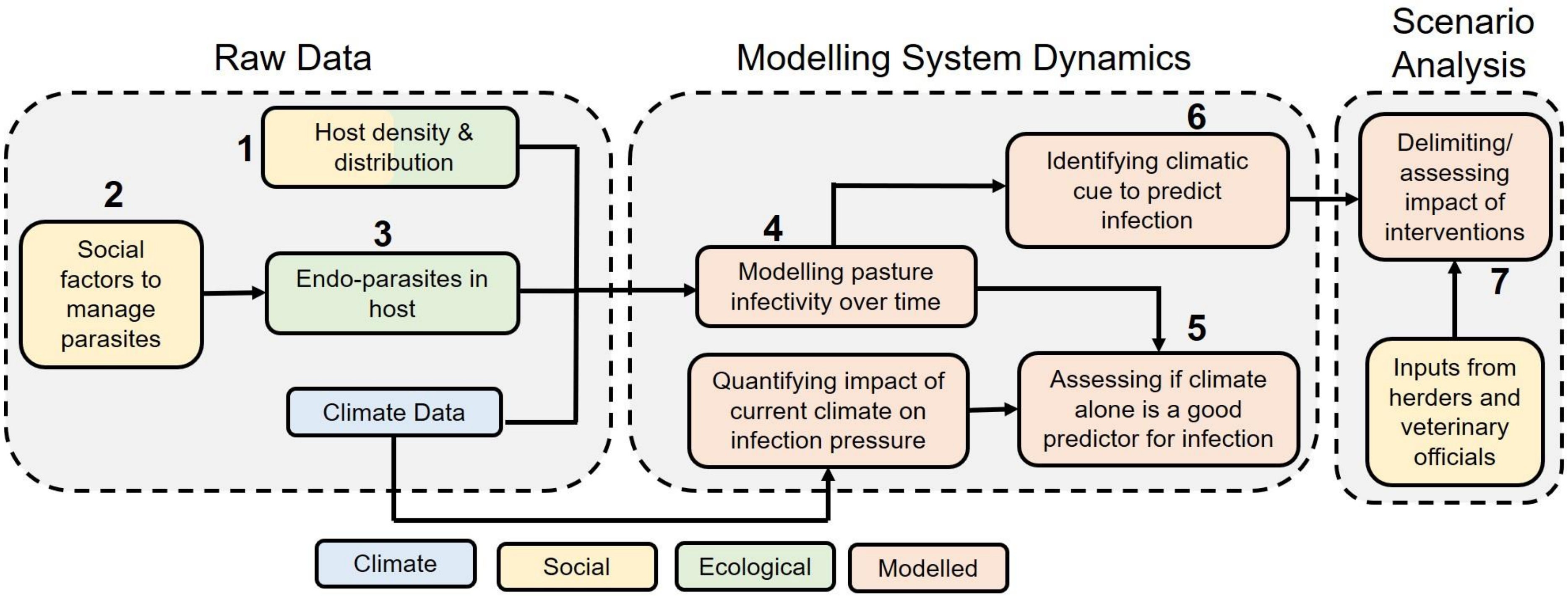

Figure 5.2. A schematic showcasing how the different forms of evidence combine to give an overall picture of the two-host (bharal, and sheep + goats combined) GIN system to inform control measures. The numbers are linked to numbers in Table 5.1 below.

Table 5.1. Research questions with reasoning and methods used to answer those questions, in order to understand two-host GIN system dynamics and inform measures using Kibber as a case study. Hosts refers to bharal and small ruminants (sheep + goats combined). GIN = gastro-intestinal nematode; FEC = faecal egg count; AUCL3_h = area under the curve of predicted infective larval (L3_h) density, a measure of overall nematode infection pressure. For explanation of GLOWORM-FL and Q_0 models, and AUC arising from the models, see text.

No.*	***Research Question***	**Method**	**Reasons**
1	*Do hosts share pasture?*	Focus group discussions and double-observer surveys	Contact patterns form the basis of GIN disease transmission (Morgan et al., 2004), and are used as inputs to the GIN transmission model.
2	*What management techniques exist for small ruminant health?*	Semi-structured interviews	Social interventions can influence GIN presence in livestock and consequently transmission to wild ungulates (Weinstein & Lafferty, 2015).
3	*What is the abundance and diversity of endoparasites in hosts?*	Faecal egg counts (FEC)	Presence of endoparasites can result in cross-transmission given appropriate contact patterns (Morgan et al., 2004). Nematode FEC are used as inputs to the GIN transmission model.
4	*What is the magnitude and seasonality of pasture infectivity?*	GLOWORM-FL model	The GLOWORM-FL tracks the number and density of infective larvae over time incorporating climate data driving the life history of nematode parasites (Rose et al., 2015)

5	*Is climate alone a good predictor of infection pressure?*	Relationship between GLOWORM-FL and Q_0 outputs	Climate alone can be considered a good predictor of infection pressure when a large proportion of variation in GLOWORM-FL output is explained by its simplified, purely climate-driven Q_0 formulation. Time and relative intensity of infections can be then determined by climatic variables alone to consequently inform interventions. This would bypass the effort needed to analyse faecal samples as inputs to GLOWORM-FL model, and to take detailed account of grazing patterns.
6	*Can we delimit climatic cues to predict infection pressure?*	$\frac{L_3 AUC\ real\ precipitation}{L_3 AUC\ high\ precipitation}$	Based on area under the curve (AUC) of infective larval (L3) abundance, as predicted by the GLOWORM-FL model, and further extracting the importance of rainfall to infection pressure (see text). Under low rainfall dependence, parasite management can be more simply guided by temperature profile.
7	*Can we delimit interventions and assess their impact?*	% reduction in intensity of infective larvae on pasture	Based on the modelling outputs (4,5,6) and consulting with local stakeholders we defined potential interventions and predicted their impacts in reducing pasture infectivity.

*corresponds to the numbers on Fig. 5.2.

Livestock density and distribution

We focused on small ruminants (sheep and goats combined), which are taxonomically closest to bharal and hence most likely to share parasite species (Walker et al., 2017). In the explanations below, therefore, livestock is taken to indicate sheep and goats combined. The abundance and distribution of livestock was estimated through focus group discussions (FGDs) and resource mapping with herders from Kibber (Nyumba et al., 2017). We conducted five FGDs, with 12, 8, 10, 6 and 7 people respectively. Each group included animal owners and shepherds. The FGDs involved discussion of the livestock distribution in pastures surrounding Kibber across the year. Each group built a resource map displaying locations of areas grazed by livestock from Kibber. Discrepancies amongst the five maps produced were settled in discussion with the village headman. The boundaries were then delimited on Google Earth Pro. Livestock abundance in Kibber was obtained from the village headman through a key informant interview. This number was triangulated with interviews of Kibber herders (see below). Total abundance of livestock was divided by the area of utilised pasture to obtain an estimate of average density.

Bharal density and distribution

We assessed bharal abundance in May 2018, using the double-observer method (Suryanwanshi et al., 2012). This method uses two observers separated in time and space to count wild ungulates, and then estimates abundance within a mark-recapture modelling framework which controls for detection probability. The study area was defined as the livestock pasture surrounding Kibber (Fig. 5.3). The area was divided into two blocks. Each block was surveyed for wild ungulates, with the aim of complying with the three main assumptions of the method: i) entire visual coverage of the survey area can be achieved; ii) the counts of the two observers are independent; and iii) the two observers collect adequate information to be able to identify individual herds based on the age-sex composition, herd location (using a Global Positioning System device) and any other peculiarities. This is so that individual herds can be identified and the proportion spotted by both observers calculated. The population-specific data collected were group size and group detection or non-detection by both the observers.

Bharal are not known to undertake long-distance vertical or horizontal seasonal migrations. Several studies on bharal in Kibber have found them using similar pasture locations at different times of year, suggesting limited (if any) defined seasonal elevation migration (Mishra et al., 2004; Suryawanshi et al., 2010; Suryawanshi et al., 2012; Kohli et al., 2014). To validate this, we conducted an ungulate mapping exercise within our FGDs, asking where and when bharal were found within the pastures surrounding Kibber.

Management of livestock health

Semi-structured interviews (Appendix D - Questionnaire) were conducted with 32 (57%) of the 56 livestock owners and herders in Kibber, to gain insights on livestock health and management practices. A local field assistant was present during interviews to help in translation. The interviews were conducted in Hindi, which is spoken well by most herders and the interviewers (MK and RS). The translator clarified doubts, if any, using the local Spitian dialect of Tibetan. The interview was designed to collect information about: i) general health of livestock, especially small ruminants, ii) prevalent endoparasites, and iii) livestock health management practices. Two key informant interviews were conducted with a government veterinarian with responsibility for the Spiti region and a veterinary assistant. To triangulate answers regarding endoparasite presence we conducted Five-Point Checks (Bath & Van Wyk, 2009) and faecal analysis (see below).The Five-Point Checks were conducted together by the livestock owners and authors (MK and RSR). Five-Point Checks provide an indication of the impact of endoparasites on host health, by scoring five signs of parasitism. The five elements consist of body condition (1 = fat to 5 = thin; reversed from original to maintain consistency of higher scores meaning poorer health), faecal breech soiling (1 = clean to 5 = dirty), anaemia (1 = red to 5 = pale), nasal discharge (0 = absent, 1 = present) and submandibular oedema or bottle jaw (0 = absent, 1 = present). Lower values are indicative of relatively healthy hosts with respect to parasitism (low impact of endoparasites), whilst higher numbers are indicative of relatively unhealthy ones with respect to parasitism (high impact of endoparasites). For simplicity, we reduced body condition, anaemia and faecal breech soiling scores to simple thresholds where the five points were converted to 0 (score < 3;

lacking signs of endo-parasitism) or 1 (score 3 or above; displaying signs of endo-parasitism). Total score for each individual was calculated as the sum of modified individual element scores, hence from minimum 0 (healthy) to maximum 5 (unhealthy); and then averaged across each livestock herd (n=32) within Kibber. For the interviews and Five-point check data, we also bootstrapped responses with replacement (10,000 iterations) and estimated means and 95% confidence intervals. Non-overlapping confidence intervals were interpreted as being statistically significant.

All surveys involving people and the Five Point Checks were approved by the University of Bristol's Ethical Committee. Each respondent was told that their identity would be kept anonymous and that they would not be identified by name or specific location in any publications or other communication. Consent was taken orally before conducting the surveys and checks and all the responses were coded, with names or other identities not recorded to ensure anonymity.

Endoparasite burdens in bharal and livestock

Fresh faecal pellet samples were collected from sheep, goats and bharal. Collection was opportunistic, with recently-voided faeces collected from the ground, and covered every month of the year. Faecal Egg Counts (FEC) were conducted on pooled faecal samples, to evaluate the density of helminth eggs and coccidial oocysts excreted onto the pasture to seed onward transmission, and as an indirect indicator of parasite burden. The mini-FLOTAC method (Cringoli et al., 2017) was used as a field-friendly, simple and cost-effective method for FEC in remote areas. This method estimates the abundance and diversity of endoparasites, using sedimentation-flotation to separate ova of nematodes and protists from the faecal matter and allow them to be identified morphologically and quantified under a microscope.

Livestock samples were pooled at the level of the overall Kibber livestock herd and bharal samples were pooled at the level of the study population (Morgan et al., 2005b). For bharal, samples were collected from all age-sex classes. The date and location of each sample collected was recorded (Appendix D, Table 1). For the sheep and goats, which are herded as one unit, we collected fresh faecal samples, taking various samples from different individuals and trying to get as many as possible at a time. Subsequently, we placed all the individual samples, each of similar volume, together into a plastic bag and mashed and mixed them thoroughly using digital pressure. From the mixed composite (pooled) sample, we took 5 g faeces and mixed that thoroughly with 45 ml saturated sodium chloride salt solution, and then examined the suspension under a microscope at medium power, following the mini-FLOTAC method (Cringoli et al., 2017). The same procedure was followed for bharal. Sample hereafter refers to a pooled sample.

The number of eggs found for each parasite was recorded for each sample and multiplied by a factor of 5 to obtain the total FEC in eggs per gram (EPG) of faeces. If multiple samples from the same host type were analysed on a given date (Appendix D, Table 1), an average EPG was taken. We were particularly interested in the FEC of strongyle nematodes as they are used as input into the GLOWORM-FL model. Nevertheless, as there are limited data available on endoparasites from the Indian trans-Himalayas, all other endoparasites that were identified were quantified as well.

5.2.3 Data Analysis

Bharal abundance

The total number of bharal groups was estimated using the two-survey mark-recapture procedure in the Bayesian ‘BBRecapture’ package of R (Fegatelli & Tardella, 2013; R Core Team, 2020). Following Suryawanshi et al. (2012), the analysis was conducted with groups as the unit. A group was coded ‘11’ if recorded by both teams, ‘10’ if only the first team recorded it, and ‘01’ if only the second team recorded it. We modelled the probability of detection for the two teams separately (using the ‘mt’ model in R package “BBRecapture”). Details on model fitting to estimate population size and confidence intervals are in Appendix D – Ungulate Analysis.

FEC data analysis

As parasite counts are typically over-dispersed, we used the non-parametric bootstrap t-test to compare the levels of faecal egg density between wild and domestic ungulates (Wilcox, 2017), running separate t-tests for each recognised type of parasite ovum. The strongyle nematode FEC, with the dates of collection and daily temperature and precipitation values, were further used as inputs into a model to predict levels of pasture infectivity over time, and therefore the potential for cross-transmission between domestic and wild ungulates (see below).

5.2.4 Transmission models

Climate data

Directly measured meteorological data were not available for Kibber, and so interpolated datasets were used to estimate parasite vital rates within the population dynamic models (below). Daily temperatures and precipitation were obtained from the POWER Data Access Viewer (DAV) which is provided by the National Aeronautics and Space Administration (NASA) (POWER, 2020). We used the POWER Single Point Data Access widget which provides access to near real-time 0.5 x 0.5 degree datasets by single point (lat/long). This was obtained for the years 1985-2018.

Transmission model - predicting pasture infectivity over time

The predictive model is based on the life cycle of the free-living stages of trichostrongylid GINs (Equations 5.1-5.7), as described in the GLOWORM-FL model (Rose et al., 2015). The GLOWORM-FL model estimates the development of parasites from eggs, after they have been deposited by host, to the third-stage infective larvae (L3), and their translation onto pasture. This results in an estimate of the magnitude (number) of L3 that are available for ingestion. The number of eggs per gram of faeces (FEC) is multiplied by host faecal output (f) and the density of the host species (D) to estimate egg output on pasture (E) (equation 5.1). Nematodes from overlapping cohorts are tracked, with new deposited eggs (E_{new}) getting added to existing eggs, upon accounting for a moisture-limited development success correction factor (C) (equation 5.2). The development of L3 in faeces ($L3_f$) from eggs (E), via the pre-infective larval stage (L), is subjected to temperature-dependent stage-specific mortality rates (μ_1) and development rate (δ) (equation 5.3-5.4).

A climate-dependent (temperature and moisture) horizontal migration rate (m_1) is used to estimate the migration of L3 from faeces onto pasture (L3_p). As L3_p can reside in either the herbage (L3_h) or the soil (L3_s), random bi-directional movement between soil and herbage is simulated with substrate specific mortality rates (μ_4, μ_5), and a temperature-dependent vertical migration rate (m_2) (equation 5.5-5. 7).

We ran the model in R version 3.6.3 (R Core team, 2020), using the *lsoda* function in the "deSolve" package (Soetaert et al., 2010), using an Adams-backward differentiation formulae (BDF) with an adaptive integration method. The output of the model is the daily number of individual GINs per hectare for each life-stage. The model predicts the density of L3 on pasture from which we calculate L3_h per kg dry herbage (L3/kgDM) by dividing L3_h (equation 7) by the biomass of dry herbage per hectare (parameterized from Bagchi et al., 2006). Annual infection pressure (i.e. number of *L3* which animal can be exposed during the year) was obtained by area under the curve (*AUCL3$_h$*), which was calculated by summing daily L3_h per kg dry herbage values. Peak infection (i.e. highest number of *L3* on herbage) day was obtained by calculating the mode of the model output (pilot analysis revealed distinct singular peaks). Lastly, to parameterize the model, FEC were used as input and host weights, averaged across sexes to account for sexual dimorphism (bharal and livestock) were obtained from literature (52 kg bharal – Mishra et al., 2019; 22.4 kg sheep/goat Spiti Livestock Husbandry Department, 2018). Faecal output was assumed to be the same for both species (Moharrery, 2011).

Model output was used to indicate pasture infectivity, and calculate changes to infectivity as a result of climate and management (see sub-sections below). The model was run for three host scenarios: only bharal; only livestock; and bharal and livestock combined. Therefore, the relative contribution of each host to overall pasture infectivity was estimated. We used *Teladorsagia circumcincta* parameters, because this species is more likely to be present over the warm-adapted *Haemonchus contortus* in cool temperate areas, and has similar responses to climate outside the host as other common genera like *Trichostrongylus* (O'Connor et al., 2006). Additionally, studies from the western Himalayan regions (similar to Kibber) have found *Trichostrongylus* species to be common in small ruminants (Dhar et al., 1982; Jithendran & Bhat, 1999). Additional details about the model can be found in Rose et al., (2015) and the parameters used here are displayed in Appendix D, Table 2.

$$E_{new} = D(f \times FEC) \qquad (5.1)$$

$$\frac{dE}{dt} = -(\mu_1 + 2\delta)E + E_{new}C \qquad (5.2)$$

$$\frac{dL}{dt} = -(\mu_2 + 2\delta)L + 2\delta E \qquad (5.3)$$

$$\frac{dL3_f}{dt} = -(\mu_3 + m_1)L3_f + 2\delta L \qquad (5.4)$$

$$\frac{dL3_p}{dt} = -\mu_4\left((1 - m_2)L3_p\right) - \mu_5\left(m_2 L3_p\right) + m_1 L3_f \qquad (5.5)$$

$$L3_s = L3_p(1 - m_2) \qquad (5.6)$$

$$L3_h = L3_p m_2 \qquad (5.7)$$

Identifying climatic drivers of predicted larval abundance

Precipitation and temperature are both drivers of larval availability, but their relative importance varies according to prevailing climate. Effective intervention strategies and appropriate weather cues consequently differ between temperature-driven and precipitation-driven systems. We evaluated the relative importance of precipitation and temperature in Kibber by comparing model outputs under actually-observed precipitation, with theoretical values generated when precipitation is set to a high, non-limiting value. First, we calculated the area under the curve ($AUCL3_h$) by summing the daily $L3_h$ per kilogram of herbage for each day over a given year. Then, we ran the model first using actual precipitation (for 2018) and then using constant high precipitation (c. 2.5 times higher than the highest daily precipitation value of 41.32mm = 100mm/day), which removes rainfall constraints on larval development and migration. The quotient $\frac{L_3 AUC\ real\ precipitation}{L_3 AUC\ high\ precipitation}$ indicates the extent to which rainfall limits transmission. Values can vary from approaching zero (transmission is strongly limited by rainfall, since larval availability under real, observed, rainfall is much lower than it could potentially be under increased rainfall) to one (increasing rainfall to saturating levels does not increase larval availability, therefore real rainfall is not limiting). This calculation is based on moisture acting on the free-living stages based on minimum thresholds that permit development in faeces and migration onto herbage, such that above these thresholds additional rainfall no longer increases transmission. A high quotient indicates that nematode transmission is effectively driven solely by temperature, with rainfall rarely, if ever, limiting. The calculation therefore suggests which climatic cue would be most useful to trigger parasite control measures, e.g. after precipitation or based on warmth.

Quantifying the contribution of current climate to infection pressure

The GLOWORM-FL model tracks the number and density of infective larvae over time, and can be condensed into a time-invariant formulation to estimate the potential for population growth under current epidemiological conditions, given additional assumptions regarding parasite lifespan and fecundity, and host density and feeding. The resulting basic reproduction quotient for parasites, Q_0, is analogous to R_0 for microparasites (Rose et al., 2016).

The Q_0 model incorporates environmental conditions (temperature and precipitation) and host factors (density and herbage intake) to estimate the second generation mature worms produced by a single adult worm throughout its lifetime, in the absence of density-dependent constraints such as immunity and within-host competition. The value of Q_0 is estimated by equation 5.8 (Rose et al., 2016):

$$Q_0 = \frac{q\gamma}{\mu} \frac{\beta \mathrm{p}}{\rho + \beta H} H m_2 \qquad (5.8)$$

Where, Q_0 is calculated from fecundity (γ), adult mortality (μ), ingestion of rate of $L3$ by the host (β), mortality rate of $L3$ on pasture (ρ), establishment rate of ingested $L3$ (p), density of hosts (H) and a vertical larval migration parameter (m_2). The parameter q, which describes the probability of an egg developing to L3 and reaching herbage, was expanded (equation 5.9) as described by Rose et al., (2016), thus incorporating climate dependence in the life history of free-living stages along with another, horizontal, migration parameter (m_1). This allows for non-linear interactions between development (δ), survival (μ_i) and horizontal migration rates.

$$q = \frac{\delta m_1}{(\mu_e + \delta)(\mu_{l3} + m_1)} \qquad (5.9)$$

As in the GLOWORM-FL model, Q_0 was estimated using parameters for *Te. circumcinta* (Table 5.2). The ‘geosphere’, ‘deSolve’ and ‘forecast’ packages in R were used to the run the model. Temperature and precipitation data were used as for the GLOWORM-FL model. An advantage of using Q_0 rather than GLOWORM-FL is that historic information on pasture occupancy is not required; rather, it estimates the extent to which current conditions favour transmission. FEC data are also not required as input, unlike for the GLOWORM-FL model, since Q_0 is scaled to the individual worm. This approach can successfully identify times and places of high transmission potential in the absence of detailed host information (e.g. Bolajoko et al., 2015) and predict future spatial and seasonal patterns of transmission under climate change (Rose et al., 2016). It is likely to be more reliable when current climatic conditions have a dominant influence on transmission success, and less reliable when historical factors such as past climate and pasture occupancy are more important.

To investigate the extent to which short term climatic variation explains infection pressure in Kibber, we ran a Pearson’s correlation test between the predicted values of Q_0 in a given year, and the predicted total level of herbage contamination with $L3_h$. To do so, daily Q_0 and its area under the curve (AUCQ_0), daily available $L3_h$ per kilogram of herbage calculated using the GLOWORM-FL model, and the area under that curve (AUC$L3_h$) were calculated for each year between 1985 and 2018. AUC$L3_h$ per kilogram of herbage (infection) and AUC Q_0 (reproductive rate) were then correlated for the period 1985-2018. We also calculated $\frac{L_3 AUC\ real\ precipitation}{L_3 AUC\ high\ precipitation}$ for each of these years to investigate if the quotient changed over time. To check for autocorrelation between the time series data points, we plotted residuals of each time series model. Time series model output, built using the "ggscatter" package in R, was reported only if the residuals were uncorrelated and had zero mean.

Investigating the impact of intervention scenarios on parasite transmission dynamics

We assessed the effectiveness of five management interventions that were shortlisted after discussions with interviewees and suggested by the veterinary official key informants (Table 5.3). Our assessment of effectiveness was based on the reduction in infection potential as defined by the amount of $L3_h$ per kilogram of herbage for the year 2018. Since carrying out health interventions for bharal would be logistically prohibitive, we concentrated on livestock-focussed interventions that might have an impact on parasite infections in both host populations. Interventions were housing and treating (with persistent anthelmintic). These are equivalent in our models in that they both simply interrupt egg supply to the pasture for a determined period. The intervention scenarios were divided into two types i) pre-peak and ii) early season. The peak infection day was identified by calculating the median date of the mode peak infection day from the GLOWORM-FL output in 1985-2018. Early season was defined both at a fixed time (related to predicted peak using the model) and much earlier than the pre-peak scenario (Table 5.3). The scenario with the greatest reduction in $AUCL3_h$ relative to baseline (= no intervention) was selected as the most effective.

Table 5.2. Extended Q_0 model parameter definitions and estimates, based on values for *Teladorsagia circumcincta*; and within-host stages in sheep.

Parameter	Definition	Value	Reference
$\boldsymbol{\gamma}$	Fecundity (eggs day^{-1} per adult)	228.261	Singleton et al., 2011
μ	Instantaneous daily mortality rate of adult nematodes	0.0307	Kao et al., 2000
$\boldsymbol{q}$	Probability that an egg will develop to L3 and migrate onto pasture	$\frac{\boldsymbol{\delta}\text{m1}}{(\mu_{\boldsymbol{e}}+\boldsymbol{\delta})(\mu_{\boldsymbol{l3}}+\text{m1})}, \frac{P}{E} \geq 1,$ $0, \frac{P}{E} \leq 1$	O'Connor et al., 2008; Rose et al., 2015
$\boldsymbol{\delta}$	Instantaneous daily development rate of eggs to L3	$-0.02085 + 0.00467\ T_{\text{mean}}$	Rose et al., 2015
$\mu_{\boldsymbol{e}}$	Instantenous daily mortality rate of eggs	$\exp(-1.62026-0.17771*T+0.00629*T^2)$	Rose et al., 2015
$\mu_{\boldsymbol{3}}$	Instantenous daily mortality rate of L3 in faeces	$10*\exp(-4.58817-0.13996T+0.00461*T^2)$	Rose et al., 2015
m_1	Instantenous daily L3 migration rate between faeces and pasture	0.21	Rose et al., 2015
ρ	Instantenous daily mortality rate of L3 on pasture	$\mu_3/3$	Bolajoko et al., 2015
m_2	Proportion of total pasture L3 that are found on herbage	0.2	van Dijk & Morgan, 2011
p	Probability of establishment of ingested L3	0.127	Gaba et al., 2006
β	Rate of ingestion of L3 on pasture	$\frac{c}{BA}$	-

c	Daily herbage dry matter intake per host (kg DM day1)	1.4	Kao et al., 2000
H	Host density or stocking density (sheep per ha)	This either varies regionally or held constant	Phelan et al., 2014
B	Standing biomass (kg DM ha^{-1})	2000 or taken regionally	Kao et al., 2000
A	Grazing area (ha)	1	-
P	Total daily precipitation (mm)	Daily variable	POWER, 2020
E	Daily potential evapotranspiration (mm day1)	$0.0023 * 0.408 * R_a \left(\frac{T_{max} + T_{min}}{2} + 17.8\right) \sqrt{T_{max} - T_{min}}$	Hargreaves & Samani, 1985
R_a	Extra-terrestrial radiation (MJ m^{-2} day^{-1})	Daily variable	Anon, 2002
T_{mean}, T_{min}, T_{max}	Mean, minimum and maximum daily temperature (°C)	Daily variable	POWER, 2020

Table 5.3. Intervention scenarios to reduce infection and align livestock and wildlife health in the Kibber grazing system. In each case, peak infection refers to the time of maximum *L3$_h$* availability, as predicted by the baseline (non-intervention) model.

Intervention	**Reasoning***	**Assumption**
House or treat livestock two weeks prior to the peak infection. – Intervention 1	Keeping livestock off pasture or treating them just before the peak might have a disproportionate impact on reducing the peak.	There is a defined peak in infection that can be targeted.
House or treat livestock four weeks prior to the peak infection. – Intervention 2	Same as above. However, the extended time period gives greater opportunity to reduce infection.	Same as above.
House or treat livestock for one month (May) early in the season – Intervention 3	Prevent the initial build-up of infection, which will disproportionately limit the increase in infection in the summer. May, driven by increasing temperature, is considered to be the beginning of the productive season in the Trans-Himalayas (Bagchi et al., 2006).	Given the harsh winters, we expect that warming spring and summer temperatures might fuel an increase in infectivity on pasture.
House or treat livestock for one month (June) early in the season – Intervention 4	Same as above.	Same as above. However, warmer temperatures in June than May are more suitable for larval development, and ceasing egg output then might have a larger effect.
House or treat livestock for two months (May – June) early in the season. – Intervention 5	Same as above. However, the extended time period may be more effective at reducing infection.	Same as interventions 3 and 4.

*Notes: *Reasoning column rationalises the reasons for the interventions, while the Assumptions column makes explicit certain conditions for this reasoning to be valid*

5.3. Results

5.3.1 Livestock and Bharal density and distribution

We estimated a population size of at least 130 (130-164) bharal in the 27 km^2 study area. Detection probability for observer 1 was 0.89 and for observer 2 was 0.73. This equated to a density of 4.81 (4.81-6.07) bharal km^{-2}. In the same area, we recorded 545 sheep and 64 goats, representing a density of 22.6 small ruminant livestock km^{-2}.

The FGDs revealed that livestock are herded to pasture each day and brought back to the village at night. They are stall-fed in pens during the harsh winters, and graze the pastures around the village through the rest of the year (including year-round when winters are mild). The Kibber livestock pasture (Fig. 5.3) is the maximum total area grazed by Kibber’s livestock throughout the year. These pastures are also where the area’s only wild ungulate, bharal, graze. All FGD members unanimously agreed that bharal, even though they exhibit fission and fusion amongst groups, were present in the Kibber livestock pasture area throughout the year; indicating year-round pasture sharing. However, it is important to note that bharal habitat and groups exist far beyond the Kibber livestock pasture as well. Kibber's pastures were used for livestock grazing throughout the year in 2018 (as has been the case in recent years) with daily rotations to new grazing depending on where the stock had grazed the previous day. Herding duties are shared by members of livestock-owning households, with the rotation decided upon collectively by the villagers. The daily-grazed area is significantly smaller than the entire pasture area (around c. 5 km^2/day). The eastern region of the Kibber livestock pasture is rarely grazed by livestock or bharal as it comprises high peaks.

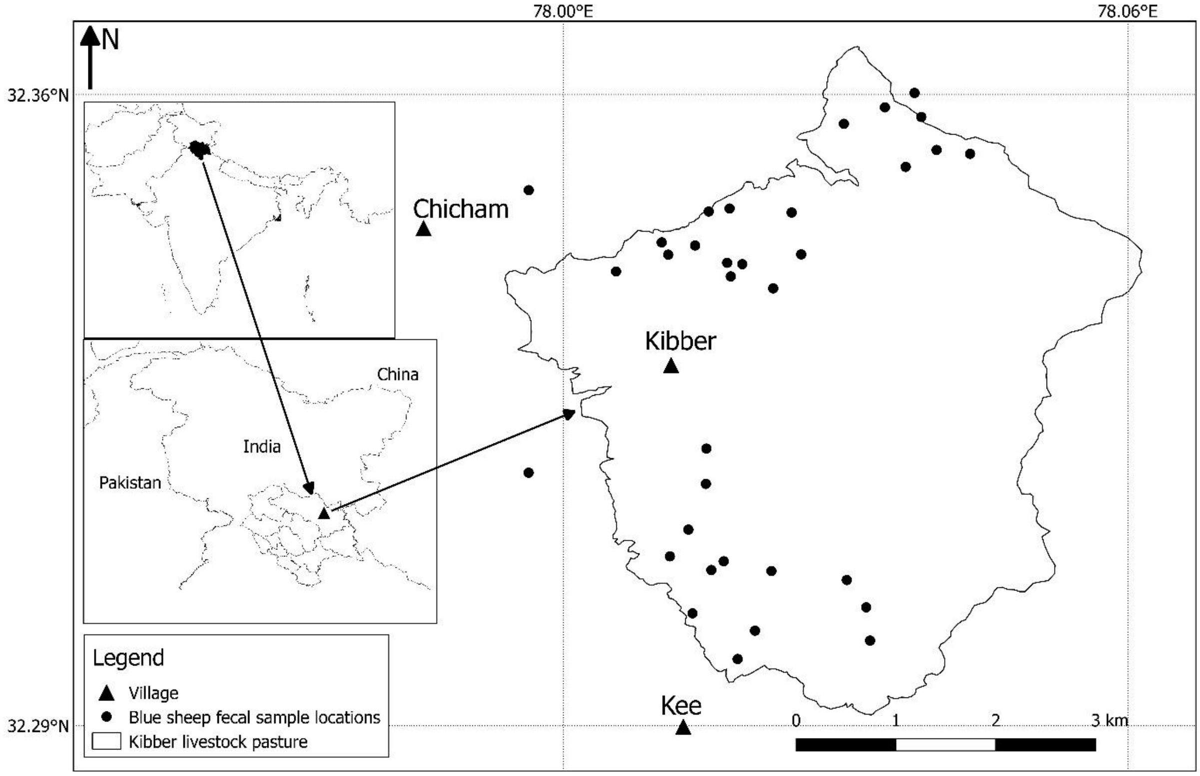

Figure 5.3. Map displaying bharal (blue sheep) faecal sample locations within the Kibber livestock pasture. The inset maps show the location of the study area within the Lahaul-Spiti district of Himachal Pradesh state, India.

5.3.2 Management of livestock health

We interviewed 32 (57%) of 56 households with sheep and/or goats in Kibber. Most of the respondents (75%, 95% CI: 66%-83%, n=24) rated the health of their livestock to be satisfactory, with significantly fewer rating livestock health as poor or good (Fig. 5.4A). Although over half of the respondents (56%, 95% CI: 46%-66%, n=18) claimed that their livestock had no disease or health issues, the rest (44%, 95% CI: 35%-54%) identified issues, most commonly ectoparasites, nasal discharge, coughing and diarrhoea (Fig. 5.4B). A few respondents gave examples of diseases of the eye, liver, and foot-and-mouth-disease (FMD) as being prevalent. Of all the respondents, 20 believed that these diseases and symptoms are more prevalent in the winter, while the rest (n=12) felt that prevalence is higher in the summer. When asked about the causes of these diseases, 10 interviewees did not know, while others attributed the onset of diseases to weakness (n=7) or the cold weather (n=6). Nearly all livestock herds (28/32) were reported to be vaccinated against FMD. According to the interviewees, no other vaccine was administered to their livestock.

All respondents were aware of ectoparasites and over half the respondents (n=17) said their livestock had them. Of these, 11/17 respondents mentioned ticks, followed by lice (5/17). The majority of respondents (n=21) stated that ticks are responsible for weakness, and possibly death, in livestock. Moreover, nearly half the respondents (n=15) claimed that ectoparasites are more common in winter, while 11 observed them to be present all year round, and six said they were more common in summer. No respondent had information about the occurrence of endoparasites and none of them treated their livestock against endoparasites. Nevertheless, Five-Point Check scores suggested negative health outcomes in livestock that were consistent with impacts of endoparasitism (Fig. 5.4D). Lastly, both the veterinary key informants suggested that the annual pasture sharing with bharal is conducive to disease cross-transmission, particularly indicating the possibility of endoparasite transfer.

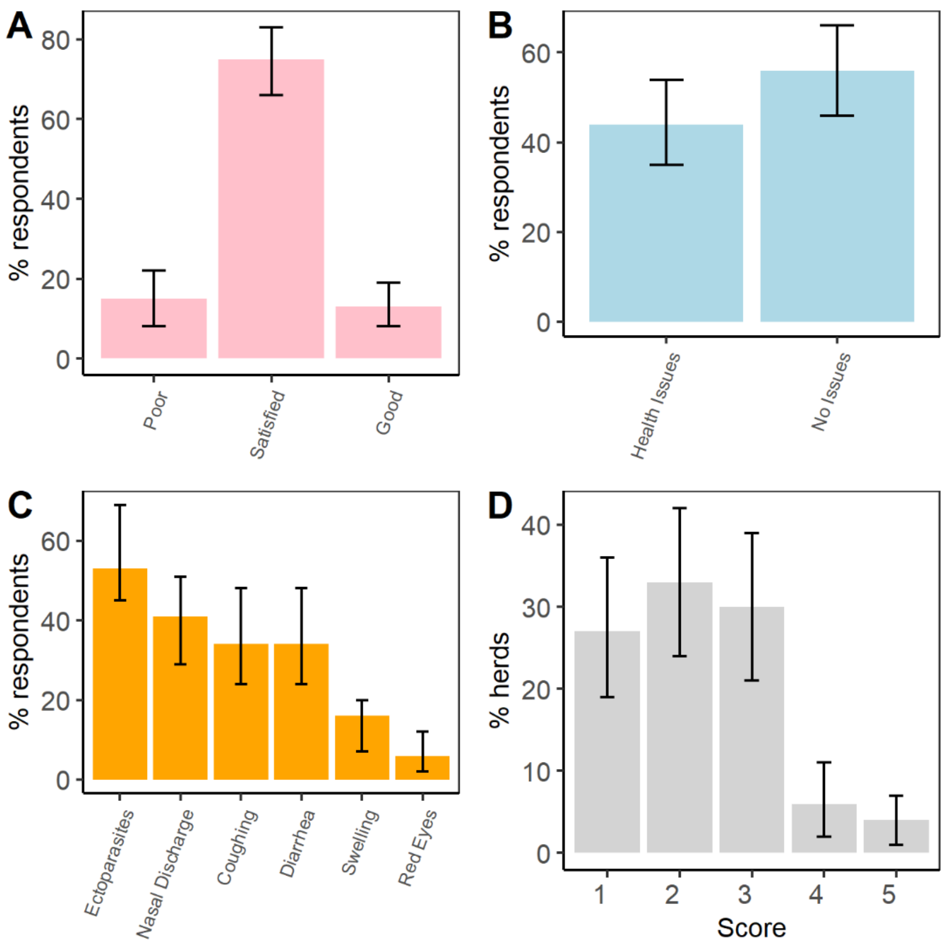

Figure 5.4. Selected results from the semi-structured interviews, including a) livestock health perception, b) reported presence of health problems in livestock and c) list of health issues and symptoms in livestock and d) the averaged composite Five-Point Check scores for livestock in each herd (n=32 herds).

5.3.3 Endoparasites in bharal and livestock

We analysed 30 unique sample days for livestock (126 pooled samples) and 38 unique sample days for bharal (115 pooled samples). Parasites identified in faecal samples included GINs (*Nematodirus* sp., *Trichuris* sp., *Strongyloides* sp., and other strongyle nematodes whose ova are morphologically indistinguishable from each other), trematodes (*Dicrocoelium* sp.), cestodes (*Moniezia* sp.), and protists (coccidial oocysts, *Eimeria* spp.) (Table 5.4). Some larvae were also observed, which were morphologically consistent with lungworm species, as well as ova resembling those of *Fasciola* spp., but because of inconsistent buoyancy of these species in saturated saline solution, levels of infection were not quantified. Endoparasite faecal density was significantly higher in livestock for *Emieria spp.*, while strongyle nematodes were significantly higher in bharal (Table 5.4). Appendix D, Table 1 shows the eggs per gram (EPG) results for all endoparasites in livestock and bharal.

5.3.4 Transmission model

Predicting pasture infectivity over time

We used strongyle FEC as input to the GLOWORM-FL model (Table 5.4 and Appendix D, Figure 1). Strongyles were found in bharal and livestock throughout the year, albeit with variation in levels of egg output (Appendix D, Figure 1). Strongyle FEC were lower in the winter months for both hosts (days 0-50 and 300-365), peaked for bharal in late summer (around day 250), and remained fairly uniformly high for livestock through summer (days 180-275). Using information from the FGDs, we estimated half of the strongyle eggs produced by livestock are deposited onto pastures, as they are housed for around 12 hours per day.

The model predicted that infective $L3_h$ larvae per kilogram of herbage peak on pasture in summer, and that the contribution of livestock to infection potential on the pasture is higher than that of bharal (Fig. 5.5A), in spite of lower average FEC (Table 5.4). Running the model for combined hosts (livestock and bharal) shows similar seasonality and summed magnitude. Infection was predicted to stay extremely low until towards day 180 of the year (i.e. July), reaching its peak just after day 200 and then tapering towards zero again by late September/early October (around day 270; Fig. 5.5A). Daily change in $L3_h$ per kilogram of herbage abundance was variable through summer (Fig. 5.5B) and not distinctly aligned with precipitation events, which occurred on most days (Fig. 5.5C). $L3_h$ levels per kilogram of herbage began to increase around 40 days after the minimum threshold temperature for development was reached, coinciding with the steady increase in spring/summer temperature (Fig. 5.5D).

Table 5.4. Endoparasites in livestock and bharal (blue sheep). Livestock samples consisted of pooled counts from mixed herds comprising mainly sheep, with some goats, and could not be separated by species. Prevalence is consequently reported at the level of the pool and not the individual animal. EPG = eggs (or, for *Eimeria* spp., oocysts) per gram; 95% CI: 95% bootstrapped confidence interval; GIN = Gastrointestinal nematode. Mean is the average egg density across positive pools .

		Eimeria	*Strongyloides*	Strongyle GIN	*Nematodirus*	*Trichuris*	*Moniezia*	*Dicrocoelium*
Blue Sheep (n=115)	**Prevalence (%)**	32	10	52	2	-	25	-
	Range (EPG)	15-565	5-15	5-35	5	-	5-220	-
	Mean EPG (95% CI)	45 (41-49)	1 (0.9-1.1)	6 (5.6-6.2)	0.08 (0.06-0.1)	-	19 (17 – 21)	-
Livestock (n=126)	**Prevalence (%)**	84	18	48	2	2	40	56
	Range (EPG)	5-15600	5-15	5-35	5-15	10-20	5-215	5-65
	Mean EPG (95% CI)	635 (570-699)	1 (1.2-1.4)	3 (2.6-3.0)	1 (0.9-1.1)	0.2 (0.1-0.3)	15 (14.0-16.4)	0.8 (0.6-1.0)
Boot-strap t-test statistics		t= 3.59 df =126 p = 0.0004	t=0.82 df=237 p= 0.41	t=-3.39 df= 182 p= 0.0009	t=3.99 df=144 p=0.0001	-	t=-0.669 df=203 p=0.51	-

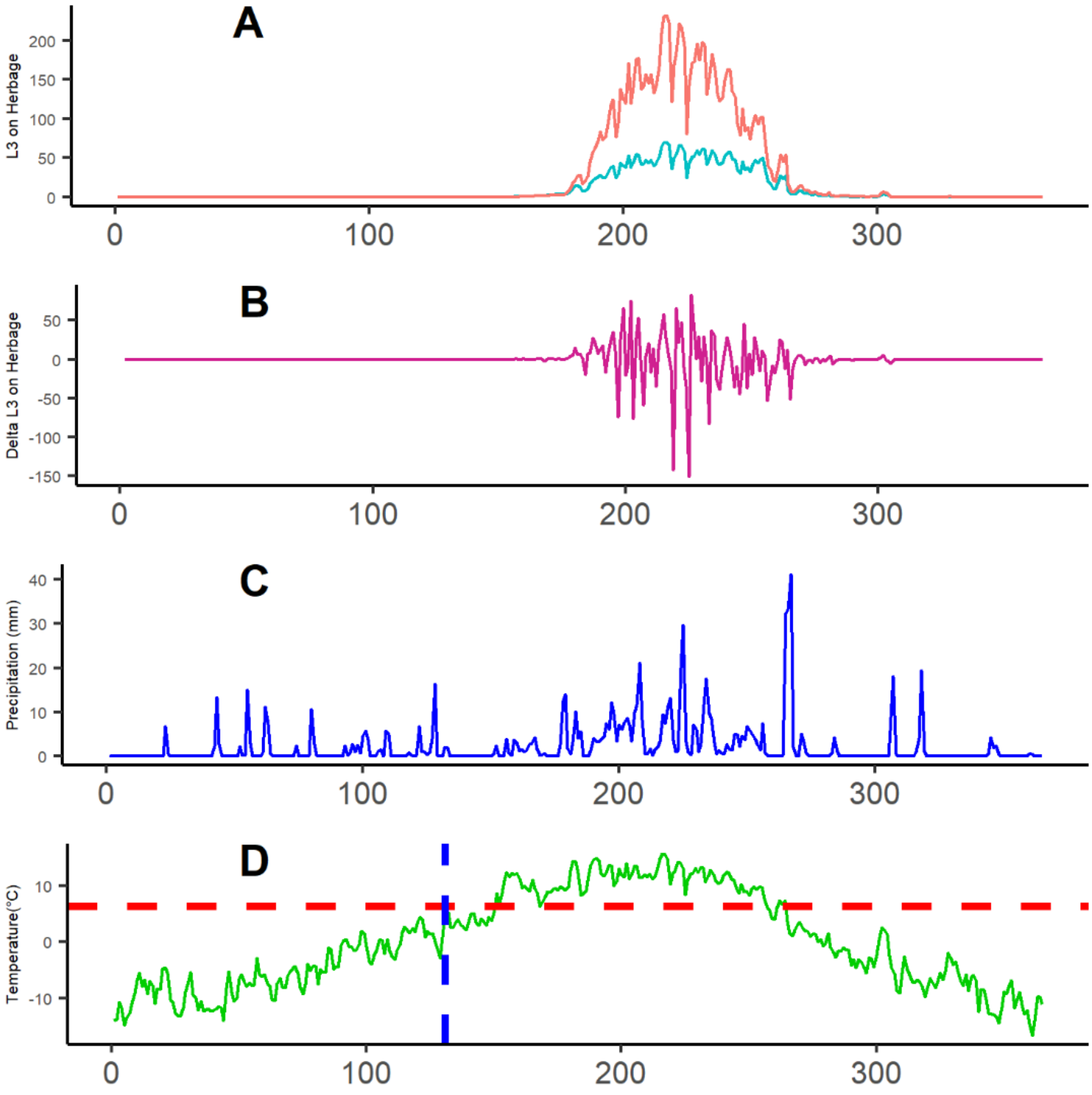

Figure 5.5. Panel graph for disease transmission dynamics in Kibber in 2018. The x-axis for each graph is day with 0= 1st January 2018 and 365 = 31st December 2018; day 200 is late July. **A:** GLOWORM-FL model output (number of $L3_h$ per kilogram of herbage) for individual hosts, Pink = livestock and blue = bharal. **B:** Daily change in $L3_h$ per kilogram of herbage, using the data in Panel A. **C:** The amount of precipitation (mm) on a given day in 2018. **D:** the average temperature (^{0}C) on a given day in 2018. The vertical blue-dotted line on Fig. 5.5D indicates the first day on which larval development is possible, based on the lower development threshold of 6.6 °C (horizontal red-dotted line).

Identifying climatic drivers of predicted infection pressure

The area under the curve of *L3* over time (*AUCL3*$_h$; Fig. 5.5A sum of both the lines) was used as an index of overall pasture infectivity over the year. When a saturating amount of precipitation was applied, removing constraints of rainfall on larval availability, *AUCL*$_3$ increased only marginally. Hence, the quotient $\frac{L_3AUC\ real\ precipitation}{L_3AUC\ high\ precipitation}$ was 0.92. A quotient close to 1 indicates marginal influence of rainfall variability, and hence a more temperature-driven transmission system. This is consistent with Fig 5.5(A and D), which shows that *L3*$_h$ abundance per kilogram of herbage rises gradually after the temperature exceeds the development threshold and peaks soon after peak annual temperature.

Quantifying the contribution of current climate to infection pressure

The time-explicit GLOWORM-FL model was used to predict total larval availability on pasture, taking into account variation in host faecal egg output and lags in development time of *L3*$_h$, as well as weather. The Q_0 model formulation, in contrast, isolates the climatic component of transmission only, with host and adult parasite factors held constant, and predicts how suitable each day is for parasite transmission success independently of historical pasture use and time lags between egg deposition and larval availability. In both cases *AUC* was used to aggregate outputs over the year. A perfect correlation between *AUCL3*$_h$ in a given year and *AUCQ*$_0$ in the same year would indicate that pasture infectivity was entirely explained by day-to-day variation in weather conditions. The correlation coefficient for *AUCL3*$_h$ versus *AUCQ*$_0$ for the years 1985-2018 was 0.49 (Pearson's correlation test, n= 34, *p*= 0.003), suggesting that factors other than current weather alone (e.g. historical pasture use) are equally important in driving transmission potential (Fig. 5.6).

To understand underlying trends and correlations in the parasite dynamics, we ran correlations between climatic variables and model outputs across time (table 5.5). The $\frac{L_3AUC\ real\ precipitation}{L_3AUC\ high\ precipitation}$ quotient showed a tendency to increase over the years (table 5.5). This indicates that over this period precipitation became less important as a constraint to transmission, and that temperature is increasingly the main driver of $L3_h$ availability on pasture. Additionally, $AUCQ_0$ increases with time but not $AUCL3_h$. $AUCL3_h$ per kilogram of herbage (infection) and $AUCQ_0$ for 1985–2018 are given in Appendix D, Table 3.

Table 5.5. Correlation matrix between climate data set and model outputs for the years 1985-2018. $AUCL3_h$ = area under the curve of predicted infective larval ($L3_h$) density on herbage, a measure of overall nematode infection pressure. $AUCQ_0$ = area under the curve of Q_0, quantifies the contribution of current weather to infection pressure. Temp = Temperature. Precip= Precipitation. Correlations in grey are non-significant, green are significant positive correlations, and blue are significant negative correlations ($\alpha = 0.05$).

	Time	Model Outputs			Climate data set	
	Year	$AUCL_3$	*Quotient*	$AUCQ_0$	*Mean Temp*	*Mean Precip*
Year	1					
$AUCL_3$	$r = 0.083$; $p = 0.64$	1				
Quotient	$r = 0.75$; $p < 0.001$	$r = 0.45$; $p = 0.007$	1			
$AUCQ_0$	$r = 0.67$; $p < 0.001$	$r = 0.49$; $p = 0.003$	$r = 0.83$; $p < 0.001$	1		
Mean Temp	$r = -0.44$; $p < 0.001$	$r = 0.31$; $p = 0.078$	$r = -0.41$; $p = 0.015$	$r = -0.25$; $p = 0.16$	1	
Mean Precip	$r = 0.74$; $p < 0.001$	$r = -0.019$; $p = 0.92$	$r = 0.77$; $p < 0.001$	$r = 0.66$; $p = <0.001$	$r = -0.52$; p = 0.001	1

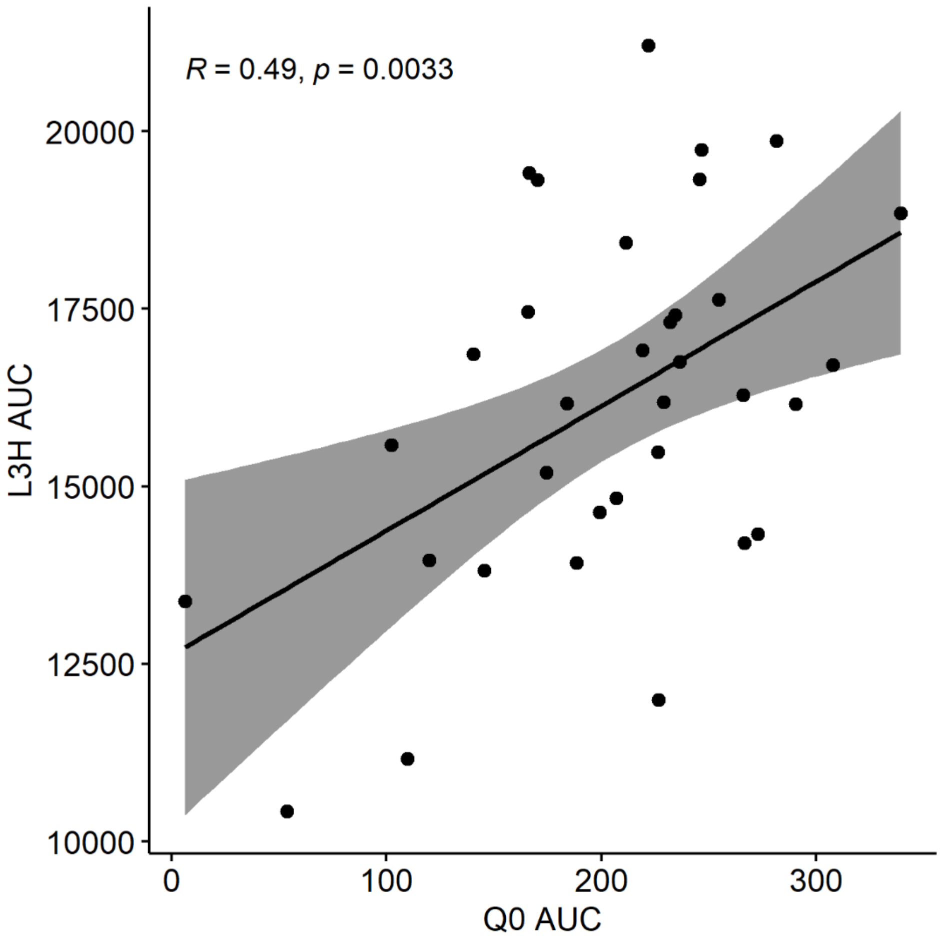

Figure 5.6. *AUCL3_h* area under the curve ~ *AUCQ₀* area under the curve.

Applying GLOWORM-FL to weather data for each year between 1985-2018 showed little change in the seasonal pattern of $L3_h$ infective larvae per kilogram of herbage on pasture over time. The general pattern conformed to the 2018 output (Fig. 5.5A); with a single peak in late summer (Figure 5.7). In the period 1985-2010, the mean peak infection day was 216 (median 215 and range 201-234). Therefore, for all five interventions (see below), the dates were defined with respect to an infection peak on day 216. Consequently, early season suppression months were selected as May and June, as that represents the transition of spring into summer, which also sees the initial rise in *L3* (Fig. 5.5A and 5.5D dotted lines).

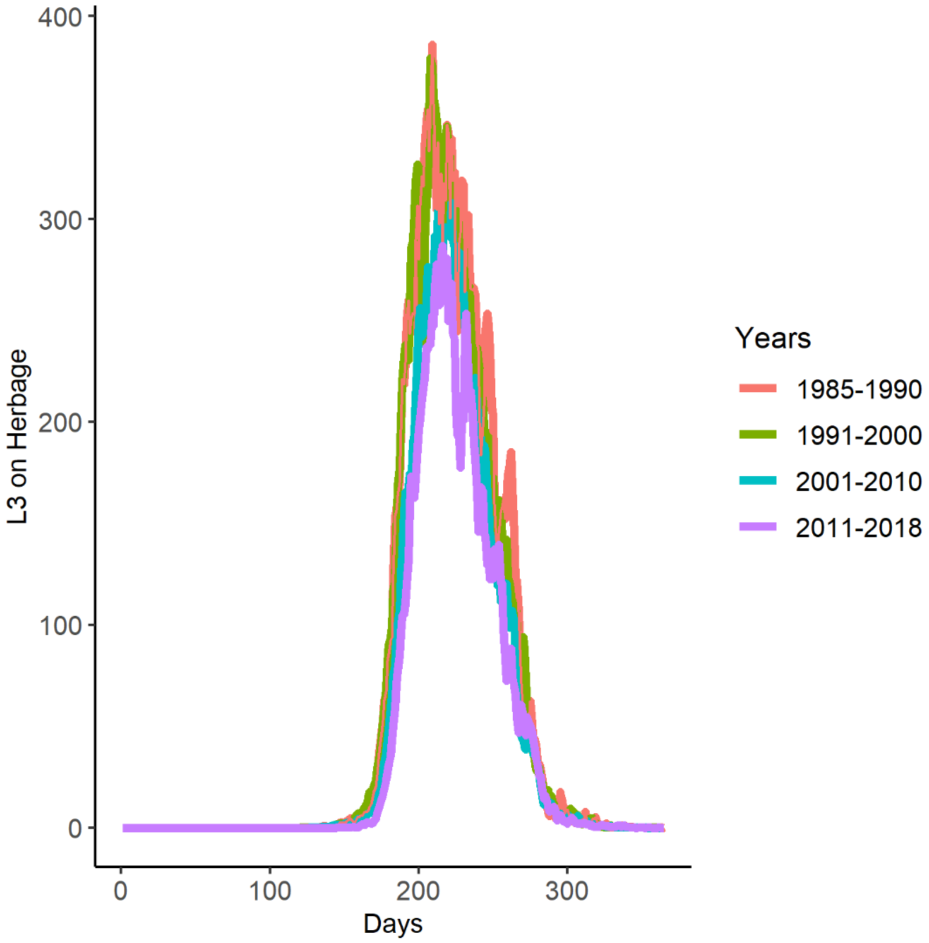

Figure 5.7. Decadal averaged GLOWORM-FL output for the years 1985-2018. The x-axis represents the days of each year starting with 0 = 1st January and 365 = 31st December.

Investigating the impact of intervention scenarios on infectivity dynamics

The first three intervention scenarios had little predicted impact on overall pasture infectivity. Interventions 4 (house or treat for one month – June- early in the season) and 5 (house or treat for two months – May and June – early in the season), however, significantly lowered the predicted number of infective larvae on pasture. The most successful interventions were therefore to house or treat livestock for one or two months (June, or May and June) early in the season (Figure 5.8, table 5.6).

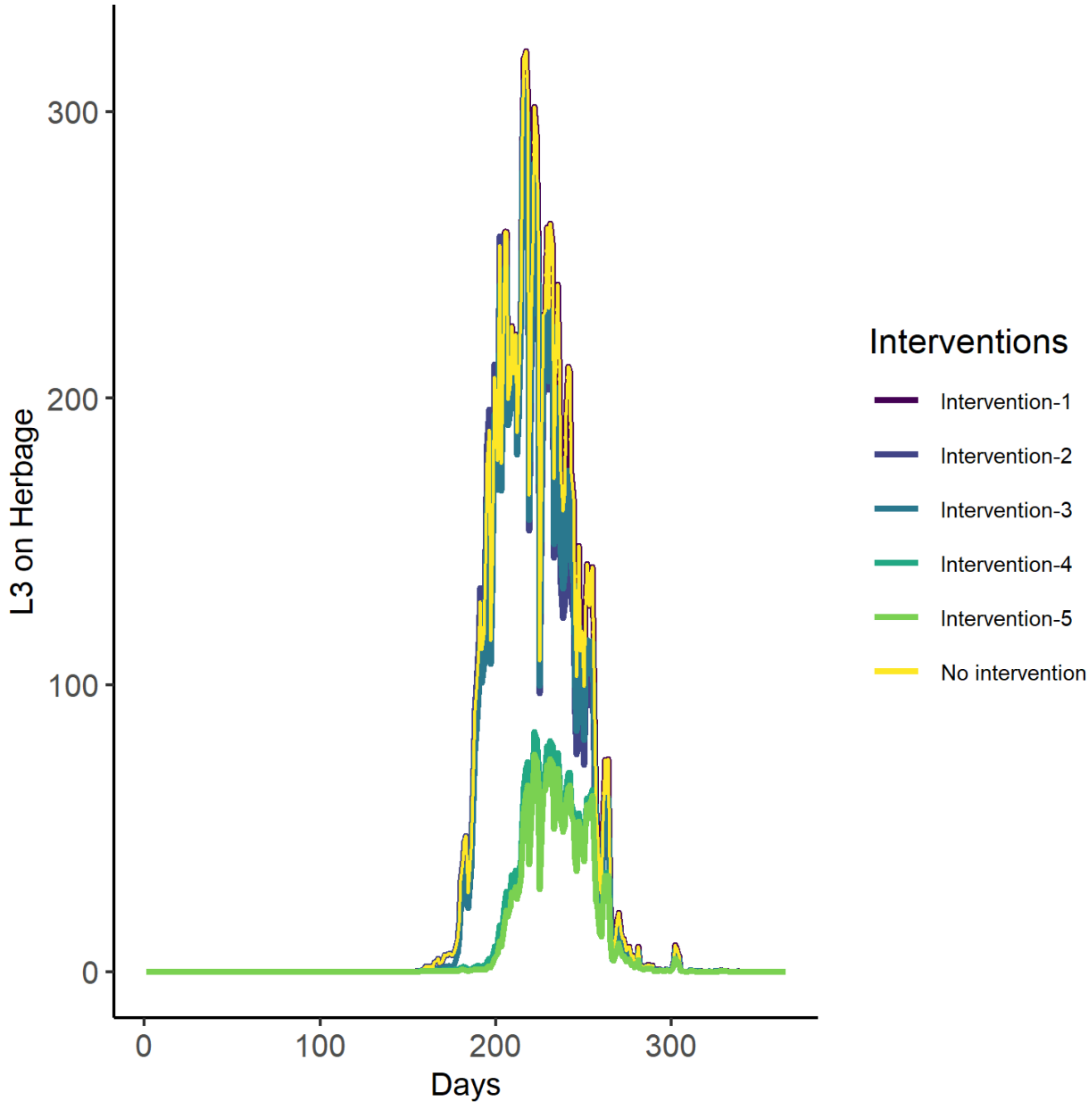

Figure 5.8. The GLOWORM-FL output for all interventions (as stated in table 5.3 and 5.6) and no intervention, for the year 2018.

Table 5.6. Intervention scenarios and their impacts in reducing infection

Intervention	**AUC Intervention**	**% reduction of AUC**
No Intervention	14,201	-
House or treat livestock two weeks prior to the peak infection – Intervention 1	13,094	7.80
House or treat livestock four weeks prior to the peak infection – Intervention 2	12,759	10.15
House or treat livestock for one month (May) early in the season – Intervention 3	12,668	10.80
House or treat livestock for one month (June) early in the season – Intervention 4	3,295	76.79
House or treat livestock for two months early in the season – Intervention 5	2,978	79.03

5.4 Discussion

We investigated disease transmission risk through a socio-ecological lens in an Indian trans-Himalayan multi-use landscape. We had the dual aim of understanding the characteristics of the system with respect to parasite transmission and, based upon that, evaluating the effectiveness of potential climatically-adapted interventions to align livestock and wild ungulate health.

5.4.1 Host distribution, social factors to manage livestock health and endoparasites

By engaging with herders, we found that livestock and bharal share the pastures around Kibber throughout the year, enabling indirect contact via pasture sharing. Host overlap is a significant factor in the epidemiology of several shared pathogens (Vosloo et al., 2002) , particularly GINs (Ezenwa, 2003). Crucially though, the scale and the nature of overlap determines whether and how transmission will actually occur (Morgan et al., 2004). Finer scale data on livestock and bharal distribution and movement on a daily or seasonal basis, would enable more sophisticated spatial modelling of disease transmission potential and also a wider range of management options such as pasture rotations. Nevertheless, given reported continual pasture use by both bharal and small ruminants throughout the year, it seems reasonable to make a starting assumption of complete overlap between populations.

Endoparasites were not raised as a common issue during group discussions or interviews, despite FEC data and Five-Point Checks suggesting their presence and potential negative impacts. Consequently, no interventions were in place to manage infection and transmission. Because endoparasites are not visible, they are often underestimated by herders, relative to the more obvious ectoparasites and in spite of health indicators suggestive of infection. This seems to be the case here. Of concern is that livestock in this region have been shown to be overstocked, with compromised productivity (Mishra et al., 2001), which would accentuate the negative impacts of even moderate parasite burdens. There is a need to more fully assess the diversity and infection intensity of endoparasites in both domestic and wild ungulates in the region, and their impacts on health, production and fitness. Where impacts are likely, it will be important to raise awareness of the issue in order for proactive management strategies to be adopted where necessary (Muthiah et al., 2013).

In the present limited study, strongyle GINs density in pooled faecal samples was relatively low (5-15 EPG, whereby the threshold for veterinary intervention in more intensive livestock-rearing systems might be 200-300 EPG), which may be testament to the general management of goats and sheep in Kibber, including housing for around 12 hours at night-time (thus potentially reducing pasture contamination by 50%), relatively low overall stocking densities of around 23 head per km^2 (equivalent to 0.23 per hectare, around 50x lower than typical stocking densities in western Europe, for example), frequent daily movement to fresh grazing within the overall grazing area, and a relatively short parasite transmission season.

Low average egg density can conceal significant effects of parasitism in some individuals due to parasite overdispersion (Morgan et al., 2005b; Morgan & Wall, 2009), however, especially when hosts are on a low plane of nutrition (Vagenas et al., 2007). We did find evidence of poor health in sheep and goats in Kibber using the Five-Point Check, which is calibrated to detect the physiologically detrimental consequences of GINs, while not being specific to them. This could be further reducing productivity of the overstocked livestock in Kibber (Mishra et al., 2001). Veterinary officials identified shared livestock-bharal grazing as conducive to disease transmission, specifically GINs, and FECs confirmed a range of endoparasite taxa were present in both hosts. This is a concern because exploitative competition between blue sheep *Pseudois nayaur* and resident livestock has been shown to reduce survival of young bharal individuals in Kibber (Mishra et al., 2004; Suryawanshi et al., 2010). In wild ruminants, GINs have been shown to correlate with poor body condition even at low levels (Irvine et al., 2006), and to reduce fecundity (Stien et al., 2002). Therefore, it is plausible that GINs might impact negatively on bharal fitness, especially if livestock act as alternative hosts and supply infection even at low bharal population density.

This potential for disease spill-over from livestock to bharal could have implications for the conservation of bharal and control of livestock diseases. For instance, a livestock-transmitted virus, Peste-des-Petits-Ruminants-Virus (PPRV), killed a significant proportion of the Critically Endangered Mongolian Saigas (*Saiga tatarica mongolica*) in 2016-17 (Pruvot et al., 2020a). Spill-over into wildlife can further undermine outbreak control spilling back into livestock. Although GINs do not generally cause disease outbreaks with high levels of mortality, impacts on host health and fitness can be considerable (see above), while also potentially exacerbating impacts of other pathogens through increased susceptibility (Ezenwa & Jolles, 2015). However there is a need to better investigate the physiological effects of GINs within hosts in Kibber before deciding whether interventions are required, and of what kind.

5.4.2 Predicting pasture infectivity over time and identifying climatic drivers of predicted infection pressure

Using the GLOWORM-FL model, we predicted that although per-capita livestock contributions to pasture loads were lower because they were housed for 12 hours a day, livestock made a greater contribution to pasture infectivity than bharal. This is likely to be due to the higher density of livestock per km^2. Given year-round pasture-sharing, this suggests the potential magnitude of parasite transmission from livestock to bharal is significantly higher than *vice versa*, whilst not disqualifying some transmission from bharal to livestock. Model simulations predicted that pasture infectivity consistently peaks in late summer, which suggests maximal transmission of GINs at this point and that mature infections are carried over into winter. This has the potential to compromise host health in the harsh winter months; a time of year when ungulate body condition is often poor (Kohli et al., 2014). In Svalbard reindeer, for example, GIN infection was associated with poor body condition in winter and subsequent low fecundity (Stien et al., 2002). However, contribution of GINs to poor body condition in bharal and hardy livestock breeds in the trans-Himalayan region is unclear, especially given the low FECs observed here.

Additionally, the model suggested that the seasonal increase in the number of infective larvae on herbage ($L3_h$) occurs after a period of steady increase in temperature. Infective larvae on pasture first appear on day 131, however peak infection is not achieved until around day 216 (around 3 months later). This "slow burn" seasonality in parasite transmission could be driven by the modest fecundity of *Teladorsagia*, which is the GINs modelled in our study (cf. the more fecund *Haemonchus*), moderate temperatures (hence slow development), and low evapotranspiration, therefore a more prolonged impact of precipitation events on transmission.

In the absence of information on GINs species composition, the transmission model was calibrated to *Te. circumcincta* as this species is well studied and has a climate envelope appropriate to the region and broadly similar to other species also common in small ruminants in temperate and montane environments, such as *Trichostrongylus* spp (O'Connor et al., 2006). However, predictions may have been different for other species. For instance, *Marshallagia spp.*, although not found in our samples, is common in Chamois *Rupicapra rupicapra* and Alpine ibex *Capra ibex* across the European Alps, mainly during the winter (Zaffaroni et al., 2000), and differs in response to temperature (Aleuy et al., 2019). Therefore further studies taking advantage of molecular approaches such as nemabiome (Avramenko et al., 2015) would be beneficial to identify specific parasites and their host distribution, enabling species-specific predictions to be made. These would, however, be subject to additional parameter uncertainty due to lack of data on response norms for many nematode species, especially in wildlife, and alternative approaches are needed (e.g. Molnar et al., 2013). Additionally, hypobiosis can affect the phenology of gastro-intestinal nematodes including in wild ungulates (Hoar et al., 2012), and should be considered if found to occur in this system.

5.4.3 Quantifying the contribution of current climate to infection pressure and investigating the impact of intervention scenarios on the disease transmission dynamics

By comparing GLOWORM-FL with Q_0 model outputs for the years 1985-2018, we found that in Kibber the historic worm burden and the developmental delay between egg and L3 on herbage were as important as current weather in driving $L3_h$ levels (Fig. 5.6). This suggests that current climate data alone are of limited use to predict infection pressure. Infection seasonality remained similar across 1985-2018, with a distinct late summer peak in pasture infectivity at a very similar time between years. The fact that over this period, $AUCQ_0$ seems to increase but not $AUCL3_h$, is also consistent with a ‘slow burn’ system; there might be more days with conducive weather for worm development, but they are not strung together in a way that translates to higher *L3* abundance (table 5.5). We also found an increasing trend in the quotient $\frac{L_3AUC\ real\ precipitation}{L_3AUC\ high\ precipitation}$ between 1985 and 2018 (table 5.5), which indicates that rainfall is increasingly not a limiting factor for GINs development and transmission, and that temperature is the primary (climatological) limitation for transmission in this area.

The fact that temperature is a better predictor of $L3_h$ abundance in this region than rainfall opens up the potential to use temperature to inform risk assessment. For example, stakeholders can use rising summer temperatures (above the minimum development threshold of 6.6 ^{0}C; Fig. 5.5D) as a an approximate predictor for increasing infection pressure. The approach taken here, to assess the relative importance of temperature vs. rainfall in predicting transmission potential based on $L3_h$ abundance, could also be used elsewhere to produce pragmatic models for risk assessments in livestock systems.

As the aim of our modelled interventions was to reduce the total infection pressure and infection peaks in the study period were reached fairly consistently in the day range 201 to 234 (mid-July to mid-August), the date appears to be a useful proxy for temperature as a cue for interventions (Tables 5.3 and 5.6). The finding that interventions four and five (treat livestock or keep them off the pasture for one month in June, or two months in May and June, thus early in the season) were the only scenarios achieving a discernible impact on infection magnitude is entirely consistent with a "slow burn" system. Historical pasture use (i.e. egg shedding) over weeks or months, along with accumulated periods of larval development, govern the standing crop of infective larvae on pasture in these types of system. This is in contrast to systems in which specific climatic events (e.g. rainfall on *Haemonchus* eggs when temperature is well above threshold) or seasonal host movements (e.g. Morgan et al., 2017; absent here) create discrete critical time points at which interventions might be focused (Besier et al., 2016).

This result is similar to many temperate systems, where the most effective intervention is to treat early in the season, i.e. "early season suppression", on the basis that it is these eggs that ignite the system and by preventing them being shed, pastures are kept clean for longer and infective larvae lack the chance to reach a high peak (Morgan & Van Dijk, 2012). Intervention 3 (early-season suppression in May) had discernibly lower impact than intervention 4 (early-season suppression in June) because in the first month after the development threshold is reached (late April into May), temperature is still low, such that stopping egg inputs then made little difference to eventual pasture contamination. A similar outcome could therefore be achieved with a shorter intervention, if this is well-timed in relation to parasite development potential, and the model can enable intervention times and weather cues to be optimised to the system in hand.

Cessation of egg output could be achieved by anthelmintic treatment or by housing. Housing livestock for one or two months early in the season might be unrealistic for various logistical and socio-cultural reasons. These include: i) a shortage of fodder in the region and reliance on continual grazing of pastures; ii) due to the short vegetative growth season, the quality and variety of vegetation is at its peak during summer, which herders try to exploit before the onset of the winter; iii) due to their Buddhist faith, the herders value the right to life of every sentient being and hence could feel that restricting livestock movement out of choice, for extended periods of time, would impinge on these rights. Treating all animals for over two months, on the other hand, would be expensive and could favour the development of anthelmintic resistance (Coles et al., 2006). Nonetheless, we evaluated this scenario to confirm the "slow-burn" nature of the system. Importantly, a key research need is to investigate if the magnitude, direction and level of infection cross-transmission is high enough to be physiologically detrimental for the hosts (Stringer & Linklater, 2014). If not, then interventions may not be required.

5.4.4 Lessons for Kibber: Integrating inputs from interviews with model outputs

Temperature can be used by herders in Kibber as a cue to be vigilant and mitigate against effects of GINs in their herds (Fig. 5.5, Fig. 5.7 and table 5.6). Nonetheless, rather than taking an effective, yet arguably impractical preventive measure, it might be more cost-effective to use timely and reactive methods such as selective treatment of individuals showing signs of parasitism. This may achieve disproportionate health improvements and epidemiological benefits using lower levels of anthelmintic treatment (Walker et al., 2015). Further adaptations to our model could enable simulation of the likely impact of selective treatments (Charlier et al., 2014). Livestock-holders and veterinary officials could use the Five-Point Check to check for parasitism in sheep and goats and identify vulnerable individuals (Bath & Van Wyk, 2009). Combining the understanding of transmission seasonality and magnitude from GLOWORM-FL with identification of those livestock individuals showing signs of parasitism, could help in selecting times and individuals at which to target treatment. This would reduce the onset of anthelmintic resistance and is a cost-effective way to treat herds where drug supplies are limited, such as in remote areas like Kibber. This has the potential to reduce the onward transmission of GINs from livestock to bharal while improving livestock health.

Additionally, our coarse analysis would need to be followed up by a finer-scale (ideally individual-based) analysis of disease and GIN loads both for livestock and wildlife, so that the heterogeneity within herds and its spatio-temporal variation can be assessed. This would enable assessment of the potential benefits of a targeted treatment approach, both for livestock and bharal. However, such interventions need consensus about their effectiveness in order to trigger channelling of resources, which often takes time to build evidence, engagement and momentum. Studies such as ours provide both the scientific foundation and the foundation of trust between researchers and herders, which could enable more targeted and effective disease control strategies in future.

5.5 Conclusion

Using a robust strategy rooted in understanding of system dynamics under a changing climate, we find that the Trans-Himalayan Kibber pastures can be characterised as a “slow-burn” parasite system that is temperature-driven. Over the years 1985-2018, this feature appears to be increasingly reinforced, while the seasonality of parasite transmission is relatively constant and predictable. Consequently, early-season suppression of GINs egg output form livestock is the most effective strategy to limit infection pressure both for livestock and bharal, particularly if consistently applied from year to year, for long enough to make a difference to overall larval abundance.

Finally, looking beyond Kibber, our study provides a transferable multi-pronged approach to investigating disease transmission risk through a socio-ecological lens in a multi-use landscape. By highlighting that disease is a socio-ecological concern, we emphasise that its understanding and management is best considered from an interdisciplinary perspective. Our holistic approach combines ecological and social knowledge to understand parasite transmission in a multi-use landscape and provide a scientific basis for interventions. Not only can this protect herders’ livelihoods but also conserve wild ungulates.

- Chapter 6 -

Predicting and attenuating parasite infection between migratory livestock and resident Asiatic Ibex in the Himalaya

In review **Khanyari, M.**, Oyanedel, R., Khara, A., Sharma, M., Milner-Gulland, E.J., Suryawanshi, K., Vineer, H.R., Morgan, E.R. (no date). *Animal Conservation*.

Authors' contribution

This study was conceptualized by me, EM, EJM and KS. RO adapted and conducted the sensitivity analysis. I and AK conducted the field work and analysed the data.. MS provided critical inputs during the writing. I and EM lead the writing of the chapter and all authors commented on subsequent drafts.

A mixed herd of Asiatic ibex grazing in the Pin pastures

Abstract

Disease cross-transmission between wild and domestic ungulates can have negative impacts on agricultural economies and wildlife conservation. Assessing how to reduce these impacts is key to maintaining people's livelihoods while also conserving wild ungulate populations. In the trans-Himalayan region of Pin valley, migratory flocks of sheep and goats share pastures seasonally with the resident wild ungulate, Asiatic ibex (*Capra sibirica),* leading to the possibility of disease cross-transmission. We focused our work on gastro-intestinal nematode (GINs) as they are common determinants of health and fitness in wild and domestic ungulates. Using a parasite life cycle model that incorporated host movements and the effects of weather on infective larval availability, we investigated the transmission dynamics and evaluated potential interventions to attenuate infection pressure for both, the livestock and ibex. We found that although ibex used the pastures year-round, parasite eggs which they shed only contributed to infective larvae on pastures during the summer. Migratory livestock enter the Pin pastures around day 152 (i.e. 1st June) and subsequently contribute eggs and hence infective larvae onto pasture. Migratory livestock were predicted to contribute the majority of infective larvae onto shared pastures, driving infections in both livestock and ibex. Our model predicts that any amount of anti-parasitic treatment of migratory livestock resulted in some reduction in infection pressure, but we found a *c.*30 day intervention towards the end of the livestock's time in Pin had the highest impact, and is likely to be effective in reducing GIN burdens in both domestic and wild hosts. Our study provides a transferable multi-pronged approach and an adaptable predictive model to investigate parasite transmission in multi-use landscapes, including those with migratory hosts. We provide a robust approach for hypothesis-testing and intervention design which can serve the dual purpose of conserving wild ungulates and protecting herders' livelihoods.

Keywords: ungulate, disease, parasite, gastrointestinal nematode, epidemiology, ibex, intervention

6.1 Introduction

Many pathogens and parasites found in domestic livestock also infect sympatric wildlife, especially ungulates. For instance, foot-and-mouth disease virus (FMDV) transmission from livestock historically led to disease outbreaks in saiga antelopes *Saiga tatarica* in Kazakhstan (Bekenov et al., 1998). Elsewhere, the importance of African buffalo *Syncerus caffer* as a source of FMDV for livestock is enhanced by its ability to persist in this species, while other ruminants such as impala *Aepyceros melampus* can act as vectors of transmission between buffalo and cattle (Vosloo et al., 2002; Hargreaves et al., 2004). Disease cross-transmission can have negative impacts on agricultural economies and conservation, of concern for wildlife and livestock managers alike (Smith et al., 2009).

Among disease-causing agents, gastrointestinal nematodes (GINs) are particularly of concern as they are major determinants of host health, production and fitness in wild and domestic ungulates (Gulland, 1992; Perry & Randolph, 1999). GIN transmission varies in time and space, driven by complex biotic and abiotic factors. A mix of pasture characteristics, precipitation and temperature determine the development and survival of free-living stages (Rose et al., 2015). Host behaviour, density, and diversity can also influence free-living stages encountering hosts (Ezenwa, 2003; Morgan et al., 2004). Many GINs infect both wild and domestic hosts (Walker et al., 2017) and are transmitted through indirect contact via shared grazing of pastures, which can be sequential and not necessarily concurrent (Morgan et al., 2004). Human interventions to control GINs in livestock can consequently affect GINs in wildlife through attenuation of shared infection pressure (Weinstein & Lafferty, 2015).

Investigating parasite transmission risk between wildlife and livestock is usually extremely challenging. Data on infection levels in wildlife are usually scarce and open to bias, and are not in themselves sufficient for assessment of cross-species transmission (Morgan et al., 2006; 2007). Investigating impacts of GIN transmission is especially difficult, yet pertinent, in remote rangelands that are home to migratory hosts. Seasonal movement of hosts can result in complex contact patterns, affecting disease transmission across species (Khanyari et al., 2021; Chapter 2). Predictive disease models offer a way to identify the risks of such transmission and to design effective interventions (McCallum, 2016). Furthermore, as there are challenges and complications regarding disease control intervention applied to wild species, GIN management is often focussed toward livestock. Nevertheless, testing control options in practice is difficult, expensive and has the possibility of being harmful to the animals involved (Learmount et al., 2018). Therefore, models can be useful tools to investigate likely interventions in virtual space before translating them into practice (Walker et al., 2018).

One situation in which cross-species GIN transmission is potentially a major, yet an understudied, issue is transhumant livestock herding in mountainous regions, where livestock and wild ungulates graze the same pastures (Mishra et al., 2021). These systems are highly seasonal, hosts are often mobile, and the areas are remote and understudied (eg. Ghoshal, 2017). They are also fragile; threatened by climate change, with communities often dependent on livestock for their livelihoods, and wild ungulate species of conservation concern (Saberwal, 1996; Mishra, 2001). Therefore, these systems are ideal candidates for model-based testing of potential interventions to support their continued viability.

Asian mountains are particularly home to many transhumant communities. There are several transhumant communities in the Indian trans-Himalayas, such as the *Changpas* of Ladakh, the *Gaddis* in Himachal Pradesh and the *Bhotias* of Sikkim (Ghoshal, 2017). We focus our work within the Indian trans-Himalayan rangeland of the Pin valley. Here the migratory livestock herders – the *Kinnaura* – share pasture seasonally (in summer) with Asiatic ibex *Capra sibirica.* Local sedentary livestock are present in the villages of Pin valley but are low in number and seldom share pasture with the ibex (Chapter 4). Ibex are not only key determinants of the viability of populations of their threatened predator the Snow Leopard *Panthera uncia*, but also play a crucial role in maintaining vegetation composition and nutrient cycling in the region (Bagchi & Ritchie, 2010). Across the trans-Himalayas, including Pin, there is increasing evidence of negative impacts of livestock grazing, manifested through competition between livestock and wild ungulates and potentially augmented by pasture degradation (Bagchi et al., 2004; Bagchi et al., 2012). Beyond affecting ungulate body condition through resource acquisition, degradation of the pasture could add to the problem of disease through nutritional stress and resource competition, in turn exacerbating GIN impacts (Kock, 2004). This is important as, in Pin, the *Kinnaura* flocks exhibit significantly higher endoparasite burdens than sedentary hosts (i.e. local livestock and ibex), and are increasing in number (Chapter 4). This suggests that GIN cross-transmission between migratory livestock and wild Asiatic ibex is possible, as GINs have free-living stages in the environment, which are acquired by grazing. In fact, given the moderate temperature and low evapotranspiration, it is likely that the short productive summer season – when *Kinnaura* flocks share pastures with ibex – is the predominant time for GIN transmission in Pin valley (Morgan & Van Dijk, 2015; Rose et al., 2015).

The long distance *Kinnaura* migration is likely to persist into the future, although there are several socio-economic changes in the *Kinnaura* society, and persistence may depend upon addressing the issues of pasture degradation and livestock productivity (Basannagari & Kala, 2013; Ghoshal, 2017). Against this background, we set out to explore GIN transmission risk between the migratory *Kinnaura* flocks and ibex in Pin valley using a parasite transmission model. We evaluated the outcomes of possible interventions to attenuate infection pressure for both the *Kinnaura* flocks and ibex, using a sensitivity analysis. Given the harsh alpine climate of Pin Valley, we hypothesized that pasture infectivity would be governed by historical pasture use and gradual accumulated larval development during the summer, driven by moderate temperatures (hence slow development of parasites), and low evapotranspiration, therefore a more prolonged impact of precipitation events on transmission (Morgan & van Dijk, 2015; Rose et al., 2015; similar to Chapter 5). Our approach could form a basis for discussions with local stakeholders, such as wildlife conservationists and livestock managers, on introducing locally-applicable and socially-relevant livestock health interventions to better align people's socio-economic priorities with wildlife conservation.

6.2 Materials and Methods

6.2.1 Study area

The study area centred on the Pin valley (32^0 N 78^0 E), which is within Lahaul-Spiti district, Himachal Pradesh, India (Fig. 6.1). Part of the study is a Protected Area, the Pin Valley National Park. The catchment of the Pin and Parahio rivers forms the Pin valley. The region is characterized by low precipitation (<500 mm annually, with most precipitation in the form of winter snow), a short growing season and low primary productivity (Mishra et al., 2001). This high-altitude (average 4,420m) region experiences extreme climatic conditions, with winter temperatures ranging from -35°C to 3°C, and summer temperatures ranging from 1°C to 30°C. Due to its arid and cold environment, the vegetation is characterized as "dry alpine steppe" with grasses, sedges and shrubs being the predominant vegetation forms. The tree layer is largely absent (Bagchi et al., 2004).

The Parahio is a large tributary of the Pin river and the local villagers (n=13 villages) within Pin valley have traditional rights over its pastures. The villagers of Pin are primarily agro-pastoralists. They keep several types of livestock including yaks, *dzos* (cattle-yak hybrids), cattle, horses, sheep and goats. Since the turn of the 21st century sheep and goat numbers have drastically declined in Pin (930 in 2003 to 55 in 2019) whilst large livestock (yaks, dzos, cattle and horses) have slightly increased (1326 in 2003 to 1866 in 2019) (Chapter 4). The other major land use is agriculture and local people grow various varieties of barley and pea (Mishra, 2001). Additionally, migratory herders – the *Kinnauras* – have traditional rights/leases over a few pastures for seasonal grazing.

The *Kinnaura* herders undertake long-distance migration with their sheep and goats. They are native to the Rupi-Bhaba area (31.5^{0} N, 77.9^{0} E), where they spend a large part of the spring (April-May) and autumn (September-October; Fig. 6.1). They graze pastures in the Pin valley during summer (June-August), and spend winters in the Himalayan foothills of the Sirmaur region (November-March). As of 2019, 28 migratory *Kinnaura* herds visit Pin valley, each with an average of 809 sheep and goats (SE ± 39.2). The *Kinnaura* herders pay an annual fee to each village committee to use these pastures for the summer months.

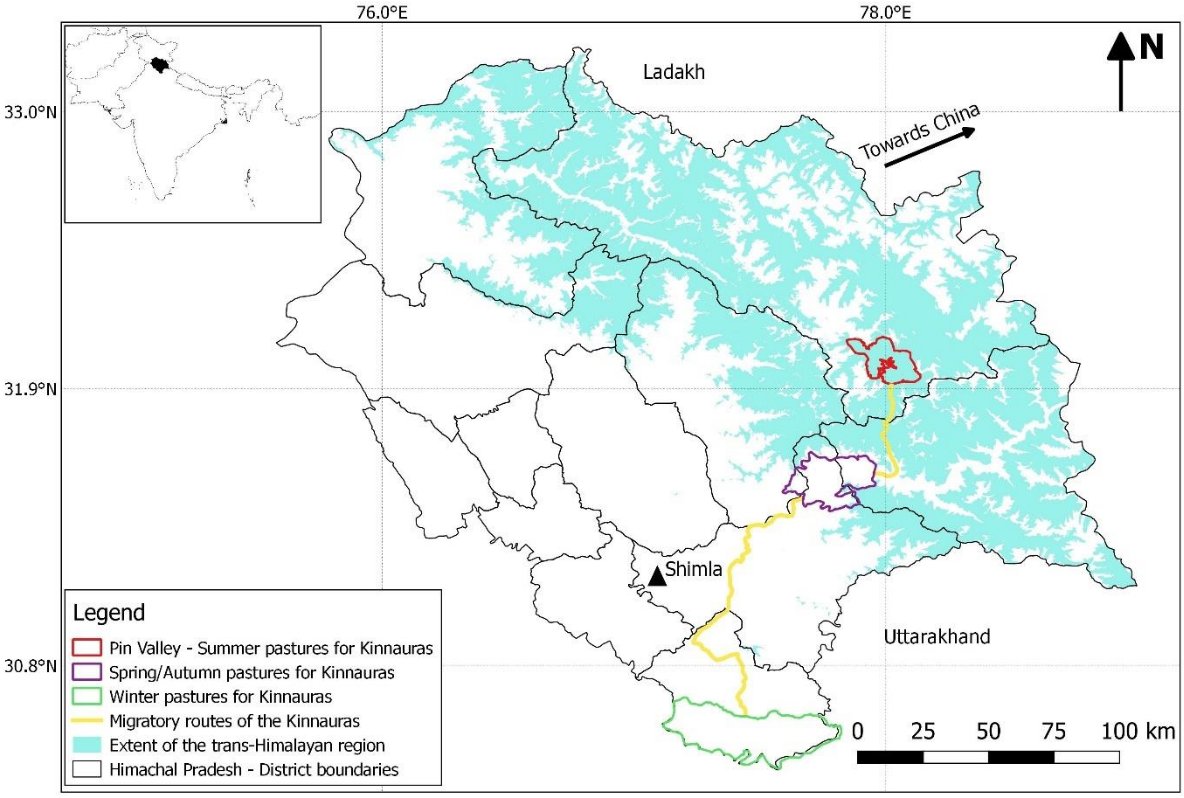

Figure 6.1. Map displaying the migratory route and seasonal pastures of the *Kinnaura* herders. The inset map situates the state of Himachal Pradesh within India. Our study area (Pin valley) is outlined in red and exists entirely within the trans-Himalayan region (c. 3,200-5,200m).

6.2.2 The significance of Pin as a study site

The Asiatic ibex is the predominant wild herbivore in Pin, and also the primary prey of the snow leopard, the apex predator of this ecosystem. They spend the entire year within Pin valley, with limited seasonal movement (Bhatnagar, 1997). Currently, Pin valley is home to *c.*240 ibex (Suryawanshi et al., in review). As the ibex is a caprine, it is most likely to share pasture and GINs with sheep and goats (Bagchi et al., 2004; Walker & Morgan, 2014); hence we concentrated our work on the migratory livestock and ibex (livestock hereafter refers collectively to the migratory sheep and goats, unless stated otherwise).

Even though the migratory livestock share pasture with other ungulates to some extent throughout their migratory range, we concentrated our work in Pin valley as its rangelands are co-grazed by livestock and ibex during the short yet important growth season (Mishra et al., 2001). To test this, we calculated annual NDVI for Pin using Google Earth Engine's LANDSAT 8 imagery. We extracted all the Normalized Difference Vegetation Index (NDVI) values from available images from 2013 to 2019 (the available date range) using equation (6.1) on a 30x30m pixel scale; where NIR represents the near-infrared band and Red represents the red band of the spectrum caught in the Landsat images respectively. NDVI values below zero represent areas covered with snow, whilst higher values of NDVI represent areas with denser vegetation cover. Additionally, there is evidence that Pin valley is particularly heavily grazed by livestock compared to surrounding rangelands, causing resource competition and conservation concern for wild ungulates, with calls for integration of social and ecological considerations into management planning for the valley (Bagchi et al., 2004; Ghoshal, 2017).

$$NDVI = \frac{(NIR - Red)}{(NIR + Red)} \qquad (6.1)$$

6.2.3 Parasitological data collection

Data collection for ibex occurred throughout 2019, whereas for the migratory flocks, it occurred in June-August 2019, i.e. during the time they spend in Pin valley. Data from local, sedentary sheep and goats were not collected as they are extremely low in number and do not share pasture with ibex (Chapter 4). Fresh faecal pellet samples were collected from migratory sheep, goats and ibex. Collection was opportunistic, with fresh faeces collected from the ground. Faecal Egg Counts (FEC) were conducted on pooled faecal samples to arrive at the number of helminth eggs reaching the pasture to seed onward transmission, and as a proxy of parasite burden. The mini-FLOTAC method (Cringoli et al., 2017) was used as a simple and cost-effective method for FECs in remote areas.

For ibex, samples were opportunistically collected from all age-sex classes. The date and location of each sample collected was recorded. As the sheep and goats are herded as one unit, we collected fresh faecal samples, taking various samples from different individuals and attempting to collect as many as possible at a given time. Next, we placed all the individual samples, each of similar volume, together into a plastic bag and mashed and mixed them thoroughly. From the well-mixed composite (pooled) sample, we took 5 g faeces and mixed that well with 45 ml saturated sodium chloride salt solution, and then examined the suspension under a microscope, following the method detailed in Cringoli et al., (2017). The same process was followed for ibex. Livestock samples (65 samples across 28 herds) were therefore pooled at the level of each migratory livestock herd and ibex samples (n=74) were pooled at the level of the study population as a whole (Morgan et al. 2005b). Sample hereon refers to a pooled sample.

The number of eggs found for strongyle parasite was recorded for each sample and multiplied by a factor of 5 to obtain the total FEC in eggs per gram (EPG) of faeces. If multiple samples from the same host type were analysed on a given date, an average EPG was taken. We were especially keen in the FEC of strongyle nematodes as they are the input into the GLOWORM-FL model.

6.2.4 Climate data

Primary meteorological data were not available for Pin. Therein, interpolated datasets were used to estimate parasite vital rates within the population dynamic models (below). We got quotidian temperatures and precipitation from the POWER Data Access Viewer (DAV) (POWER, 2020). We used the POWER Single Point Data Access widget which offers access to almost real-time 0.5 x 0.5 degree datasets by single point (latitude and long), for the years 1990-2019. Potential evapotranspiration (evaporation) was estimated based on the daily mean air temperature and day length (number of daylight hours) using the Hamon method (Xu & Singh, 2001). Day length was estimated based on the latitude of the study site and date using the *daylength* function of the *geosphere* R package (Hijmans, 2019).

6.2.5 Transmission model - predicting pasture infectivity over time

The predictive model is based on the life cycle of the free-living stages of trichostrongylid GINs (Equations 6.2-6.8) (Rose et al., 2015). The GLOWORM-FL models the journey of the parasite eggs upon deposition by hosts to the third-stage infective larvae (L3), and then migration onto pasture. The output is an estimated number of L3 that are present on herbage per unit area for ingestion by the grazers. To obtain egg output on pasture (E), the number of eggs per gram of faeces (FEC) is multiplied by the density of hosts and host faecal output (f). Temperature-dependent stage-specific mortality ($\mu_{1,2,3}$) and development (δ) rates govern the growth of L3 in faeces ($L3_f$) from eggs (E), via the pre-infective larval stage (L). Overlapping nematode groups are traced, with existing eggs being replenished by newly deposited eggs (E_{new}), after taking into account a moisture-limited development success correction factor (C).

The progress from L3 from faeces onto pasture ($L3_p$), is done by accounting for a climate-dependent horizontal migration rate (m_1). $L3_p$ can either be in the herbage ($L3_h$) or soil ($L3_s$). To reflect this, we simulated random bi-directional movement between herbage and soil using substrate-specific mortality rates (μ_4, μ_5), and a vertical migration rate (m_2) dependent on temperature.

We ran the model in R version 3.6.3 (R Core team, 2020), using the *lsoda* function withing the “deSolve” package (Soetaert et al., 2010). The output of the model is the daily number of individual GINs per hectare for each life-stage. We calculate $L3_h$ per kg dry matter of herbage (L3/kgDM) by dividing $L3_h$ (equation 8) by the biomass of dry herbage per hectare (parameterized from Bagchi et al., 2006). Henceforth, pasture infection denotes $L3_h$ per kg dry herbage (L3/kgDM). Annual infection pressure was estimated by summing daily L3/kgDM for the whole year, i.e area under the curve ($AUCL3_h$). Finally, FECs were inputted to seed the model. Total egg output per hectare was estimated based on host weight, obtained from the literature and averaged across sexes to account for sexual dimorphism (52 kg ibex and 22 kg sheep/goat – Mishra et al., 2019). Faecal output (wet weight, g per day) was assumed to be the same per kg of body weight for both species (Moharrery, 2011).

To estimate relative contribution of each host to pasture infectivity, the model was run for three host scenarios: only ibex; only livestock; and ibex and livestock combined, for 30 years of climate data. To obtain mean and 95% confidence intervals for each scenario, we bootstrapped the 30 model outputs (one for each year of climate data, run independently) with replacement (10,000 iterations). Pasture was assumed to be cleared of infection each winter due to the extreme negative temperatures observed in Pin, and predicted GIN mortality rates at these temperatures (Rose et al., 2015), with transmission each year seeded anew from faecal deposits; hence the pasture parasite population was tracked from zero in each independent simulation.

We used *Teladorsagia circumcincta* parameters, because this species tends to dominate over the warm-adapted *Haemonchus contortus* in cool temperate areas, and has similar responses to climate outside the host as other common genera such as *Trichostrongylus* (O'Connor et al., 2006). Studies from the western Himalayan regions (similar to Pin) have found *Trichostrongylus* species to be ubiquitous in small ruminants (Jithendran & Bhat, 1999). Additional details about the model, including parameters used, is in Rose et al., (2015).

$$E_{new} = D(f \times FEC) \qquad (6.2)$$

$$\frac{dE}{dt} = -(\mu_1 + 2\delta)E + E_{new}C \qquad (6.3)$$

$$\frac{dL}{dt} = -(\mu_2 + 2\delta)L + 2\delta E \qquad (6.4)$$

$$\frac{dL3_f}{dt} = -(\mu_3 + m_1)L3_f + 2\delta L \qquad (6.5)$$

$$\frac{dL3_p}{dt} = -\mu_4\left((1 - m_2)L3_p\right) - \mu_5\left(m_2 L3_p\right) + m_1 L3_f \qquad (6.6)$$

$$L3_s = L3_p(1 - m_2) \qquad (6.7)$$

$$L3_h = L3_p m_2 \qquad (6.8)$$

6.2.6 Simulation model – identifying optimum times and duration of intervention

We concentrate on livestock-centred interventions for two reasons: i) carrying out health interventions in ibex is logistically challenging and ii) interventions in sympatric livestock are likely to impact parasite infections in both hosts. Interventions were based on treatment with repeated or persistent anthelmintics. This was operationalized in our model by turning egg supply to zero for a defined time period. Our output of interest was the sum of $L3_h$ per kilogram of herbage, integrated over the defined time period ($AUCL3_h$), which enabled evaluation of the reduction in infection pressure attributable to an intervention.

To identify the most effective time and duration of an intervention in migratory livestock to reduce overall infection pressure ($AUCL3_h$), we developed a sensitivity analysis following the approach used by Oyanedel et al., (2021). Here, we assessed the mix of intervention attributes - start date and length - that caused the most reduction in $AUCL3_h$. For the sensitivity analysis, we varied the intervention features by changed the intervention start day from day 152 (1st June) to day 243 (31st August) and its length (1 day to 30 days). The former was selected to overlap with the period in which the migratory livestock visit the Pin pastures, while the latter was chosen based on conversations with livestock herders which confirmed that treatment over 1 month was unlikely to be feasible due to issues of cost and anthelminthic availability. Longer treatments also increase the peril of anthelmintic resistance (Charlier et al., 2014). We ran 10,000 GLOWORM-FL model simulations, drawing random values from the intervention attribute ranges (starting on day 152-243 and persisting for 1-30 days). Results from each simulation were calculated as the reduction in $AUCL3_h$, and the attribute pairs used in the simulation were recorded for subsequent visualization.

6.3 Results

6.3.1 Predicting pasture infectivity over time

Our fieldwork found Strongyles in ibex throughout the year, albeit with variation in levels of egg output, and in migratory livestock throughout the time they were in Pin (Appendix E, Table 1). Even though ibex used the Pin pastures throughout the year, our model suggested that eggs which they shed only developed successfully to contribute to infective larvae on pastures ($L3_h$) during the summer (*c.* day 180 – day 265, i.e. 1st July - 22nd September). Migratory livestock contribute to peaks of pasture contamination throughout their time in Pin (c. day 152 - day 243 i.e. 1st June - 31st August; Fig. 6.2). Moreover, even after their departure, eggs which they shed continue to develop, contributing to the ongoing supply of infective larvae on pasture into the autumn (i.e. between *c.* day 244 – day 304, 1st September – 31st October), albeit at lower levels than during the time they spend in Pin. The total number of infective larvae on pasture ($L3_h$) contributed by migratory livestock is three orders of magnitude higher than that contributed by Asiatic ibex ($AUCL3_h$ ibex = *c.*1 100, $AUCL3_h$ migratory livestock = *c.*92 000). Parasite transmission seasonality in Pin has remained relatively similar across a 30 year time period (Fig. 6.3D), with infective larvae ($L3_h$) peaks occurring in late summer-autumn. This follows the summer period which is warm (average daily temperature between 6°C-11°C; Fig. 6.3A), has relatively high levels of precipitation (Fig. 6.3B) and the time of peak NDVI (Fig. 6.3C).

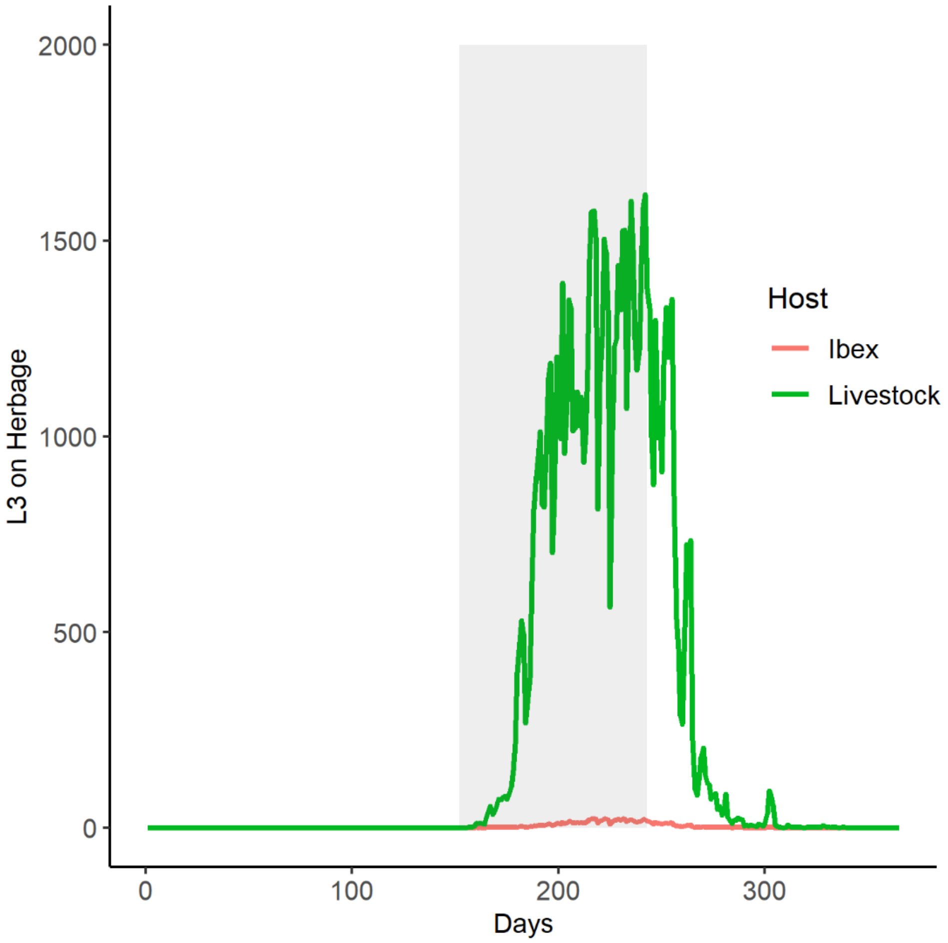

Figure 6.2. GLOWORM-FL model output (predicted number of infective nematode larvae, $L3_h$ per kilogram of herbage) arising from eggs shed by infections in Asiatic ibex (purple), migratory livestock (green) and combined total host population (pink). The x-axis is days with 1= 1st January 2019 and 365 = 31st December 2019. Shaded area (grey) indicates when the migratory livestock are present in Pin (day 152 – 243; 1st June – 31st August). *Note:* running the model for combined hosts (livestock and ibex) shows similar seasonality and summed magnitude We don't display it here as it is only slightly higher than the livestock only output.

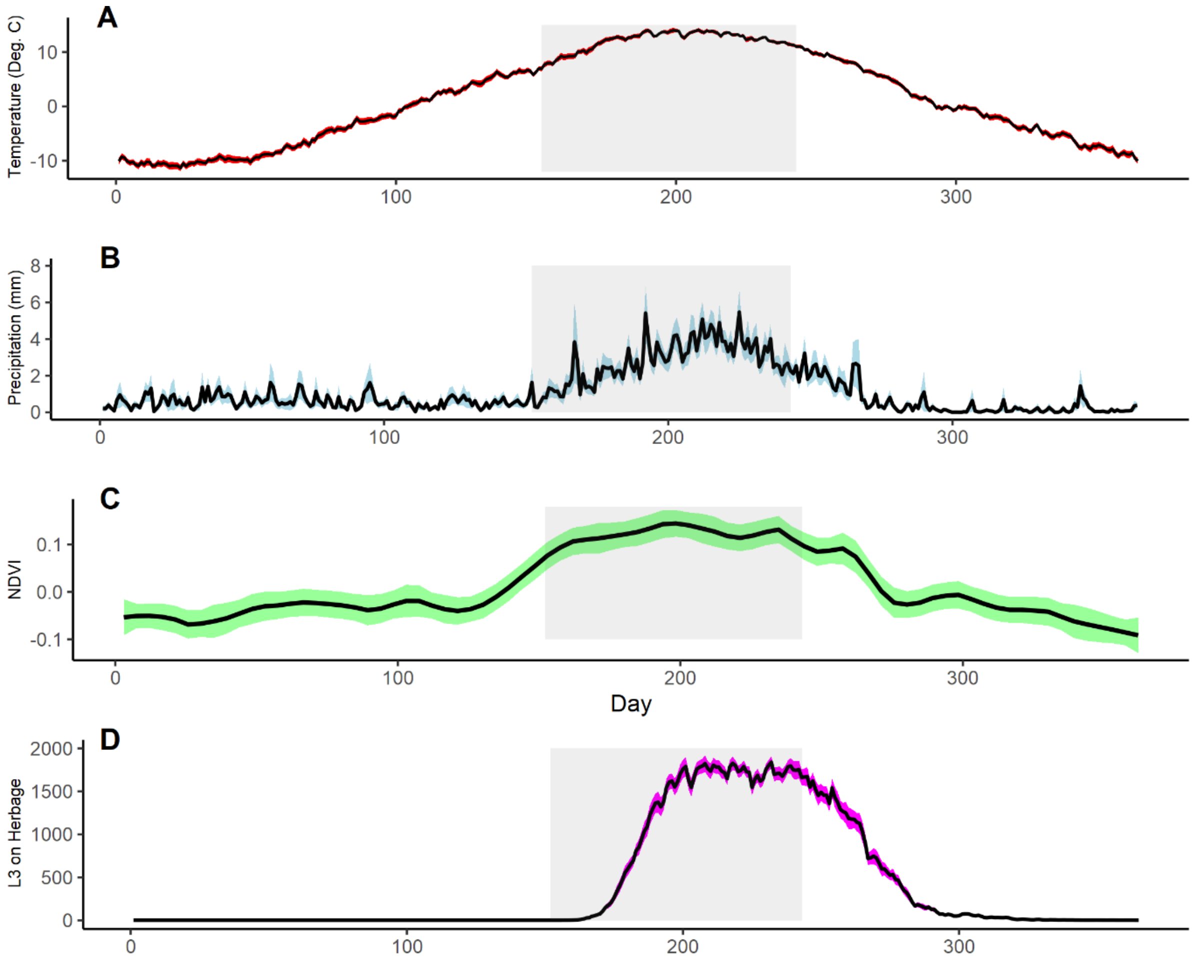

Figure 6.3. Panel graph for disease transmission dynamics in Pin. The x-axis for each graph is day with 1= 1st January and 365 = 31st December; day 200 is late July. **A:** Average daily temperature (°C). **B**: Daily precipitation (mm).**C:** NDVI in Pin. **D:** GLOWORM-FL model output (number of $L3_h$ per kilogram of herbage) arising from ibex and migratory livestock combined. Shaded colour band for each panel indicates the 95% bootstrapped confidence intervals using the 1990-2020 climate data set, and black line is the bootstrap mean. The grey shaded polygon indicates the time migratory livestock are present in Pin (day 152-243, 1st June-31st August).

6.3.2 Identifying optimum times and duration of intervention

The modelled GIN-control interventions in migratory livestock whilst they co-grazed pastures in Pin with ibex resulted in reductions in predicted infection pressure ($AUCL3_h$; Fig. 6.4). The simulation output had a clear peak in infection reduction for a 30 day intervention starting around day 194, suggesting that, given the constraints discussed above, the longer and later an intervention took place, the more effective it was. The peak represented a *c.*70% drop in infection pressure (i.e. $AUCL3_h$) compared to a no-intervention scenario, during the time livestock are present in Pin.

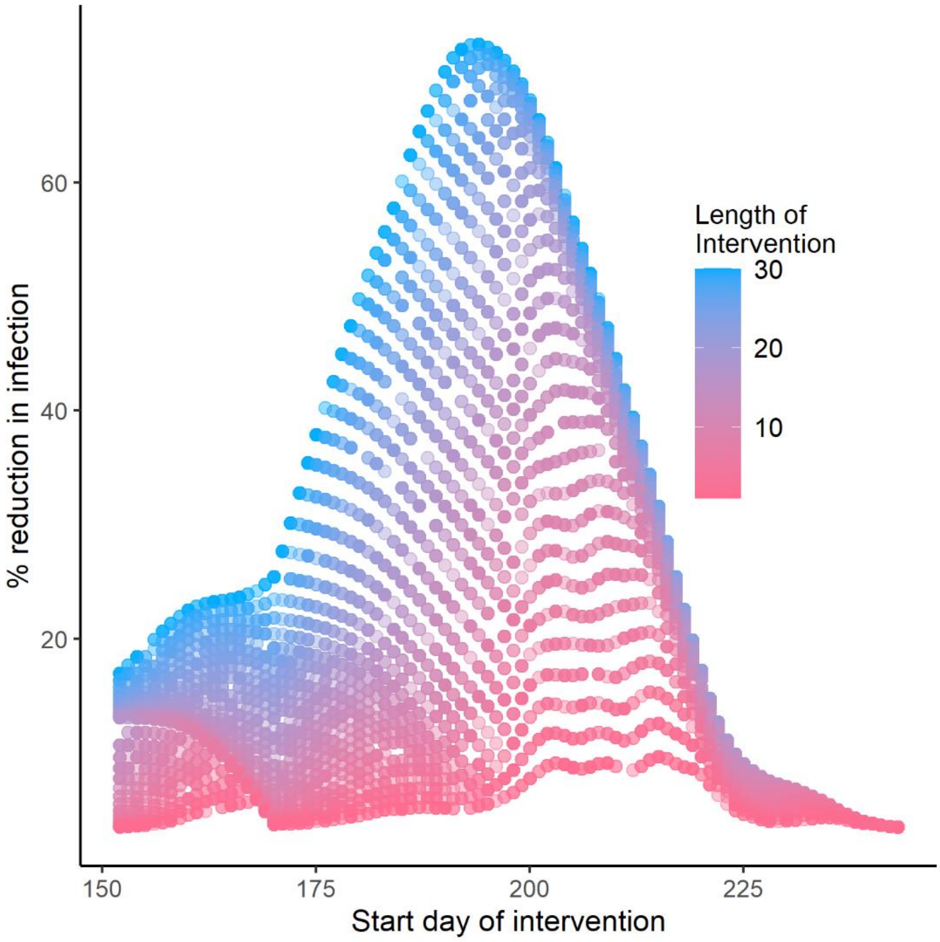

Figure 6.4. Simulation output showing the effect of start day of intervention in migratory livestock (x-axis), and length of intervention (legend) on % reduction in infection (measured as change in $AUCL3_h$), upon intervention, for the time period migratory livestock graze pastures in Pin (day 152-243; 1st June till 31st August). Please note the y-axis is a % reduction in infection, rather than lowest total pasture contamination for the season.

6.4 Discussion

We investigated disease transmission risk in an Indian trans-Himalayan multi-use landscape, where migratory livestock share pasture with sedentary Asiatic ibex on a seasonal basis. We had the dual aim of understanding the characteristics of the system with respect to parasite transmission and evaluating the effectiveness of potential interventions to align livestock and wild ungulate health.

6.4.1 Understanding predicted pasture infectivity and its potential consequences

Using the GLOWORM-FL model, we predicted that pasture infectivity peaks during the mid-late summer months when migratory livestock co-graze Pin pastures with ibex. Livestock, although using those pastures for merely three months, made a far greater contribution to pasture infectivity than ibex, primarily due to their higher density and significantly higher parasite burdens (Chapter 4; Appendix E, Table 1). Given pasture sharing at those times, this suggests the potential magnitude of parasite transmission from livestock to ibex is significantly higher than *vice versa*, whilst not precluding some transmission from ibex to livestock.

Although the model suggests that infection seasonality in Pin has remained similar for the last 30 years, there is reason to believe that the magnitude of infection pressure has increased, as migratory livestock numbers have increased in Pin valley since the turn of the 21st century, while ibex numbers have remained relatively stable (Ghoshal 2017; Chapter 4). We weren't able to model these trends as we don't have accurate time series information on both livestock and ibex numbers. Additionally, changes in climate into the future are projected to result in a hotter and drier climate across the Indian trans-Himalayas (eg. Li et al., 2016). Although warming temperatures can result in faster infective larvae developed and continued development into the autumn, drier periods can compensate for this by restricting development, particularly in the summer period (van Dijk et al., 2008).

Besides potential disease spill-over, there is evidence that the co-grazing of pastures, along with climatic changes, is resulting in increased exploitative competition for grazing resources between wild and domestic ungulates, and potentially increased pasture degradation in Pin (Bagchi et al., 2004; Ghoshal

2017; Chapter 4). This is of concern as livestock and ibex share the Pin pastures during a short period of vegetative productivity, which even at its peak is lower than other temperate grasslands of Asia (peak NDVI in Pin is *c*.0.1-0.2 compared to *c*.0.4-0.5 in other temperate grasslands, e.g. Liu et al., 2017). Degradation and resource competition could add to the problem of disease through nutritional stress, in turn exacerbating GIN impacts (Kock, 2004).

Moreover, pasture infectivity peaking in late summer suggests maximal transmission of GINs at this point, meaning that mature infections are carried over into winter. This has the potential to compromise host health in the harsh winter months; a time of year when ungulate body condition is often poor, particularly in the harsh environment of the Indian trans-Himalayas (Kohli et al., 2014). In Svalbard reindeer *Rangifer tarandus*, for instance, GIN infection was associated with poor body condition in winter and low fecundity in the subsequent year (Stien et al., 2002). However, more research is needed to understand the impact of GINs on body condition and fitness of ibex and livestock.

Additionally, the fact that the Pin pasture has a single broad peak of infective larvae on herbage ($L3_h$), is consistent with a "slow burn" system. Pasture infectivity in this system is governed by historical pasture use and gradual accumulated larval development during the summer. This seasonality in parasite transmission is likely to be driven by the modest fecundity of *Teladorsagia*, which is the GIN modelled in our study (in comparison to the more fecund *Haemonchus*), moderate temperatures (hence slow development), and low evapotranspiration, therefore a more prolonged impact of precipitation events on transmission (Morgan & van Dijk, 2015; Rose et al., 2015). This is consistent with other temperate regions, including landscapes from the trans-Himalayas (Chapter 5).

Finally, since we lacked information on GIN species composition, the transmission model was calibrated to *Te. circumcincta* as this species is well studied and has a climate envelope broadly similar to other species that are also common in sheep and goat in temperate and montane environments, such as *Trichostrongylus* spp. (Dhar et al., 1982; Jithendran & Bhat, 1999). Nevertheless, predictions may have been different for species like *Haemonchus* – although the harsh winter conditions and low annual precipitation of our study site do not favour *Haemonchus* life history (Anderson, 2000), so it is likely not to be present in significant numbers. We further assume that livestock and ibex are equally suitable hosts for the modelled GIN. Although a high degree of overlap in GIN species is expected (see Walker et al., 2015), this simplifying assumption probably ignores some degree of host specificity within a mixed species parasite fauna. More information on species composition in the Pin multi-host GIN system is needed, and could be generated using molecular approaches like ‘nemabiome’ deep amplicon sequencing (Avramenko et al., 2015).

6.4.2 Identifying optimum times and duration of interventions: Lessons learnt and future avenues

The simulation output suggested that a *c.*30 day treatment of migratory livestock in the last 30 days of their time in Pin valley was the most effective timing and duration of treatment to achieve the highest reduction in magnitude of infection (i.e. $AUCL3_h$) on pasture. Treating livestock at this time has the potential not only to reduce pasture infectivity which in turn reduces the infection pressure faced by ibex as summer transitions into winter, but also to lower GIN burdens in livestock as they undertake the strenuous migration back from Pin into Rupi. This is important because long-distance migration in domestic and wild ungulates come with heightened metabolic costs (Bischof et al., 2012), which can be exacerbated by endoparasites (Teitelbuam et al., 2018), potentially resulting in compromised body condition and fitness (Hughes et al., 2009).

The months spent by migratory herders in Pin are often the most productive in terms of their livestock gaining body condition (e.g. increased weight and size; Ghoshal, 2017) – traits that are favoured when livestock are sold for their meat (Saberwal, 1996). Upon returning to Rupi in autumn (*c.* September-October), the herders often sell several livestock, with the price of an individual being calibrated based on its weight. Therefore, treating livestock for a 30-day period just prior to their return migration, as suggested by our simulations, holds the potential of reducing GIN burdens in livestock and increasing the chances of retaining the body condition gained in Pin. This has the dual potential of ameliorating people’s food security while improving the income they receive from their flocks. Nevertheless, continual whole herd treatment has the potential to drive the development of anthelmintic drug resistance, which can also transmit to wild ungulates (Charlier et al., 2014; Barone et al,. 2020). Our simulation model could be used in future to test the effectiveness of treating a proportion of the livestock flock, by scaling reductions in faecal GIN egg outputs in the model, thereby lessening the selection pressure for anthelmintic resistance. However, the ‘optimal’ intervention time for treatment at 30 days prior to migration was based on the metric of maximal percentage reduction of pasture burden, rather than the lowest total pasture contamination for the season. It is arguable whether using the maximum percentage reduction would actually translate to lower infection levels in across the herds compared to treating earlier in the season and preventing pasture contamination from taking place. Given the complexities in such socio-ecological systems, it will be important to validate these model outputs with empirical on-ground interventions. A key next step could be to trial treatments in partnership with herders, where one treatment is done early in the season and another 30 days prior to the migration. Subsequently, livestock faecal output can be tracked and actual reduction in pasture contamination can be quantified to challenge our current model/simulation outputs.

Nevertheless, treating livestock during this period (i.e. 30 days prior to the migration) could also have significant benefits for ibex health and fitness. Studies offer evidence for parasite mediation of multiple life history trade-offs and support the value of considering life history investment, immunity, and parasitism simultaneously when examining the fitness consequences of disease (e.g. Albery et al., 2021). Reducing infection pressure during late summer into autumn has the potential not only to attenuate parasite-related negative health and fitness impacts during ibex rutting – usually the months of winter (Bhatnagar, 1997) – but also can potentially reduce over-winter parasite burdens, leading to improved fecundity (Albon et al., 2012). Importantly, a key research need is to investigate to what extent the magnitude, direction and level of infection cross-transmission is physiologically detrimental for the hosts, and how this may change with changes in climate and pasture quality – factors that interact in determining host health and fitness (Stringer & Linklater, 2014)

Finally, migratory livestock grazing has been considered to be one of the most important threats to ibex conservation across the trans-Himalayas (Ghoshal et al., 2017). Our approach to analyse potential interventions could be undertaken in other such landscapes within Himachal Pradesh and beyond.

Additionally, it could help predict and attenuate parasite infection in other multi-ungulate rangelands, whether they be ungulate communities consisting of several species intermittently sharing pasture as they migrate across the Mara plains (Ogutu et al., 2009), reindeer sharing pastures seasonally with livestock in parts of Scandinavia (Hrabok et al., 2006), or rangelands with non-migratory species exhibiting seasonal variation in host contacts. For example, white-tailed deer *Odocoieus virginanus* are known to have small annual home ranges, often overlapping with livestock, with seasonal variation driven by access to water and feed (Berentsen et al., 2014). The approach of collecting data using robust but feasible methods to parameterise models such as GLOWORM-FL, and then using these models to understand parasite dynamics and virtually trial interventions, is a powerful one that deserves to be widely implemented.

6.5 Conclusion

Using a robust modelling strategy rooted in understanding of system dynamics, we find that the Pin pastures face their highest GIN infection pressure during the months when the migratory *Kinnaura* flock co-graze its pastures with the resident ibex. We also find that treating livestock for around 30 days prior to their return migration in late summer to Rupi (autumn pastures) results in the greatest reduction in pasture infectivity. This can reduce GIN burden in both the domestic and wild hosts, with a range of benefits for both herder livelihoods and conservation. Beyond Pin, our study provides a transferable multi-pronged approach to investigating disease transmission risk in a multi-use landscape, including those with migratory hosts, and provides a scientific basis for interventions. This can serve the dual purpose of conserving wild ungulates and protecting herder’s livelihoods.

- Chapter 7 -

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Authors' contribution

This study was conceived by me, EJMG, NJS, SR and ERM. I and AS conducted the field work. HVR developed the GLOWORM-FL model and advised on its adaptation. RO developed and adapted the sensitivity analysis model. I analysed the data and led the writing. All co-authors contributed to the writing subsequently.

Two saiga females with their calves in Ural, Kazakhstan

Abstract

Contact between wild and domestic ungulates is increasing across rangelands, enabling disease co-transmission, whose management is difficult due to uncertainties in complex system behavior, lack of empirical data, and logistical and ethical obstacles to interventions. Working across a rangeland where critically endangered migratory saiga antelopes, *Saiga tatarica*, share pasture with livestock, we explored gastrointestinal nematode (GIN) transmission dynamics using a model parameterised from observed faecal nematode egg output and host numbers and distribution. The objective was to assess how GIN infection in saigas might be managed under current and future scenarios. Results showed that seasonal saiga migration leads to asymmetry in parasite transmission, with the majority of GIN acquired in their autumn and winter range from pastures contaminated by earlier livestock grazing. Consequently, intervening to reduce parasite burdens in livestock early in the season in these areas could disproportionately lower GIN cross-transmission to saigas. Similarly, early season GIN suppression in livestock in the saiga's spring and summer range was predicted to have less overall effect on parasite transmission to saigas, but would reduce infections in the critical calving period. These findings were robust under projected changes, negating the effect of increasing livestock numbers on GIN infection pressure. Climate warming predicted increased frequency of climate anomalies associated with saiga mass mortality events from bacterial infection, but independently of impacts on GIN transmission, which were marginal. Outcomes support better understanding and mitigation of factors affecting saiga health and rural livelihoods, using an approach transferable to other systems, particularly those with migratory hosts.

7.1 Introduction

7.1.1 Parasite transmission in co-grazed rangelands

Rangelands cover *c*. 40% of the earth's land surface and are grazed by livestock and wildlife (Asner et al., 2004). Climatic variations, ecosystem fragmentation and changes in livestock management practices are altering rangelands, with implications for the people and wildlife that reside there (Berger et al., 2013; Reid et al., 2014). Shared pasture use can also facilitate disease transmission, with potentially severe implications for wildlife health and conservation (Smith et al., 2009).

Among disease-causing pathogens, endoparasites - particularly Gastro-intestinal nematodes (GINs) - can determine health and fitness of wild and domestic populations (e.g. Gulland, 1992). Seasonality and climate change can affect GINs, as part of their life-cycle is completed outside the host. A mix of pasture characteristics and climate determine the development and survival of these free-living stages (Rose et al,. 2015). Host behaviour, and the density and diversity of hosts, also influence the probability of free-living stages encountering hosts (Morgan et al., 2004). Many GINs infect both wild and domestic hosts (Walker et al., 2017) and human interventions to control GINs in livestock can affect GINs in wildlife (Weinstein & Lafferty, 2015).

Investigating GIN transmission is especially hard, yet pertinent, in migratory ungulates across remote rangelands. The interactions between migration and parasitism are often complex. Escape from parasites is a proposed evolutionary driver of seasonal migration (Folstad et al., 1991). Yet, migratory hosts can have both higher (e.g. Koprivnikar & Leung, 2015) and lower (e.g. Altizer et al., 2015) levels of parasitism than year-round residents. Seasonal host movement can result in complex contact patterns, affecting disease transmission (Morgan et al., 2006; 2007). Working with migratory hosts in remote rangelands is associated with logistical, technical, economic and political challenges (Khanyari et al., 2021; Chapter 2). Consequently, many rangelands with migratory species are data-poor and it is challenging to estimate facets of GIN transmission, like seasonal and spatial variation in infective larval density (Morgan et al., 2005a).

Given the uncertainties of disease control directed at wild hosts, GIN management in shared rangelands is often focused on livestock (Kosmala et al., 2016). Nevertheless, trialling control options *in vivo* is difficult, expensive, and can be damaging to the hosts if infection intensity is high (Coles et al., 2006; Walker et al., 2018). Furthermore, *in vivo* intervention studies may not adequately capture variability in weather patterns over extended periods (Vineer, 2020). Therefore, using multi-host GIN models within a scenario analysis framework provides a useful virtual testbed for understanding parasite transmission dynamics and exploring the consequences of potential interventions. Scenarios are accounts of potential futures, creating a possibility space within which to explore the consequences of uncertainty (Peterson et al., 2003); their systematic exploration can anticipate future uncertainties regarding the interaction between people and biodiversity outcomes, in order to inform interventions (Bohnet & Smith, 2007). Scenario analysis can provide managers with evidence to underpin decisions, and researchers with testable hypotheses with which to advance understanding of system dynamics.

7.1.2 The case of migratory saigas in Kazakhstan

The majority of the world's critically endangered saiga antelopes, *Saiga tatarica*, inhabit Kazakhstan's rangelands across three populations – Betpak-Dala, Ustiurt and Ural. They undertake latitudinal annual migrations, driven by precipitation and vegetation green-up (Singh et al., 2010a). After the Soviet Union collapsed in 1991, saiga numbers drastically declined by >90% due to overhunting. Following a partial recovery, a Mass Mortality Event (MME) killed more than 200,000 individuals in the Betpak-Dala population in May 2015, representing 62% of the global population (Kock et al., 2018). Haemorrhagic septicaemia, a form of pasteurellosis, was implicated as the proximate cause, possibly linked to a climate anomaly (Kock et al., 2018). Livestock seemed to play a negligible role in this MME (Khanyari et al., 2021; Chapter 2). Another MME occurred in the Mongolian sub-species *S.t. mongolica* in 2016-17, caused by spillover of a virus, Peste-des-Petits-Ruminants-Virus (PPRV), from livestock, which killed a significant part of the saiga population (Pruvot et al., 2020a).

Livestock and saiga numbers are increasing in Kazakhstan, producing both a threat of disease spillover to saigas, and opportunities to understand shared disease drivers. Therefore, saiga conservation strategies need to consider disease (including MMEs) alongside threats like poaching, to ensure the continued viability of the species (CMS, 2015). MMEs are often associated with multiple stressors that can work solely or in combination (Kock et al., 2018). Pasteurellosis-related MMEs in saigas (in 1984, 1988 and 2015) were linked with high humidity and temperature, particularly around the time of mass calving aggregations (Robinson et al., 2019)

As well as bacterial and viral pathogens, saigas are infected by various GINs and their migrations have implications for GIN cross-transmission with livestock across their range (Morgan et al., 2007). GINs have been linked to pasteurellosis as a source and trigger in reindeer, *Rangifer tarandus* (Kummenje et al., 1976). A die-off in Chamois *Rupicapra rupicapra* from pasteurellosis was possibly exacerbated by GIN infestation (Posaultz et al., 2014). As mortality from pasteurellosis events is low in other species, it is plausible that the high death rate of saigas due to pasteurellosis MMEs in 1984, 1988 and 2015 was associated with the presence of other pathogens, possibly GINs (although Kock et al., 2018 found no evidence of this), or that GINs could exacerbate future MMEs, in combination with other factors, including environmental conditions. Moreover, there is evidence of GIN-induced immune suppression facilitating the invasion of diseases in wild ungulates (Ezenwa et al., 2010). Because the climate anomaly in 2015 involved elevated temperatures, which also tend to favour GIN development, we hypothesise that years in which an anomaly occurs will generate relatively high GIN infection pressure, which could contribute to MME aetiology and/or impair population recovery from such events.

Given this background, our primary aim was to understand GIN transmission dynamics in migrating saigas, focusing on the Ural population, which increasingly shares pasture with growing livestock populations. We assessed how GIN parasitism might change for saigas given the anticipated changes in their habitats, using scenario analysis. Lastly, we tested an intervention scenario to reduce GIN parasite transmission to migrating saigas. We focused on sheep and goats, which are most numerous on the rangelands, are taxonomically closest to saigas, and most likely to share parasites (Walker et al., 2017). Our work seeks primarily to support the understanding and mitigation of factors damaging saiga health. We do so by developing an approach that is adaptable to other shared rangelands globally.

7.2 Materials and Methods

Data collection aimed to assess the relationship between livestock and saigas based on seasonal overlap and potential GIN parasite cross-transmission in the Ural saiga population in Western Kazakhstan (2.1). Data on levels of nematode eggs in faeces in both hosts over time were collected and used to calibrate a parasite transmission model (2.2), which was then applied to explore effective intervention strategies (2.3) and to evaluate the consequences of changing habitat conditions for cross-transmission risk (2.4).

7.2.1 Study site and populations

We focused on the Ural saiga population in Western Kazakhstan (Fig. 7.1). Saiga habitat is primarily flat, treeless steppe in the north of the range, and semi-desert in the south, both characterized by hot and dry summers and extremely cold winters. Annual rainfall varies from 300mm in steppe to <250 mm in the semi-desert. Saigas migrate to summer grounds in the north and winter areas in the south, and aggregate for mass calving along their northward migration, in early-mid May (*c.*9th May - 22nd May).

Ural saigas decreased from 236,000 in 1991 to 26,400 in 2013, due to hunting following massive post-Soviet social change, but recovered to *c.*545,000 in 2021 due to better protection and economic recovery (ACBK official statistics, 2021). Livestock numbers and densities are currently recovering from an equivalent sharp post-Soviet decline across Kazakhstan, linked to economic collapse in rural areas (Kerven et al., 2016). With the dramatic recent increase in saiga and livestock numbers in Ural, concerns for potential resource competition are emerging (Satke, 2020). Given that livestock and saiga densities remain relatively low in the other populations (Khanyari et al., 2021; Chapter 2), saigas are much more likely to come into close contact with livestock in Ural, making it a relevant case study site and a test-bed for potential increases in ungulate populations in other regions. The Ural population also has a history of MMEs and GIN parasite overlaps between saigas and livestock (Bekenov et al., 1998). In 1984 pasteurellosis killed 73% of the population and similar mortality levels in 2010 may have been attributable to fog fever toxicosis (Robinson et al., 2019).

Livestock holdings in Kazakhstan, including Ural, can primarily be divided into two types; village-based and outlying farms. Village-based livestock predominantly use village lands (typically <3km around the village) designated for common use. Outlying farms are land parcels leased by private farms. We combine these two types of holding into a single livestock density figure.

7.2.2 What is the parasite infection pressure faced by migrating saigas?

Endoparasites in saigas and livestock – Faecal Egg Counts (FECs)

The density of GIN eggs in faeces was used in combination with host density to estimate rates of pasture contamination, and to seed climate-driven models of parasite development to predict the subsequent density of infective larvae on pasture over time. Parasite data collection was divided into two spatial compartments: a) the spring/summer saiga distribution and b) autumn/winter saiga distribution (Fig. 7.1). Calving occurs within the spring/summer compartment for a period of 2 weeks starting 9th May – date obtained from multi-year data upon which a median date for calving was estimated (Kock et al., 2018); results referring to the calving period are consequently a subset of outputs of spring/summer compartment. Calving is a crucial life history stage for saigas when females aggregate in large numbers in relatively small areas to give birth to calves over a short period (*c.*7-10 days), before migrating northward for the rest of spring and summer (Bekenov et al., 1998).

Data were collected during calving and early summer (5th May – 10th June 2019) for saigas and livestock in the spring/summer compartment and during rutting (10th December – 25th December 2019) for saigas and livestock in the autumn/winter compartment. As faeces could not be distinguished between sheep and goats they were aggregated and referred to as livestock. Samples were pooled at the level of the Ural saiga population for saigas and per sheep/goat herd for livestock, following Morgan et al., (2005b). A total of 155 pooled faeces samples were collected: 79 from saigas and 76 from livestock. We were interested in the faecal egg count (FEC) of strongyle nematodes as they adversely impact ungulate health and fitness and are inputs for the GLOWORM-FL transmission model (Rose et al., 2015). We used the mini-FLOTAC method (Cringoli et al., 2017) to estimate the abundance of strongyle nematodes, which uses sedimentation-flotation to separate nematode ova from the faecal matter which are then morphologically identified and quantified under a microscope (Appendix F – Faecal Egg Count).

Transmission model (GLOWORM-FL) to predict pasture infectivity over time

The GLOWORM-FL model is based on the life cycle of the free-living stages of trichostrongylid GINs (Equations 7.1-7.7) (Rose et al., 2015). It estimates parasite development rates from eggs in faeces, once deposited by hosts, to the third-stage infective larvae (L3), and their migration onto pasture, while accounting for simultaneous climate-dependent mortality at each stage. This results in an estimate of the number of L3 that are available for ingestion over time. Host faecal output (f) is multiplied by the host species density (D) and number of eggs per gram of faeces (FEC) to estimate egg output on pasture (E_{new}) on the sampling dates. E_{new} values were interpolated linearly between sampling dates to obtain daily time series, which were used as input for simulations at daily intervals. The development of L3 in faeces ($L3_f$) from eggs (E), via the pre-infective larval stages (L; Equations 2-4), is subjected to temperature-dependent stage-specific mortality rates (μ_i, where i corresponds to the life cycle stage) and development rate (δ). Upon accounting for a moisture-limited development success correction factor (C), overlapping nematode cohorts are tracked with newly deposited eggs (E_{new}) added to existing eggs.

A temperature- and moisture-dependent horizontal migration rate (m_1) is used to estimate the L3 migration from faeces onto pasture ($L3_p$). As $L3_p$ can be in either the herbage ($L3_h$) or the soil ($L3_s$), random bi-directional movement between soil and herbage was simulated with substrate-specific mortality rates (μ_4, μ_5), and a temperature-dependent vertical migration rate (m_2).

We ran the model in R version 3.6.3 (R Core team, 2020), using the “deSolve” package (Soetaert et al. 2010). The model output is the daily number of individual GINs per hectare for each life-stage, from which we calculate $L3_h$ per kg dry herbage (L3/kgDM) – referred as "L3 infective larvae" - by dividing $L3_h$ (equation 7) by the biomass of dry herbage hectare^{-1} (Eisfelder et al., 2017). The model was run independently for the two spatial compartments – spring/summer saiga distribution (Days 91-244 on a

365 day annual scale, i.e. 1st April – 31st August) and autumn/winter (Days 1-91 and 245-365 on a 365 day annual scale, i.e. 1st September – 31st March; Fig. 7.1), as that was the available saiga distribution data resolution. The magnitude of seasonal infection was obtained from the area under the curve of L3 abundance ($AUCL3_h$), by summing daily $L3_h$ per kg dry herbage values for the days that saigas spent in a given compartment. To parameterize the model, total GIN FEC were used as input (see 2.2.1) and host weights, averaged across sexes to account for sexual dimorphism (saigas and livestock) were obtained from Bekenov et al., (1998). Faecal output per body mass was assumed to be the same for both livestock and saiga (Moharrery, 2011; grams of faces per kg liveweight of wild/domestic host). To estimate onward development and survival rates of free-living GIN stages on pasture, we obtained daily temperature and precipitation average from 1000 randomly selected points within the two seasonal compartments – spring/summer and autumn/winter for the years 2000-2020 (POWER, 2020) (Appendix F - Climate data).

Model output was used to predict pasture infectivity, and to calculate changes to infectivity based on scenarios. The model was run for three host combinations: only saigas; only livestock; and saigas and livestock combined, to estimate the relative contribution of each host to pasture infectivity (Morgan et al., 2007). We used parameters for *Teladorsagia circumcincta* because this species tends to dominate in cool temperate areas, has similar responses to climate as other common genera like *Trichostrongylus* (O'Connor et al. 2006), and is found in both saigas and livestock (Morgan et al., 2005a). Details about the model can be found in Rose et al. (2015) and the parameters used are given in Appendix F, Table 1.

$$E_{new} = D(f \times FEC) \qquad (7.1)$$

$$\frac{dE}{dt} = -(\mu_1 + 2\delta)E + E_{new}C \qquad (7.2)$$

$$\frac{dL}{dt} = -(\mu_2 + 2\delta)L + 2\delta E \qquad (7.3)$$

$$\frac{dL3_f}{dt} = -(\mu_3 + m_1)L3_f + 2\delta L \qquad (7.4)$$

$$\frac{dL3_p}{dt} = -\mu_4\left((1 - m_2)L3_p\right) - \mu_5\left(m_2 L3_p\right) + m_1 L3_f \qquad (7.5)$$

$$L3_s = L3_p(1 - m_2) \qquad (7.6)$$

$$L3_h = L3_p m_2 \qquad (7.7)$$

Predicting pasture infectivity across the Ural rangelands

Figure 7.1 illustrates the likely dynamics of *Te. circumcinta* in Ural, which the model seeks to quantify. Saigas are in their spring/summer distribution in April-August, and spend September-March in their autumn/winter range. Livestock are sedentary and do not mix between compartments (Chapter 3).

Saigas shed eggs via faeces onto pastures in their spring/summer distribution (April-August). Given temperatures above the development threshold (O’Connor et al., 2006), these eggs develop into infective larvae on pasture (equations 1-7), subject to a lag between faeces deposition and appearance of infective larvae on pasture. Parasite eggs shed by saigas as they leave their spring/summer distribution are likely to infect pastures for some time following their departure, given the lag between egg shedding and pasture infectivity (Rose et al., 2015). Livestock occupy and shed eggs onto pasture via faeces in the spring/summer compartment year-round, assuming no housing in winter. Eggs shed in the winter months are unlikely to become infective larvae on pasture given freezing temperatures. They don't undergo hyperbiosis, hence all eggs on pasture in the winter are killed. Livestock eggs in this compartment are therefore likely to become infective larvae in the same months as eggs from saigas; albeit for an extended period of time given their continual pasture occupation (Fig. 7.1).

In their autumn/winter distribution, saigas shed eggs via faeces onto pastures in September-March. Low temperatures during this period, with precipitation predominantly in the form of snow, suggests eggs are unlikely to develop successfully to infective larvae on pasture. Eggs from livestock are likely to have similar dynamics as in the spring/summer compartment, for the reasons articulated above

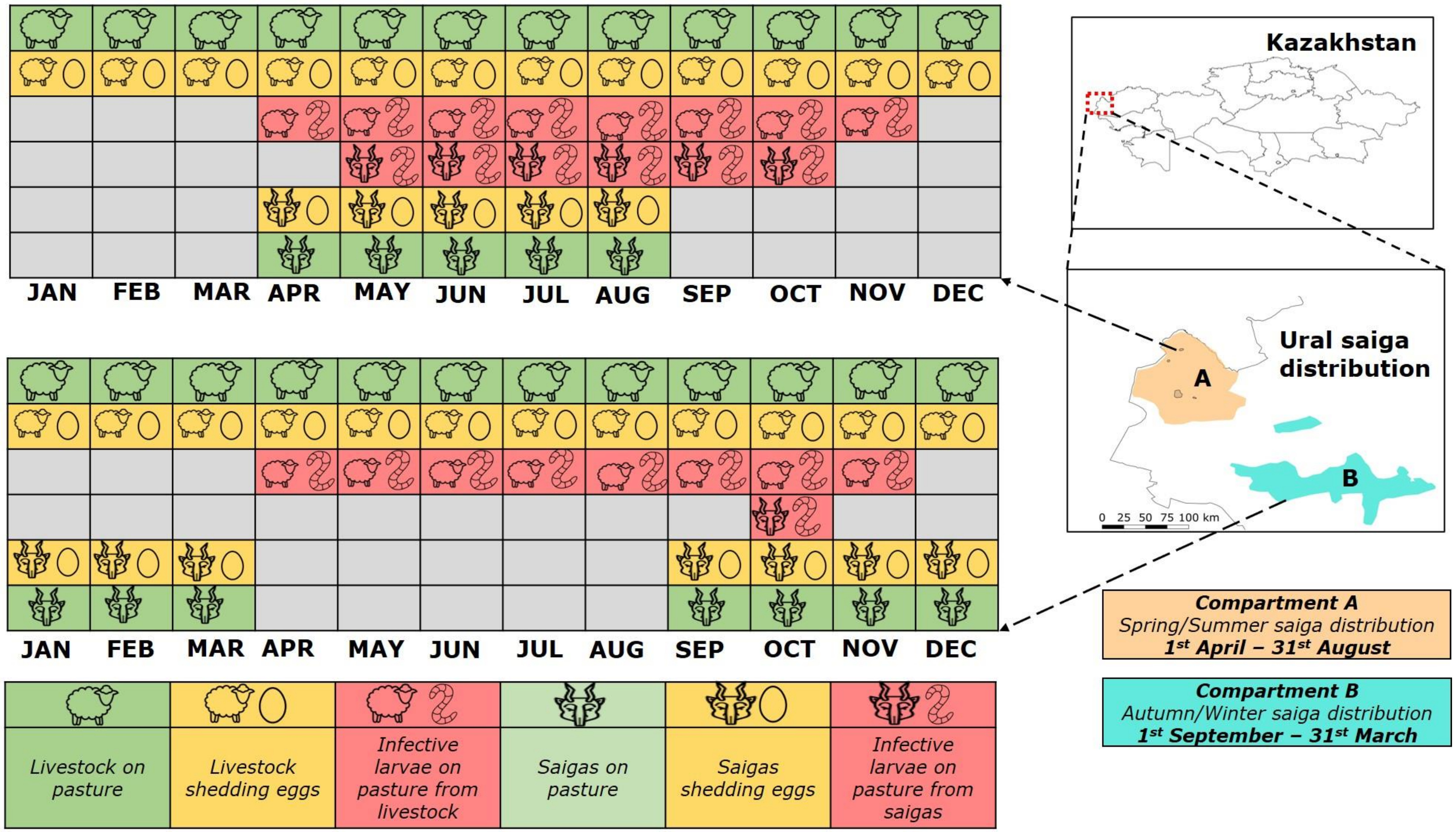

Figure 7.1. A schematic of the two-host parasite system in Ural, in the absence of intervention against parasites. Top map - location of the Ural saiga population in Kazakhstan, bottom map - seasonal distribution of saigas in Ural. Calving locations (small shaded polygons) are within the spring/summer saiga distribution. See text section 2.2.2 for detailed explanation. Icons courtesy of Noun Project.

7.2.3 Is early-season suppression a robust intervention strategy in our case study area?

Pasture use and egg shedding over weeks or months, along with development of those eggs into larvae during climatically appropriate periods, governs infective larvae on pasture in most temperate systems worldwide. Therefore, the most effective intervention against GIN populations in temperate systems is to treat animals with anthelmintics early in the grazing season, following commencement of conditions suitable for development. This "early-season suppression (ESS)" decreases parasite egg output that would otherwise ignite the system. By preventing egg shedding, pastures are kept clean for longer, fewer generations of nematodes are produced, and contamination by infective larvae is limited before the weather again becomes unsuitable for development (Morgan & van Dijk, 2012).

We tested the impact of ESS in livestock on the GIN infection pressure on saigas. Interventions were either prolonged housing or treatment with a persistent anthelmintic. These are equivalent in our models in that they both simply switch off egg supply for a determined period. We assessed reduction in infection potential as defined by the sum of available infective larvae ($L3_h$) per kilogram of herbage (i.e. $AUCL3_h$) when an intervention was applied, compared with a scenario of no intervention.

To test the potential effectiveness of ESS, we developed a sensitivity analysis following Oyanedel et al., (2021). We assessed the combination of intervention attributes that achieved the highest $AUCL3_h$ reduction, by varying the intervention start date (between day 1 - 1st January - and day 365 - 31st December), and the length of intervention (1 to 30 days). The maximum 30 day intervention length, derived from interviews with herders- was chosen as a realistic period over which livestock can be treated given the cost and limited availability of anthelmintic treatment (or, for housing, the additional feed costs given that grass is available on pasture). We then ran 10,000 GLOWORM-FL model simulations for each compartment, drawing random values for each run from the intervention attribute ranges. Results from each simulation were calculated as reduction in $AUCL3_h$ relative to no intervention for a given attribute combination.

To test the effectiveness of ESS over time, we ran the GLOWORM-FL model on climate data for the period 2000-2020 with no changes to FEC input into the model (i.e., no intervention) and with FEC input to reflect ESS for a month between 10th April and 10th May (i.e., intervention). This period was chosen based on the result of the sensitivity analysis above.

7.2.4 How could future climate change and livestock numbers affect infection pressure in saigas?

We assessed the impact of likely future scenarios developed based on the literature around the likely increases in livestock numbers and climate changes (Table 7.1). The baseline (business-as-usual) model was generated by running the GLOWORM-FL model on a 50 year simulated climate data set (temperature and precipitation). To generate the simulated "baseline" climate, we used climate data from 2000-2020. We used historical ranges to produce a mean and distribution for each date. For each day in the simulation, we selected values at random from the temperature and precipitation distributions to generate 50 baseline simulated climate data sets. For the climate change scenario, we repeated this but shifted the distribution by the mean predicted changes for temperature and precipitation, whilst maintaining the variance (Table 7.1 and Appendix-F, Fig. 1).

Additionally, years in which pasteurellosis-related MMEs occur in saigas, on average, have *c.*2.2 ˚C higher average minimum temperature in the 10 days leading up to calving (onset at 9th May), but non-significant precipitation differences (Kock et al., 2018). Given our simulations, we estimated how often this climate anomaly occurred under current ("baseline" climate) and future conditions ("climate change" scenario) as a proportion of simulated years (n=50 each of current and future). We tested whether years with a climate anomaly had higher infection pressure for saigas during calving than years without a climate anomaly using a t-test on $AUCL3_h$.

For the increased livestock scenarios, sheep and goat numbers were increased by 45% in each compartment (Table 7.1) and these new densities were used to estimate how many eggs are being shed onto the pasture by livestock, assuming similar infection levels to those measured.

To evaluate consequences of changes in livestock numbers and climate, alone or together, and with or without ESS, on GIN infection pressure in saigas, model-predicted $AUCL3_h$ were compared between scenarios. Scenarios with higher average $AUCL3_h$ values were considered worse. For all scenarios we also assessed the impact of ESS for each compartment, separately and together. We obtained 50 outputs with and without ESS, for each scenario, which were bootstrapped with replacement (10,000 iterations) to estimate means and 95% confidence intervals. Non-overlapping 95% confidence intervals were interpreted as statistically significant.

Table 7.1. Future scenarios for host numbers and climate in Ural, Kazakhstan, explored in the simulations. FEC = nematode faecal egg count.

Scenario	**Reasoning**
*Baseline**	Current host numbers and FEC inputs with the "baseline" simulated climate data (2000-2020)
Increased livestock	Sheep/goat numbers in the districts where saigas are found have seen an increase by *c*.45% in the past decade (Kazakh Statistics Bureau, 2020); a further 45% increase is assumed.
Climate change (temperature and precipitation)	Mean annual temperature is predicted to increase c. 0.9 °C by 2030. Precipitation is projected to decrease by c.2 % in December to May, with a c.1 % increase in June to November (Reyer et al., 2017; World Bank Climate Change Portal, 2021).

* livestock are assumed to be on pasture throughout the year.

7.3 Results

7.3.1 What is the parasite infection pressure faced by migrating saigas?

Migrating saigas enter their spring/summer distribution around day 91 (1st April), finding relatively uncontaminated pastures due to hostile conditions for survival and development of larvae over winter. However, over the course of their stay they are predicted to encounter high $L3_h$ levels, including rapidly increasing infection levels during mass calving (day 129-142, Fig. 7.2A) as conditions become favourable for larvae development and survival. Saigas (7.2B) and livestock (7.2C) both contribute to pasture infectivity in the spring/summer compartment although livestock contribute more. Total predicted infection faced by saigas in their spring/summer compartment was 7,680 $AUCL3_h$, while the total infection available in the spring/summer compartment over the whole year was 11,043 $AUCL3_h$. As saigas migrate to their autumn/winter distribution, they enter already-contaminated pasture (Fig. 7.2D). Here, pasture infectivity is almost entirely contributed by livestock that were grazing over the summer period (7.2F), with saiga contributions being negligible ($AUCL3_h$ <10) and confined to late September/October (7.2E). Because the total annual available L3 for the autumn/winter compartment was high, at 21,498 $AUCL3_h$, despite their late arrival the saigas encounter similar overall L3 levels as in their spring-summer range (7,547 $AUCL3_h$). This is because the autumn/winter compartment has higher livestock density (Appendix F, Table 1) and slightly warmer weather (Appendix F, Fig. 1), which favours parasite development. The infection pressure for saigas in the autumn/winter compartment is experienced between September (*c.* day 245) and rutting in December (*c.* day 340), after which the conditions become too cold, hence inhospitable for L3 larvae. In both compartments, the infective larvae on pasture are contributed predominantly by the livestock, as livestock densities are higher than those of saigas and their presence is permanent (Figure 7.2C,F).

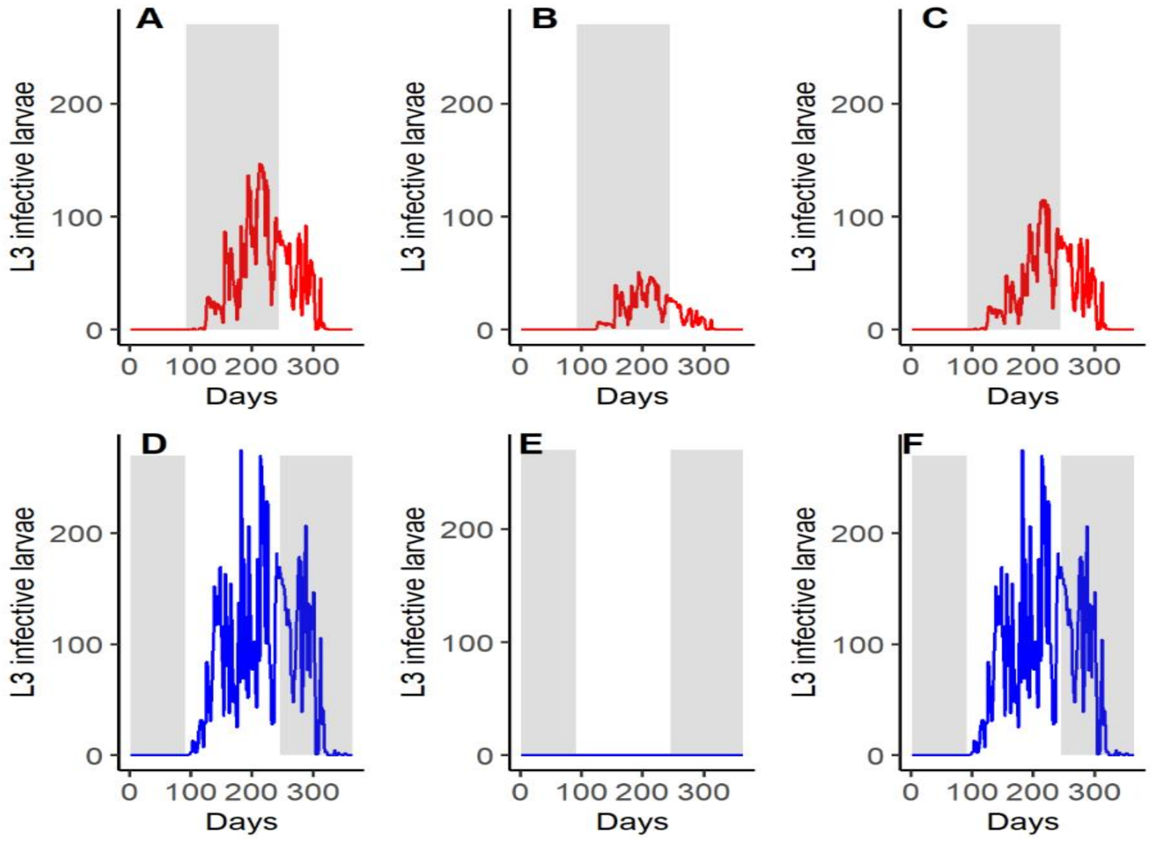

Figure 7.2. GLOWORM-FL output ($L3_h$ per kilogram of herbage) contributed by hosts in Ural in 2019. The x-axis: 1= 1st Jan. 2019 and 365 = 31st Dec. 2019. **A:** combined hosts in the spring/summer saiga distribution, **B:** saigas in the spring/summer saiga distribution, **C:** livestock in the spring/summer saiga distribution. **D:** combined hosts in the autumn/winter saiga distribution. **E:** saigas in the autumn/winter saiga distribution. **F:** livestock in the autumn/winter saiga distribution. Seasonal saiga presence is denoted by the grey shaded area.

7.3.2 Is ESS an effective intervention strategy in our case study area?

The simulation output based on the FEC data collected in 2019 and an average 50 years "baseline" of simulated climate data for both compartments, suggested that a c.30 day intervention (treating/housing) starting around day 100 was most effective. This corresponds to ESS (Fig. 7.3A,C). For a given day, the longer the intervention, the more effective, in both compartments. There is an optimal start date in both compartments, corresponding to a clear peak in attenuation at day *c.*110 in the spring/summer compartment and day *c*.100 in the autumn/winter compartment (early-mid April). Starting an intervention on or close to the optimal start date was especially important if intervention length was less than 30 days (Fig 7.3B,D). The maximum achievable reduction in infection for saigas was far higher in the autumn/winter compartment than the spring/summer compartment, as saigas are still actively contributing eggs to the pasture during the intervention in the spring/summer compartment.

Applying ESS - an intervention for 30 days starting on day 100 (10th April) - led to attenuation of infection in both compartments using climate data simulated from the period 2000-2020, although the magnitude of attenuation was far higher in the autumn/winter compartment (Appendix F, Fig. 2). The autumn/winter compartment had a more pronounced late-season small/secondary peak than the spring/summer compartment (Figure 7.2A and 7.D), which is probably due to the slightly warmer weather in this compartment (Appendix F, Fig. 1).

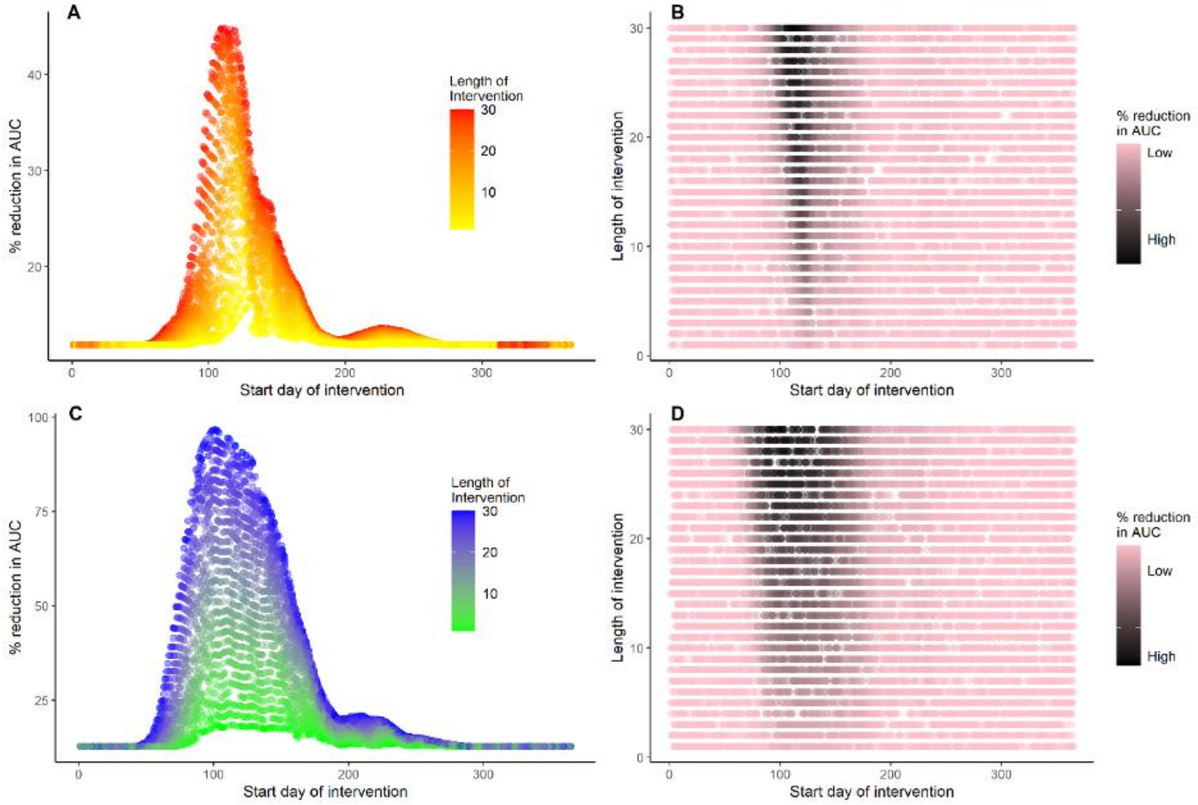

Figure 7.3. The simulation output for anthelmintic treatment in spring/summer **(A and B)** and autumn/winter (**C and D**) compartments of the Ural saiga distribution. For plots **A** and **C** the x-axis is

the start day of intervention on a one year scale (day 1 to day 365), while the y-axis is the % reduction in $AUCL3_h$ for a given combination of intervention length and start date. The colour of the points represents the length of intervention (days). Note that the y-axes are different for the two compartments, with a far higher $AUCL3_h$ reduction attained in the autumn/winter compartment. For plots **B** and **D** the x-axis is the start day of intervention on a one year scale (day 1 to day 365), while the y-axis is the length of intervention (1-30 days). The colour of the circles represents % reduction in $AUCL3_h$, with high (black) corresponding to >40% reduction in **B** and >90% reduction in **D.**

7.3.3. How is the parasite infection pressure likely to change with climate and livestock density?

In both compartments, most future scenarios involving increases in livestock led to predicted increases in $AUCL3_h$ experienced by saigas (Fig. 7.4 blue bars), whilst scenarios with climate change alone did not show a discernable trend (overlapping bootstrapped confidence intervals suggests no statistically significant difference from the baseline). Increased livestock alone caused the largest increase during spring/summer (statistically significant) (Fig. 7.4, Appendix F, Table 3). Increased livestock and climate change together caused the largest increase in $AUCL3_h$ during calving and autumn/winter, which is statistically significant. Overall, the climate change scenario caused a slight decrease (non-significant) in $AUCL3_h$ experienced by saigas, whilst increased livestock and increased livestock plus climate change caused a statistically significant increase (Fig. 7.4; Appendix F, Table 3).

Climate change simulations further showed that in future the probability of having a year with a climate anomaly correlated with MMEs in saigas will increase from 6% (3 anomalies in 50 simulated years) in the baseline climate dataset to 10% (5 anomalies in 50 simulated years). Nevertheless, years with a climate anomaly did not have significantly higher $AUCL3_h$ experienced by saigas during the calving period (Appendix F, Table 4).

ESS significantly reduced $AUCL3_h$ for all seasons and scenarios (Fig. 7.4, Appendix, Table 3). Within each compartment, ESS had similar impacts across all scenarios. Nevertheless, the effectiveness of the intervention varied substantially between compartments. It was highly effective (>80% reduction in *AUCL3*$_h$) for all scenarios in the calving and autumn/winter saiga ranges but only moderately effective (40-50% reduction in *AUCL3*$_h$) during the spring/summer distribution (Fig. 7.4 and Appendix F, Table 3). This is because saigas continue to contribute eggs during the period of amenable weather for larval development in the spring/summer distribution. However, in the spring/summer compartment, ESS had a proportionally higher impact on exposure of saigas to infection during the particularly sensitive time of calving, which occurs early within the spring/summer compartment, and hence arises largely from eggs shed by livestock and removed by ESS.

AUCL3$_h$ experience by the saigas was reduced by 31% on average if ESS was applied in one compartment only, comparted with 63% if implemented range-wide. ESS applied solely in the autumn/winter compartment was consistently more effective at reducing *AUCL3*$_h$ for saigas than solely in the spring/summer compartment. These outcomes were very similar for all scenarios (Appendix F, Fig. 3).

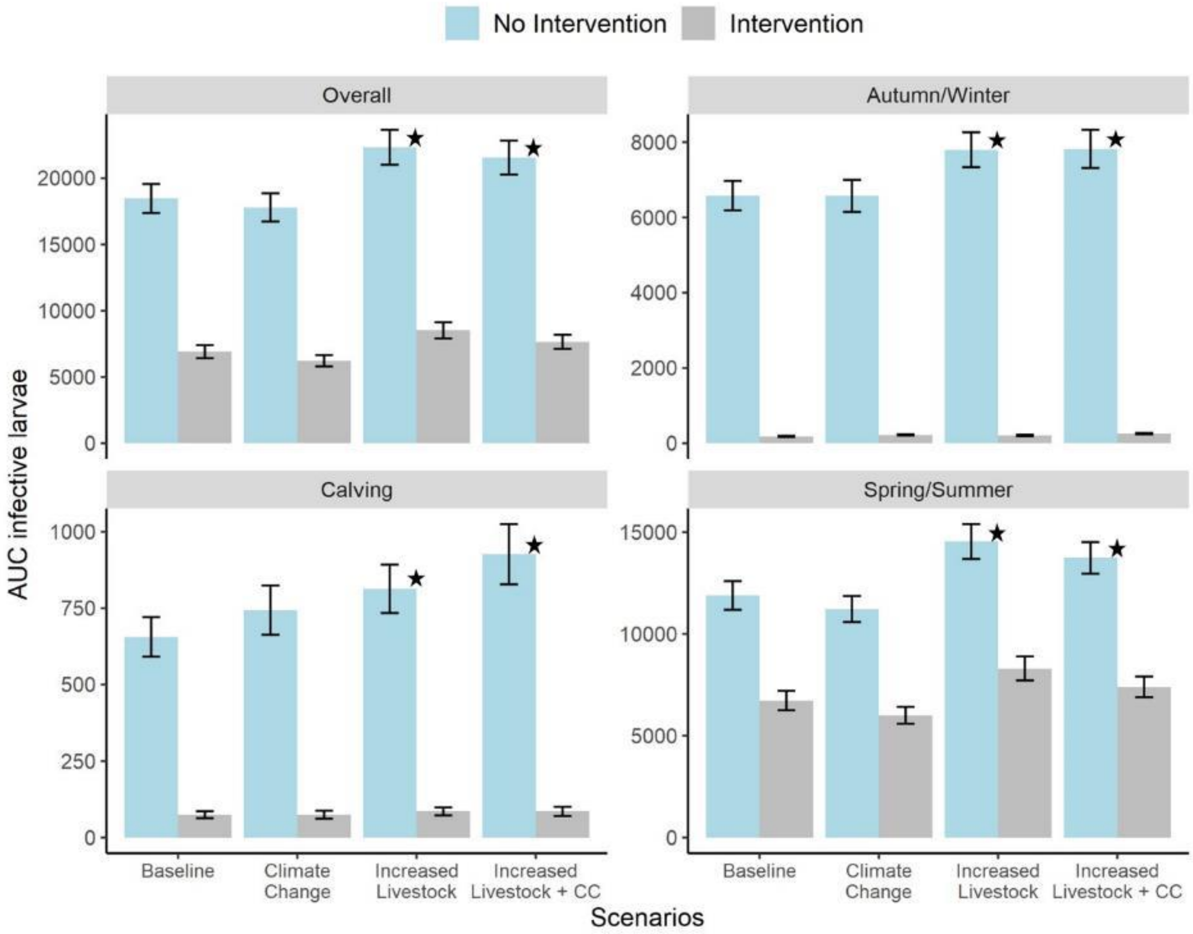

Figure 7.4. Panel graph displaying the mean *AUCL3$_h$* (i.e., area under the curve of L3 density, an index of infection pressure, see text) experienced by saigas (with simulated 95% confidence intervals) for four different scenarios: baseline (current conditions), climate change, increased livestock, and increased livestock plus climate change, with (grey) and without (blue) an early-season suppression intervention across the entire saiga range. The scenarios are split by compartments for (i) The entire saiga range (overall), (ii) Autumn/Winter, (iii) Calving (within spring/summer), iv) Spring/Summer. Blue bars with stars represent statistically significant differences relative to the baseline for that compartment. Overlapping 95% confidence intervals are interpreted as not being statistically significantly different.

7.4 Discussion

Our work investigated GIN transmission dynamics across the range of migratory saigas in Western Kazakhstan, whilst also assessing how GIN parasitism might change for saigas into the future and how this might interact with the risk of MMEs. We tested several potentially feasible combinations of intervention attributes to reduce GIN parasitism in saigas through ESS of eggs from livestock.

A key caveat is that we divide the saiga distribution into two seasonal compartments, although saiga migration is more nuanced. For instance, we do not model the saiga mass calving aggregations separately, despite mass calving leading to locally elevated densities in spring. This could be where heightened saiga-saiga parasite transmission occurs, as saigas usually aggregate away from livestock (Singh et al., 2010b). Additionally, saiga numbers are also increasing dramatically, but we focussed our scenarios on livestock trends. Models and simulations that incorporate broad- and fine-scale saiga population dynamics in space and time are required (Morgan et al., 2007). In the case of the autumn/winter range, higher saiga numbers would have minimal impact on the dynamics or levels of GIN infection in saigas, since most infection pressure here comes from livestock, but this might not be true for the spring/summer range or calving areas within it.

Nevertheless, we found through model simulations that saiga migration broadly resulted in saiga experiencing lower overall infection pressure ($AUCL3_h$) than if they remained in their autumn/winter range. The spring-summer range tends to be unusable in the winter due to deep snow (Bekenov et al., 1998). Migration can inhibit parasite transmission by reducing host availability (Altizer et al., 2011) and could be adaptive to avoid infection (Folstad et al., 1991). Whether this is true for saigas needs further investigation. Obstacles to saiga movement like infrastructural development are altering migration routes, sometimes resulting in sedenterization (Singh & Milner-Gulland, 2011), and could increase disease impacts. Given sharing of GIN parasite species between saigas and livestock, increasing livestock densities in the saiga range could also pose challenges to saiga health and population viability.

The changes in pasture infectivity predicted in the simulations could have direct effects on saiga worm burden, body condition, and fitness. Strategic anti-parasitic interventions in livestock that decrease exposure of saigas to infection could reduce these effects and have positive impacts on saiga populations. Assuming saiga herbage dry matter intake of 1.6 kg dry matter day^{-1} in summer (Bekenov et al., 1988), predicted L3 density on herbage (Fig. 7.2) might lead to *c.*160 L3 being ingested per saiga day^{-1}, on average. Over 6 months, assuming 50% L3 establishment rate in the host and neglecting adult parasite mortality, this would generate around 14,600 adult GINs. In naturally infected farmed reindeer and wapiti, no relationship between parasite burden and growth rate was detected at GINs burdens of 400-25,083 worms (Mackintosh et al., 2014). Cross-sectional correlations between GIN burden and body condition are, however, notoriously limited in wildlife (Irvine et al., 2006). Lack of such correlations can conceal delayed and negative impacts of parasites on fecundity, for example in wild reindeer (Albon et al., 2002). Sheep ewes subjected to experimental infection with 110,000 *Te. circumcincta* L3 produced 11% less milk relative to anthelmintic-treated controls, with lower milk protein and poorer body condition also observed (Cruz-Rojo et al., 2012); accumulated L3 ingestion by saigas using the above values would average 29,200 L3, much lower than the dose shown to negatively affect milk production in sheep, and perhaps unlikely to result in significant lactation costs. Conversely, Morgan et al., (2005a) found that parasite burden was negatively correlated with body condition in 6-month old female saigas in Betpak-Dala, at burdens less than 100 adult worms. The infection pressure predicted by our simulations could, therefore, have impacts on saiga fitness at current levels. The impacts of parasitism might be amplified in saigas in certain conditions or seasons; for example, poor body condition impacting survival through especially harsh winters (Bekenov et al., 1998), or reduced fecundity or milk yield impeding population recovery following MMEs. Until better information is available on the population consequences of GIN parasitism in saigas, especially experimental data on the effects on fitness parameters of parasite infection, it will be impossible to fully compare the benefits of proposed livestock treatments in support of saiga conservation, to alternative interventions.

Future scenarios with increased livestock suggested increased infection pressure on saigas. Historically, saigas shared vast areas with high livestock numbers with relatively limited disease consequences, although there were major Foot-and-Mouth Disease spill-over events in the 1970s, which were subsequently eradicated through livestock vaccination (Bekenov et al., 1998). However, this coexistence might be precarious into the future, with higher livestock and saiga densities likely to occur along with increasingly degraded pastures (Hu et al., 2020). This is likely to render saigas vulnerable to increased GIN infection and other shared pathogens. Illustrating this, the 2018/19 PPRV MME in

Mongolian saigas was exacerbated by the depleted state of their pastures due to high livestock densities (Pruvot et al., 2020a), and undernutrition is known to exacerbate GIN impacts in ungulates (e.g. Gulland & Fox, 1992).

Our simulations suggest that climate change alone may not discernibly change the GIN infection pressure faced by saigas. This could be due to the modest fecundity of *Te. circumcincta,* which is the GIN modelled here (c.f. the more fecund *Haemonchus contortus*), moderate temperatures (hence slow development; modelled here), and low evapotranspiration, therefore a more prolonged impact of precipitation events on transmission (Rose et al., 2015). While warming temperatures (as projected for Ural) can facilitate faster development of infective larvae and prolonged development into the autumn, drier spells can compensate for this by limiting development, particularly during summer (van Dijk et al., 2008). *Te. circumcincta* is present in saigas and shares climatic constraints on development and survival with related GIN species. It co-occurs with other GINs like *Marshallagia* spp. and *Nematodirus* spp. (Morgan et al., 2005a), which differ in ecology, seasonal transmission patterns and response to climate change, and expansion of the model to include those species could alter conclusions. Currently, however, knowledge of the vital rates of the free-living stages of those species is inadequate to replicate the modelling exercise presented here (Morgan et al., 2007).

Despite limited predicted impact of climate warming on GINs in Ural, into the future we predict higher likelihood of climate anomalies associated with pasteurellosis-related saiga MMEs (Kock et al., 2018). GIN infection in saigas did not vary between anomaly and non-anomaly years, perhaps because of rainfall constraints. MME are often associated with multiple stressors including highly transmissible infections and exposure to toxins or extreme weather, hence not all years exhibiting climate anomalies translate into MMEs (Fey et al., 2015). Regardless of the lack of a discernible change in GIN infection pressure in years with a climate anomaly, saigas calve at a time of year when GIN infection pressure is high (see Fig. 7.2). It is likely that GINs further stress individuals nutritionally and immunologically, particularly calving females (Gulland, 1992). This could have implications for saiga health and fitness, and may increase susceptibility to MMEs (Posaultz et al., 2014), as well as reducing fecundity and hence population recovery following an MME.

We found that ESS is likely to be effective and robust in attenuating GIN infections in saigas arising from livestock. Treating all livestock for a prolonged period of time (30 days in our simulations), however, can be expensive and could favour the development of anthelmintic resistance in livestock (Coles et al., 2006), which could also then transmit to saigas (Barone et al., 2020). An alternative method of reducing pasture contamination is to keep livestock housed in spring, but this is the period of increased forage availability and would probably be socially and economically unfeasible. When considering saiga range compartments separately, ESS had higher predicted efficacy on saiga infection when applied to livestock in the autumn/winter compartment than the spring/summer compartment. This is likely to be because during the time of intervention (April), saigas still contribute GIN eggs onto pasture which developed to infective larvae in the spring/summer compartment, unlike in the autumn/winter compartment where saigas are absent during most of the period suitable for GIN larval development. Applying ESS in the autumn/winter range therefore appears to have disproportionate benefits for saigas. However, more nuanced insights are needed. For example, suppression in the autumn/winter range could help reduce over-winter worm burdens in the host, which are known to affect ungulate body condition and suppress fecundity and calf weights in the subsequent year (Albon et al., 2002). Conversely, applying the intervention during spring/summer comes with the advantage of reducing infection pressure during the critical calving period. To guide decision-making, saiga conservationists could use disease risk prioritization frameworks to delimit times and locations of concern where intervention may be most effective on a range of different dimensions (e.g. Khanyari et al., 2021; Chapter 2). This aligns with the suggestions for migratory species in general that intervening where it matters the most is critical for cost-effective management (Singh & Milner-Gulland, 2011; Allen & Singh, 2016).

Alongside benefits for saigas, ESS has the added advantage of reducing infection in livestock, thereby ameliorating agricultural livelihoods. Such interventions, especially when leveraging awareness about the saiga’s ecological importance, may foster a positive attitude in the livestock owners towards wildlife conservation, creating “win-win” situations (e.g. Walker et al., 2018). This is especially crucial in Ural, where increasing livestock numbers are co-grazing increasingly degrading lands with a growing saiga population, causing negative perceptions of livestock owners towards saigas (Chapter 3).

Beyond saigas, our approach is transferable to other spatially-compartmentalised multispecies ungulate ecosystems. For instance, in the Makgadigadi Pans, Botswana, parasite transmission was similarly modelled as a combined process involving sympatric wild ungulates and livestock (Walker et al., 2018). Further nuance can be added by incorporating diverse life history and movement strategies exhibited by host species into the model. Lastly, disease transmission between wildlife and livestock is a global concern not only among ungulates, but also other host taxa. With appropriate adjustments to the parasite life-history models, our approach could be applied to other systems, such as brucellosis cross-transmission between Elk *Cervus canadensis*, Bison *Bison bison* and livestock in parts of North America (Rhyan et al., 2013) and to predict risk of cross-transmission in migratory taxa beyond ungulates, such as transmission of avian influenza in birds (Li et al., 2017).

7.5 Conclusion

We used modelling, informed by empirical work, to develop an understanding of GIN parasite infection pressure experienced by saigas across the Ural rangelands. Additionally, we assessed how infection pressure is likely to change into the future with increases in sympatric livestock and climate change. Lastly, we tested the effectiveness of ESS of GINs in livestock as a strategy for attenuating infection pressure for saigas. Our study provides a transferable multi-pronged approach to investigate current and future disease transmission risk in a multi-use spatially-compartmentalised landscape. Our holistic approach combines ecological and social knowledge to understand parasite transmission and provides a scientific basis for wildlife conservationists and animal husbandry managers to develop interventions. Appropriately-designed interventions can support herders’ livelihoods and improve the conservation status of wild ungulates.

-   Chapter 8 –

Discussion

A livestock herd trying to find pasture during the winter in the Indian Trans-Himalaya

8.1 Meeting the aims and objectives

8.1.1 Overview of lessons learnt from each chapter

My thesis aimed to ***investigate the impact of environmental and social factors on GIN transmission dynamics between interacting domestic and wild ungulate hosts, exhibiting varying spatio-temporal dynamics, in temperate Asian rangelands.*** By addressing this aim, I aimed to fill a major gap in empirical understanding of disease dynamics in this particular geography, and more widely for multi-host, spatio-temporally varying systems where controlling GIN disease is important both socio-economically and for wildlife conservation. This overarching aim was addressed by five objectives, whose connections to chapters, their field site and its spatio-temporal dynamic is displayed in figure 8.1 below.

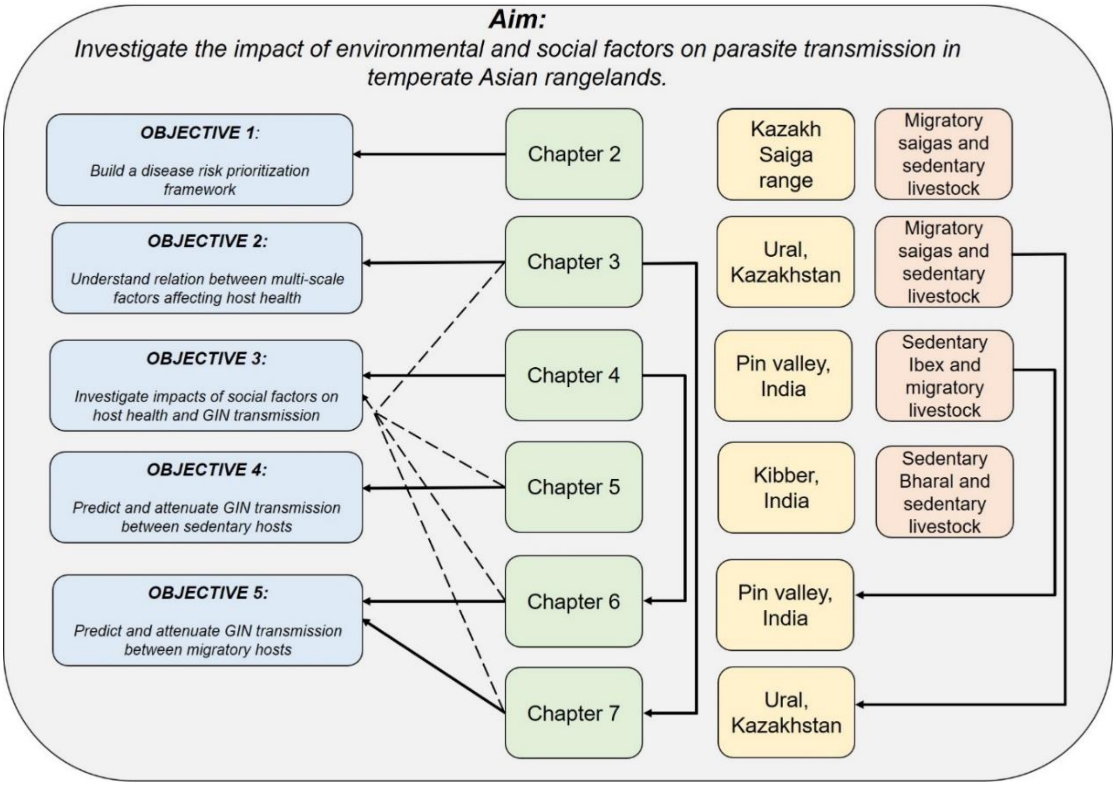

Figure 8.1 A schematic displaying the connections between different objectives (blue) and chapters (green), their field sites (yellow) and its spatio-temporal dynamics (red). Solid lines indicate direct connections, whereas dashed lined indicate partial connection (eg. a section of a chapter contributes to a certain objective). Note: Objective 3 permeated through all the subsequent chapters hence the dotted lines.

Objective one was to build a disease risk prioritization framework to assess disease spill-over risk from livestock to wildlife in mixed-use rangelands. This was achieved by ***chapter two*** where I built a three-step framework to assess disease transmission between wildlife (especially migratory life) and livestock, particularly in data-limited circumstances and across social-ecological scales. Within this framework, step one identifies diseases with transmission risk to hosts within multi-use landscapes. Subsequently, step two uses an epidemiological risk function to represent transmission-relevant contact patterns, using density and distribution of the host to map locations and time of disease transmission risk. Lastly, step three uses fine-scale data on livestock management and wildlife-livestock interactions to provide insights relevant to the local scale on disease risk. I applied the framework to characterize disease transmission between livestock and saiga antelopes *Saiga tatarica* in Central Kazakhstan. Step one identified peste-des-petits-ruminants (PPR) as posing a high risk of transmission from livestock to saigas, foot-and-mouth-disease (FMD) as low risk, lumpy skin disease as unknown risk and pasteurellosis and GINs as uncertain risk. Step two delimited regions having high disease transmission risk at different times of year. Step three aimed to assess the role of livestock in the 2015 saiga mass mortality event from pasteurellosis, concluding that it was likely minimal. Our case study demonstrated the value of combining ecological and social information to inform management of targeted interventions to reduce disease risk.

Because GINs include persistent free-living stages in their life cycles, indirect contact between hosts through shared pasture use (even at different times) supports transmission. The framework in chapter one is consequently of limited use in predicting the transmission risks of GINs between species. These parasites are ubiquitous, sensitive to climate, and have insidious impacts on host health; but predicting transmission requires spatially and temporally explicit approaches. The remainder of the thesis develops methodologies to address this more complex problem, while continuing to espouse the social and ecological factors relevant to disease risks which I articulated in chapters one and two.

Objective two was to understand the relationships between multi-scale factors affecting host health in rangelands. This was achieved by ***chapter three***, where I used the example of the Western Kazakhstan rangelands, home to critically-endangered saigas and livestock, to investigate relationships between ecological, social, economic, political and climatic factors that affect host health in mixed-use landscapes and act at multiple scales. I focused on Gastro-intestinal Nematodes (GINs) because they are transmitted between hosts that share pasture and affect ungulate fitness. Additionally, our framework (***chapter two***) indicated GINs to be of uncertain risk to saigas. Focusing on our case study, I find that a combination of factors may increase GIN prevalence and transmission: Veterinary services are limited; both saiga and livestock numbers are rising; and climate change is increasing farmers' dependence on co-grazed pastures for hay. I find that it will be key for saiga conservationists to engage in various complementary conservation interventions, with special care taken to evaluate and adapt them while considering rural livelihoods and livestock health. The outputs of ***chapter three*** provide researchers and practitioners with a means to improve understanding of complex inter-relationships and plan interventions within rangelands, considering host health from an interdisciplinary perspective.

Objective three was to investigate the impacts of social factors on host health and GIN transmission. This was primarily achieved by ***chapter four*** where I investigated the effects of herding practices on livestock health and disease transmission. I focused on GINs as they interact with nutrition, climate and host body condition. I worked with two pastoral communities, the migratory *Kinnauras* that visit the trans-Himalayan Pin valley in summers and the resident pastoralists of Pin valley. I found that GIN transmission between hosts is possible as the *Kinnaura* flock share pasture with ibex during their time in Pin, having significantly higher endoparasite loads than sedentary livestock, and the *Kinnaura* flocks are increasing in number. I also found that sedentary livestock are unlikely to transmit endoparasites to ibex as they rarely share pasture with ibex, have low helminth burdens and are low in abundance. Additionally, parts of ***chapter three*** (see previous paragraph) and ***chapters five, six and seven*** (see below) contribute to this objective as well.

Objective four was to model GIN transmission between sedentary ungulate hosts, through a socio-ecological lens, and evaluate the likely effectiveness of potential interventions. This was achieved through ***chapter five*** where I explored GIN transmission dynamics in Kibber through a socio-ecological lens. This was done by integrating information on the management of livestock health, a parasite transmission model with field surveys and local knowledge and also evaluated the plausible effectiveness of potential interventions. Livestock were predicted to contribute to more infective larvae on pasture than sympatric Bharal *Pseudois nayaur*. Simulations revealed that in Kibber, pasture infectivity is governed by historical pasture use that facilitates the gradual accumulation of larvae on pasture during the summer. Transmission did not have any distinct flash-point(s). Therefore, the most effective solution was to treat livestock early in their grazing season using ambient temperature as a trigger. Pausing egg inputs by a month at this time resulted in attenuation of infection pressure for both domestic and wild ungulates by 76%. This chapter provides a multi-pronged approach, one that incorporates social and ecological sources of knowledge to not only investigate GIN transmission, but also support herder's livelihoods and conservation wild ungulates; in a relatively tractable system with permanent host presence.

Objective five was to model GIN transmission between hosts displaying spatio-temporal movement, investigate likely changes in transmission dynamics due to socio-ecological changes in the system and evaluate the likely effectiveness of potential interventions. I achieved this objective by ***chapters six and seven*** wherein both chapters have largely similar objectives and structure, but are split between two study sites. ***Chapter six*** is based in Pin valley, i.e. the Indian trans-Himalaya and ***chapter seven*** is based in Ural, i.e. the Kazakh rangelands. I centred ***chapter six*** on investigating the dynamics of GIN parasitism and the potential for attenuation of infection in migratory livestock, with potential positive knock-on effects on the infection and health of sympatric Asiatic ibex. ***Chapter seven*** was set up to investigate GIN parasitism in migratory saigas and possible ways to attenuate parasite infection through intervention in sympatric sedentary livestock.

For ***chapter six,*** I investigated parasite transmission between migrating livestock and sedentary ibex using a population model. Sensitivity analysis was applied to virtually evaluate the best time and length of interventions (i.e. treating livestock with anthelmintics), informed by understanding of the constraints faced by local herders. The number of infective larvae on pasture contributed by migratory livestock was predicted to be orders of magnitude higher than that by Asiatic ibex. Although any amount of intervention in migratory livestock resulted in some reduction in infection pressure, we found a *c.*30-day intervention towards the end of the livestock's time in Pin to have the highest reduction in infection pressure, in relation to intervention length. Not only can this reduce parasite burdens and their consequent health impacts in migratory livestock – thus, having a likely positive impact on the herders' economic and food security – it can also benefit wildlife by reducing parasite transfer to sympatric ibex. The nuanced and contextual modelling done in ***chapter six*** was only possible due to the understanding of the system created by the predominantly descriptive ***chapter four.***

For ***chapter seven***, I investigated GIN transmission dynamics between the migratory saigas and sedentary livestock using a parasite transmission model and also virtually tested an intervention scenario to attenuate GIN infection pressure. Taking a step forward from ***chapter six,*** I used a scenario analysis approach to assess how GIN parasitism might change for hosts (saigas) into the future given the anticipated changes in their environment. I found that saigas experience comparable infection levels in their spring/summer and autumn/winter range, although migration out of their autumn/winter range results in them experiencing lower infection levels than if they were based there throughout the year. The scenarios of increased livestock numbers, and increased livestock numbers combined with climate change, resulted in increased infection levels for saigas, albeit with differences across their seasonal distribution. The scenario of climate change alone did not result in discernible change in GIN infection pressure, although warming was predicted to increase the frequency of spring temperature anomalies that were associated with outbreaks of pasteurellosis in saigas elsewhere, and hence could increase the impacts of parasites on saigas subject to coinfections. As in Kibber (***chapter five***), we found evidence through the model that early-season suppression is a robust strategy to attenuate infection pressure in hosts, across the scenarios investigated. This chapter provides new scientific understanding to support efforts to mitigate parasitism that can affect saiga health, while also having a positive impact on agricultural livelihoods.

8.1.2 Evaluating our results in light of existing parasite transmission theories

Although our work did not directly test the applicability of various theories/hypothesis relating to parasite transmission, chapter outputs do provide material that can be discussed in the light of previously available knowledge. Table 8.1 below aims to illustrate the contribution of the thesis to these existing theories/hypotheses, which were highlighted as relevant in Table 1.1.

Table 8.1 Contribution of the thesis to existing parasite transmission theories/hypothesis. Color corresponds to theme where green = host-scale, yellow = movement and blue = changes (see Table 1.1).

Theory/Hypothesis	***Knowledge gained through the thesis***
Population-level disease transmission	Throughout the thesis, we model disease transmission (*chapter five, six and seven*) at the level of the host (livestock and wild ungulate) populations. For instance, in the GLOWORM-FL model we incorporate host density and seasonal migration of hosts (as a unit – i.e. entire population migrating). This required extension of the existing model to account for the spatio-temporal complexities of mixed-use systems, especially when one host group is migratory. Knowledge of the impact of these factors, and availability of the refined model, will support a more nuanced consideration of parasite transmission in other similarly dynamic systems.
Individual-level disease transmission	Our disease modelling doesn't incorporate individual-level disease transmission. Nevertheless, there is evidence within the thesis to consider this nuance. For instance, in *chapter four,* it appears that goats rather than sheep might be more likely to transmit parasites to ibex, necessitating at least a species-specific nuance within the transmission model. The five-point checks illustrate parasites impact certain individuals of livestock more than others (*chapters three and four*) and as parasites are often clumped (Morgan et al., 2005b), this suggests these individuals might be disproportionately contributing

	to pasture contamination; which could consequently be disproportionally reduced by selectively treating more highly infected individuals.
Escape hypothesis	We find in *chapter seven*, that the migratory life-history of saigas results in them experiencing lower overall infection pressure than if they remained in their autumn/winter range annually. This lends support to this hypothesis, especially as the spring/summer range tends to be unusable in the winter given deep snow (Bekenov et al., 1998). However, the mechanism behind the potential of parasites to drive saiga movement needs further investigation.
Perturbation hypothesis	The scenario analysis in *chapter seven* indicated that perturbations like increasing livestock numbers will lead to increased parasite infection experienced by migrating saigas. However, perturbation doesn't lead to ubiquitous increase in parasite infection in our models, as seen by the fact that the climate change scenario resulted in no discernible change in GIN transmission. This suggests that in this, and possibly other systems, perturbations acting indirectly on parasite transmission via host population density or movement might be more important than climatic change.
Pathogen pool hypothesis	Our results don't directly provide information about this hypothesis. Nonetheless, there is evidence from literature that migrating saigas actually carry parasites from their southern range and infect livestock in their norther range; albeit in another population (Morgan et al., 2006). Additionally, as shown by Rose et al., (2016), parasite distribution is likely to be altered due to climate change, potentially exposing naïve hosts to novel infection pressure.

8.2 Weaving common threads between chapters: parasitism, wildlife conservation and pastoral livelihoods

8.2.1 Disease is a social-ecological concern, especially in rangelands

A social-ecological system (SES) is a combination of social and ecological actors and processes that influence each other in discernable ways (Ostrom, 2009). Through the course of each chapter we see that the temperate Asian rangeland sites have intricate interconnections between people, their livestock, wildlife and their collective social, political and ecological surroundings. Consequently, host health and disease management in rangelands is a social-ecological concern (Valente et al., 2020).

For example, Mogotsi et al., (2016) emphasized that complex social-ecological dynamics such as rampant cross-border livestock theft, illegal immigrants and livestock interactions with disease-susceptible wild ungulates on co-grazed rangelands are interacting with each other and hampering the control and eradication of FMD in Eastern Botswana. As a means forward in such a situation, multi-pronged policy considerations such as targeted FMD awareness campaigns, improving FMD risk assessments and collaborating on surveying and control strategies with neighboring countries are required. These policy intervention need to go beyond just the epidemiology of the disease causing agent – in this case the FMDV. Looking beyond FMD, Alexander and McNutt (2010), empirically show that human behavior influences infectious disease emergence at the human-animal interface, further advocating for the incorporation of behavioral theory models in disease mitigation.

More generally, while the aim of disease ecology is to study host-pathogen interactions in the context of their environment and evolution, Garine-Wichatitsky et al., (2021) argue that given the intricate interconnections between wildlife and livestock in rangelands, the emerging discipline of disease ecology is also relevant to ameliorating our understanding and management of diverse and complex wildlife-livestock interfaces globally. For instance access to resources, interspecific competition, and predation can shape contact patterns that could potentially drive disease transmission. Furthermore, there is a growing understanding of the importance of anthropogenic factors that shape wildlife-livestock-human interface, with pathogen emergence being particularly driven by changes in livestock husbandry and biodiversity conservation practices (Mishra et al., 2021). It is crucial to have interdisciplinary integration of ecological, biomedical, and social sciences (termed as “disease socio-ecology” by Garine-Wichatitsky et al., 2021) for improving the management of wildlife-livestock interactions.

In my thesis, a key innovation is the embedding of social-ecological awareness into disease models. Whilst this integration is limited in the literature to date, studies have alluded to its importance and need (eg. Morgan et al., 2004). Zooming into studies in parasitology, only recently are studies emerging which examine how herders respond to advice and change behaviour, which in turn impacts disease transmission. For example, Vande Velde et al., (2018) reviewed the current uptake of sustainable GIN control practices with a focus on the herder’s socio-psychological factors. Similarly, Charlier et al., (2016) suggest that combining economic assessments of GIN infections with a nuanced understanding of non-economic factors that can influence an individual’s decisions on animal health, can lead to more effective control strategies.

Zooming out beyond parasites, studies in various conservation sectors have linked social and ecological systems. For instance, Daw et al., (2009) link the social and ecological systems to conserve coral reef fisheries. They examined the relationships between human population density, socioeconomic development, reef complexity, and coral reef fishing condition in five countries within the Indian Ocean. They highlight that to sustain coral reef fisheries would require an integrated approach that combines creating protected areas alongside empowering local societies by building their capacity to address the complicated underlying causes of reef degradation. This example speaks of a larger paradigm shift in conservation, with the discipline seeing an increased push to incorporate the human dimension in species and ecosystem conservation; arguably converting the domain once described as conservation biology (Soule, 1985) into conservation science (eg. Bennett et al., 2017)

8.2.2 Issues of disease transmission often don’t occur in isolation

Throughout the thesis, as we worked across rangelands where wildlife shares space with people and their livestock, it became apparent that these ecosystems are products of various interactions that have manifold conservation implications for wildlife and livelihood implications for the people that call them home.

Increasingly degraded pastures – often due to resource competition between wild and domestic ungulates – can exacerbate parasite transmission due to various mechanisms including tighter contact patterns and loss of body condition (Martin et al., 2011). It would be wise to devise interventions that consider the interactions between disease transmission and resource competition, if the interventions are to be long-lasting and contextually appropriate (Williams et al., 2020). While there are examples of studies exploring these links from various rangelands around the world, particularly in Africa and Europe (Ferroglio et al., 2010; Martin et al., 2011; Sun et al., 2018), studies in temperate Asian rangelands have seen lesser integration of these ecological factors.

Thinking specifically for Ural, the issues of resentment towards saigas and poaching are perhaps amplified as a result of interacting concerns about disease and loss of rangeland productivity. Conversely, a veterinary intervention could lead to positive amplification – for instance vaccination which limits or eliminates disease transmitted from saigas to livestock can result in herders feeling less antagonistic against saigas, thereby promoting coexistence. However, to truly achieve a positive sentiment towards saiga while safeguarding livelihoods, there are several data gaps to be filled and then applied. For instance, there are no data on people's views of saigas and how they think they should be managed. There is limited information on sustainable hunting and how that can be intertwined into conservation and livelihood projects. All these things can be integrated into future studies to achieve an integrated management plan for the region, its species and its people (CMS - Sustainable use of saiga antelopes, 2021)

Moreover, there is a link between livestock density and GIN transmission, whereby more livestock using the same areas can contribute to both increased degradation related to resource competition and GIN transmission (Grenfell, 1992). Although the research in my thesis was not set up to evidence this specific link, further work could specifically address these issues. If co-existence of viable wild ungulate populations along with healthy livestock that support herder livelihoods are to be maintained into the future, it will be crucial for managers to proactively tackle interconnected issues of resource competition, disease transmission and pasture degradation. Tackling singular issues can have unintended consequences. For instance, a commonly used intervention in Trans-Himalayan India to reduce resource competition between livestock and wild ungulates is to set up reserves free from livestock grazing (Mishra et al., 2016). However, these reserves tend to be small, hence wild ungulates don’t solely use them. Therein, the concentration of livestock (often at orders of magnitude higher densities in this region than wild ungulates; Mishra et al., 2001) and, periodically, wild ungulates, in regions outside the livestock grazing free reserves can result in tighter contact patterns. This can facilitate, albeit unintentionally, parasite and disease transmission (Morgan et al., 2006).

Zooming out from disease, there are lessons to be learnt from the large literature on human-wildlife conflict and coexistence (eg. Redpath et al., 2015). Human–wildlife conflict refers to the negative interactions between human and wild animal that can lead to undesirable outcomes for people and wildlife (eg. Dickman, 2010) For instance, the community based natural resource management (CBNRM) programs across various countries in Africa, aims to achieve the dual goals of biodiversity conservation and improving rural livelihoods. Dressler et al., (2010) evaluated six case studies of CBNRM programs from around the world. While there were several nuances to consider, given the multi-pronged nature of CBNRM programs, they did provide an integrated approach towards ensuring social justice, material well-being and environmental integrity.

All of this collectively calls for looking at rangelands from a “One health” perspective. One Health is a collaborative, multisectoral and transdisciplinary approach, working at various levels (eg. local, regional and national), with the ultimate goal of achieving optimal health outcomes, whilst realizing the interconnections between people, organisms (domestic and wild) and their shared environment (Buttke et al., 2015) (Fig. 8.2). However, as seen from figure 8.2 there are various components to consider when operationalizing a one health approach. For instance, Machalaba et al., (2021) allude to the need for multidisciplinary and multisectoral approaches which require collaborations between sectors and organizations, synergising expertise to address complex health-related issues. Additionally, Destoumieux-Garzon, (2018) outline a list of training, research, political and economic barriers that need removing for effective application of the “One Health” approach. An example of one such barrier is the lack of communication and cross-training between human and veterinary medicine, agronomy and ecological, environmental, and evolutionary science.

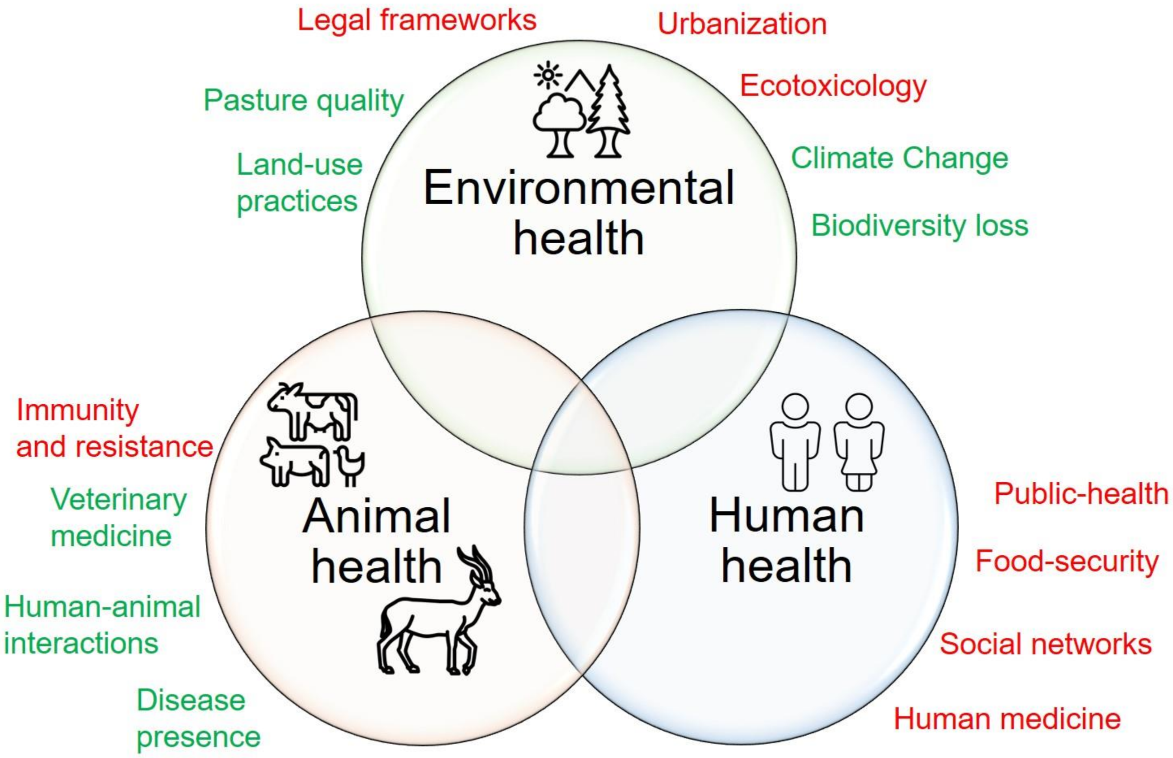

Figure 8.2. Figure displays the One health concept, with elements in green highlighting sub-components that my thesis addressed, whilst elements in red are sub-components not directly worked upon in my thesis. The aim of the figure is to show what is needed in order to set up a One Health approach and areas of further research need beyond my thesis. Please note the sub-components are indicative and not exhaustive.

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8.2.3 When considering GIN transmission dynamics, host movement matters

Understanding the role of wildlife and livestock in multi-host disease systems is complicated by varying ecological and behavioral attributes unique to the species in those systems, along with the dynamics of the natural and human systems within which they are embedded. All of this complicates modelling of disease transmission (Hassell et al., 2017). Particularly concerning GINs, for instance, even if livestock are a source of infection to wild hosts, the timing and extent of transmission will be governed by contact patterns. Seldom are these straightforward (Morgan et al., 2006). When contact between hosts is seasonal or sporadic, its timing is likely to be more important to the direction of disease transmission than relative levels of infection (Morgan et al., 2004).

A clear example of host movement affecting GIN transmission dynamics can be seen in ***chapter seven*** (also see Morgan et al., 2006). I find that even though saigas don't contribute infective larvae on pasture in their autumn/winter range, their movement out to their spring/summer range in April means they avoid the summer infection peaks (contributed to by resident livestock) in their autumn/winter range. This can be considered as a case supporting the parasite escape hypothesis (Table 8.1). However, more empirical and experimental studies are needed to elucidate the mechanism. For instance, Folstad et al., (1991), empirically show that high intensities of warble fly larvae *Hypoderma tarandi* cause post-calving migration in reindeer in Norway. Alternatively, Normandeau et al., (2020) show that migratory elk *Cervus canadensis* had higher parasite diversity, prevalence and intensity. Recent theoretical work suggests that parasites and pathogens could be drivers of partial migration, either as escape from infected areas or individuals, through loss of infected individuals during migration, or to promote recovery from infection when parasites cannot adjust to environmental changes that occur during migration (Altizer et al., 2011; Fritzsche McKay & Hoye, 2016; Shaw & Binning, 2016). Future work can attempt to test such claims for saigas, especially as changes in land-use and climate are altering and even limiting saiga migration (Singh et al., 2011).

To do so, there is value in using models as a hypothesis-generation tool, helping researchers to design focused and informative (efficient/tractable) experiments and observations (see Chapter 5), and achieving insights that might be out of reach without such guidance. For instance, quantitative models and simulations can aid in designing experiments of suitable power to evaluate hypotheses, with large enough effect sizes to differentiate between them. Any equation that aims to convert a process or relationship from a conceptual model to a quantitative one can be considered as an example of hypothesis generation (Hilborn & Mangel, 1997).

Even while using models as hypothesis-generation tool to understand parasite dynamics in rangelands, we still can't truly quantify the impacts of parasites on fitness of hosts using the current data. This is so because we can’t the map the realized health and fitness impact of parasite burdens from abundance of parasites alone. While is this is especially hard in wild ungulates, this issue is ubiquitous and extends to livestock (eg. Friesen et al., 2017) and host movement makes this even more complicated (Morgan et al., 2006). The consequences of negative parasite impacts on health might not relate simply to growth rate and farm fat price per kg livestock. Into the future, therefore, we need experiments on both systems to compare fitness to untreated controls; and for livestock better contextual understanding of what is meant and needed in relation to animal “health”, which is difficult when parasites are relatively unseen and unappreciated.

Moreover, Macpherson, (1992) suggests that transhumance movement in areas of the globe characterized by changing weather, for instance cycles of dry and wet climate, have evolved to escape wetter and hotter areas as parasite presence is either high or exclusively present in such areas. As an example, the Fulani pastoralists in West Africa move northwards away from tsetse infested areas, which build up during the warm and wet season to avoid drastic damages from *Trypanosoma spp.* infection (Ford, 1971). They move their livestock south again, during the dry season once the tsetse population recedes. However, if reasons beyond climatic variation - for instance loss of institutional and communal support for livestock herders - were to manifest themselves as limits on long-distance migration, maybe even leading to sedenterization, as seen in large parts of Central and South Asia (Weber & Horst, 2011), this might render traditionally transhumance societies increasingly vulnerable to disease threats. This will inevitably hamper local livelihoods**.**

These examples illustrate the fact that the relationship between host movement, GIN parasitism and its consequences, are often not linear and interact with various other factors resulting in complex net results on parasite burdens and hence host health and fitness (Gaillard et al., 2000). In this thesis, complex host movement patterns were successfully incorporated into parasite population models alongside climate, to predict infection patterns and the impacts of socially realistic interventions. Moreover, I showed that interventions in livestock can be calibrated to maximum effect by taking account of the consequences of complex host movements and climate for cross-species transmission, thereby protecting wild ungulates from infection and its consequences. While social and ecological considerations were included in model calibration and intervention design, it remains challenging to incorporate these more explicitly into parasite dynamic models, especially in a way that can be transferred to other systems. A key means to tackle this complexity is multi-sectoral collaborations, where people from different backgrounds provide insights which are integrated in order to tackle an issue (eg. Tomaselli et al., 2018 on using social and ecological knowledge to understand wildlife health).

8.3 Next steps: key shortcomings and avenues for future research

8.3.1 Frameworks for wildlife disease management in shared spaces with livestock

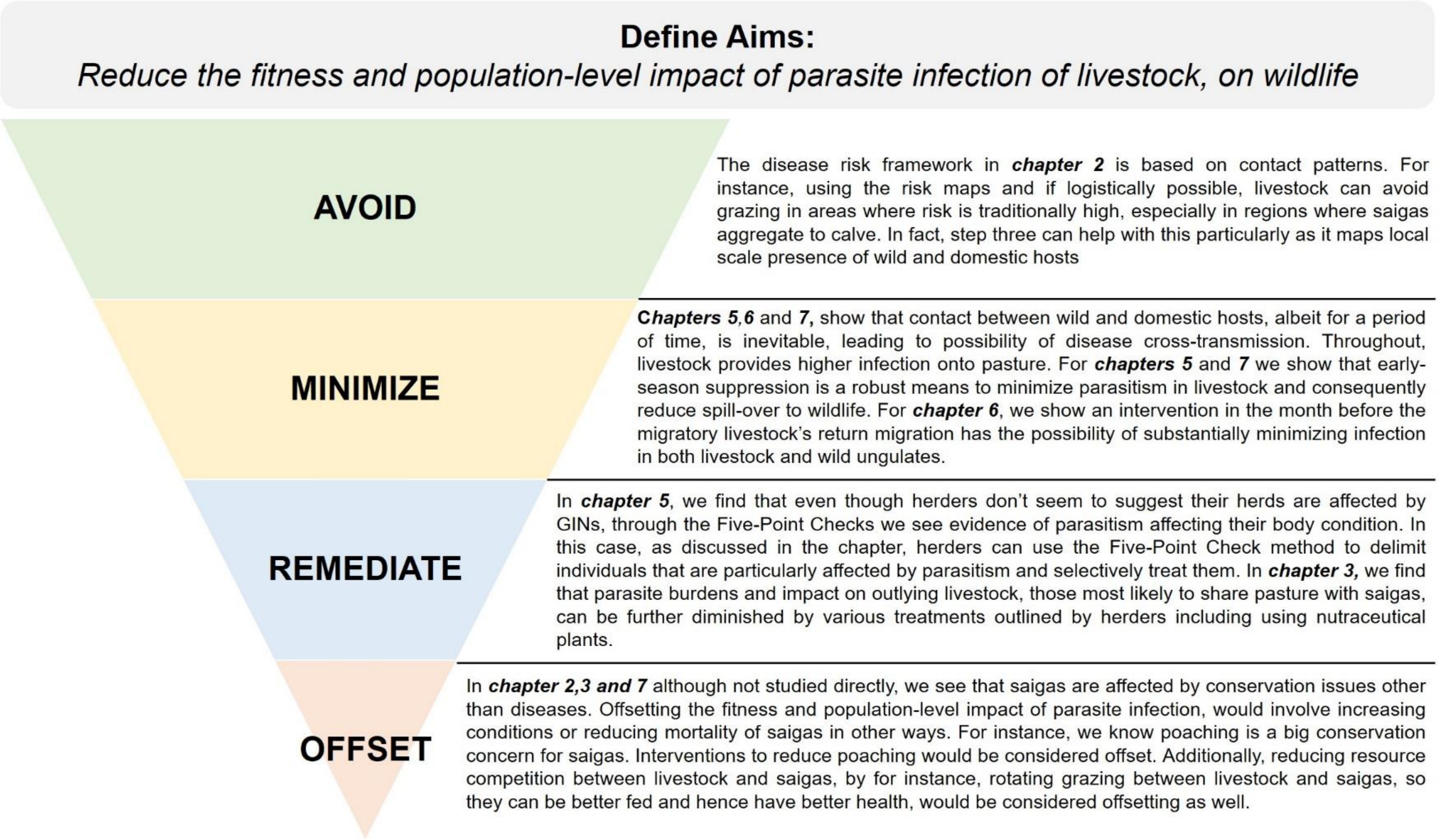
Considering the complexities and nuances of rangelands globally, along with the known negative impacts of disease transmission for wildlife conservation and livelihoods that are accelerating in the contemporary world, there is an urgent need for an overarching approach to helping stakeholders make decisions to reduce disease cross-transmission. A key component of this overarching approach needs to be its simplicity in interpretation for stakeholders of varied expertise so that it is actually applied. In conservation, an analogous field, frameworks have been developed not only to provide overarching guidance for planning and decisions support, but also featuring a variety of specific tools which can help support conservation planning and decision making (Schwartz et al., 2018). I took this approach when developing the framework in ***chapter two,*** which can help stakeholders assess and predict disease spill-over at management-relevant temporal and spatial scales in regions where livestock overlap in space with wildlife. However, Schwartz et al., (2018) caution that no one framework can be all-encompassing and highlight the importance of using multiple frameworks in concert to support decision-making. Different frameworks can be used for different aspects, for instance one framework can be used for conservation planning, while another for conservation implementation.

Linked to the above point, given that wildlife conservation and veterinary health management are often resource-limited domains, especially in remote regions such as where we worked, managers need to decide whether or not to intervene on health or other conservation-relevant aspects. Information can help to guide this decision. For instance, Value of Information (VoI) methods can be used to understand

and manage uncertainty from the view of the decision maker (Bolam et al., 2018). We know from the literature that knowledge about conservation issues and ways to mitigate them, doesn’t necessarily translate into action (Lauber et al., 2011). This translation into action is often hindered by the availability of resources and time (McDonald-Madden et al., 2008). It is unrealistic to expect every conservation and animal husbandry issue to be considered and acted upon. Prioritization tools and frameworks can be used to delimit the issues that needs most urgent consideration. If disease impact is not contextualized within the varied impacts occurring on species and within an ecosystems, stakeholders may hit a blind spot.

Acknowledging these challenges and opportunities, the mitigation hierarchy (MH) could be a framework for holistic, risk-based management of disease transmission between domestic and wild hosts. The MH is essentially a step-wise, precautionary approach initially developed to reduce the negative impacts of economic development on biodiversity (Arlidge et al., 2018). It has subsequently been translated to management of marine fisheries and bycatch mitigation (Booth et al., 2020). Typically, the MH proceeds in four sequential steps: i) avoid, ii) minimize, iii) remediate and iv) offset, in order to achieve a specified – if possible quantitative – goal for a specific target issue (see figure 8.3). Considering these steps from the perspective of disease transmission, the first step (*avoid*) would involve avoiding any interactions that could lead to disease cross-transmission (e.g. through separation of livestock and wildlife). The second step (*minimize*) involves reducing the extent or impact of disease transmission in the affected populations even though some probability of cross-transmission exists (e.g. through improving condition of potentially affected individuals so they are more able to cope with disease). The third step (*remediate*) involves remediating the negative impact of disease on individuals and therefore populations, following cross-transmission (e.g. through treatment). Lastly, the fourth step (*offset*) requires that any residual negative impacts of disease are compensated for. In this case this could be actions which enhance fitness of individuals separate from disease (for example through reducing neonatal mortality with better postpartum care for livestock or less disturbance for wildlife). And the overall goal which managers aim for might be that disease transmission does not lead to an overall decline in livestock productivity or wildlife population size (equivalent to the common "no net loss goal" that the MH often supports).

Through figure 8.3, I show how results from different chapters can be used under the MH framework to provide stakeholders (in our case wildlife conservationists and livestock managers) with avenues to make on-the-ground decisions, ultimately reducing disease transmission and its associated impacts. Zooming out, for effective disease management planning and decision-making in a landscape, our framework in ***chapter two*** can help delimit areas and times of disease spill-over risk, while the MH can subsequently help think through the type of interventions can be used to achieve reduced negative effects of disease of livestock in wildlife. Therefore, when used in tandem, these frameworks can enhance conservation planning, decision making and management of disease transmission at the interface between livestock and wildlife.



Define Aims:

Reduce the fitness and population-level impact of parasite infection of livestock, on wildlife

AVOID

The disease risk framework in ***chapter 2*** is based on contact patterns. For instance, using the risk maps and if logistically possible, livestock can avoid grazing in areas where risk is traditionally high, especially in regions where saigas aggregate to calve. In fact, step three can help with this particularly as it maps local scale presence of wild and domestic hosts

MINIMIZE

Chapters 5,6 and ***7,*** show that contact between wild and domestic hosts, albeit for a period of time, is inevitable, leading to possibility of disease cross-transmission. Throughout, livestock provides higher infection onto pasture. For ***chapters 5*** and ***7*** we show that early-season suppression is a robust means to minimize parasitism in livestock and consequently reduce spill-over to wildlife. For ***chapter 6***, we show an intervention in the month before the migratory livestock's return migration has the possibility of substantially minimizing infection in both livestock and wild ungulates.

REMEDIATE

In ***chapter 5***, we find that even though herders don't seem to suggest their herds are affected by GINs, through the Five-Point Checks we see evidence of parasitism affecting their body condition. In this case, as discussed in the chapter, herders can use the Five-Point Check method to delimit individuals that are particularly affected by parasitism and selectively treat them. In ***chapter 3,*** we find that parasite burdens and impact on outlying livestock, those most likely to share pasture with saigas, can be further diminished by various treatments outlined by herders including using nutraceutical plants.

OFFSET

In ***chapter 2,3 and 7*** although not studied directly, we see that saigas are affected by conservation issues other than diseases. Offsetting the fitness and population-level impact of parasite infection, would involve increasing conditions or reducing mortality of saigas in other ways. For instance, we know poaching is a big conservation concern for saigas. Interventions to reduce poaching would be considered offset. Additionally, reducing resource competition between livestock and saigas, by for instance, rotating grazing between livestock and saigas, so they can be better fed and hence have better health, would be considered offsetting as well.

Figure 8.3. A schematic displaying the applicability of the mitigation hierarchy to reducing impacts of parasite infection of livestock on wild hosts using examples from the chapters. Note that the aim here is general reduction of parasite infection– rather than a specific quantified reduction, which is what would normally be required in a mitigation hierarchy context; the specific target is best agreed in a participatory and consultative manner (Milner-Gulland et al., 2021).

8.3.2 Key shortcomings of the thesis and opportunities

Working through the thesis has revealed several key shortcomings that need to be made explicit, not only to ensure we interpret the results with caution, but also delimit future avenues for continued research.

Firstly, none of our studies incorporate eco-immunological dimensions. It is increasingly recognized that disease presence and magnitude are not the sole determinants of disease expression and impact (Martin et al., 2011). For instance, studies show that natural ecosystems may have a stable level of endemic disease which reduce disease expression (Martin et al., 2011), raising questions of whether disease control is constructive or not, inherently linked to the question of what the optimal ecological condition is for a mixed system of livestock and wildlife (Stringer & Linklater, 2014). The question to then unpick is whether a moderate and regular exposure to livestock parasites is more positive for wild ungulate health and fitness than intermittent extraordinary exposure, which may well cause disease outbreaks. This presupposes that immunity is effectively acquired and serves to attenuate parasite impacts, for which evidence for GINs in saigas is mixed (Morgan et al., 2005a). With perturbations like climate change in these landscapes, the threat from emerging infectious diseases and sporadic spill-over (including GINs), especially from poorly managed livestock populations vectoring disease to wildlife, becomes increasingly real (Kock, 2014). If hosts survive this initial effect, they might adapt to new climatic and/or land-use regimes. However, the level and frequency of exposure will be key. For instance, evidence from Rift Valley Fever outbreaks, which occur once in a decade in an ecosystem, is that wildlife and livestock suffer equally suggesting that immunity and/or adaptation isn't enough at the decadal time-step (LaBeaud et al., 2008). A linked line of research would be to consider the relationship between ecosystem resilience and disease expression. Research on PPR shows that susceptible species in resilient healthy ecosystems are infected but do not express disease, whilst the same or phylogenetically closely related species in unhealthy ecosystems suffer severe disease and mortality (see Fine et al., 2020 and Pruvot et al., 2020a for PPR outbreaks in Mongolia saigas which seemed to exacerbated due to poor body condition due to low levels of pasture quality). This is important for GINs as they are generally ubiquitous and interact with host nutrition. Based on this, a crucial next step in research extending from the thesis would be to assess if GIN burdens differentially impact host fitness in landscapes differing in their quality and quantity of forage availability, levels of pasture degradation and levels of epidemic diseases of other types.

Furthermore, throughout my thesis (particularly in ***chapters five , six and seven***), while we model pasture infectivity, we are unable to map the impacts of infectivity on actual parasite burdens within hosts and consequently the health and fitness impact of those burdens. There is a need to model the parasitic stage of GINs (Vineer et al., 2020), complementing GLOWORM, which models the free-living stage of GINs. This would allow us to quantify the translation of infective larvae on pasture to adult worm burdens within hosts, from which we could better infer impacts on health and fitness. For instance, Vineer et al., (2020) developed a flexible framework to simulate the population dynamics of the parasitic phase of gastrointestinal nematode infecting grazing livestock. While this has been applied only to livestock farms in Europe, there is a possibility of extending this to other multi-species ecosystem globally, after experimental studies are used to parameterize the model to the parasite species of concern in those landscapes. There is also the possibility of using this model to facilitate research into alternative parasite control strategies including vaccine development and novel treatment approaches, and to understand GIN epidemiology influenced by climate change and differential host management. Besides as applied throughout the thesis, we run GLOWORM-FL model parameters for well-studied parasite species (*Teladorsagia sp.*) when others might be more important and behave very differently in the species and system we are concerned with (eg. *Nematodirus sp.* undergoing hypobiosis in winter within saigas).

Coupled with this, experimental manipulation of adult worm burden in captive wild hosts – done with all critical ethical considerations – can help explicitly map the impact of worm burdens on host health and fitness. While models can be extended to whole-GIN life cycles using observational datasets (eg. Morgan et al., 2006; ***chapters five, six and seven***), extending them to predict impacts on fitness parameters will need experimental support. Even where this exists in sheep and cattle, the models get complex and sometimes researchers have to make heuristic compromises (Berk et al., 2016). There is a grave paucity of such experimental studies, primarily due to the logistical challenges of carrying them out. For instances Albon et al., (2002) implanted slow-release anthelmintic boluses in 1994 over winter in Svalbard Reindeer and then followed this up with investigating calving rates in known, tagged, individuals. Arguably the only solid evidence around GINs and wild ungulate fitness is for wild reindeer *Rangifer tarandus* (eg. Albon et al., 2002) – although there is some evidence in other species like Soay sheep (eg. Coulson et al., 2018) and Red Deer (eg. Albery et al., 2021). Even then, outcomes vary between host populations. For instance, Albon et al., (2002) found that anthelmintic treatment increased the probability of a reindeer having a calf in the next year, compared with an untreated control – highlighting the negative impact of parasites on reindeer fitness. However, Carlsson et al., (2016), contrary to what was expected, found that reindeer infected with parasites had similar levels of stress hormones compared with uninfected reindeer. Their results raise questions of whether moderate infection intensities with GINs are beneficial to hosts, as reindeer may use a tolerance strategy to cope with GINs. Therefore, impacts of GINs on fitness are likely to vary with host and parasite species, host sub-populations and potentially even year and other factors. A way forward perhaps is to set up long-term research programs in each species of interest. Alternatively, there is scope to develop comparative avenues nestled in metabolic theory of ecology (O'Connor & Bernhardt, 2018). For instance, Kirk et al. (2018) highlight how warming effects parasites in a manner that is consistent with general temperature dependence of host and parasites metabolism, showing that parasite transmission rate can be predicted across temperature and host size using the metabolic theory of ecology.

Disease is one of the top five threats to biodiversity, globally. As a case in point, diseases pose grave threat to various taxa including chytridiomycosis in hundreds of amphibians globally, facial tumor disease in Tasmanian devils (*Sarcophilus harrisii*), white-nose syndrome in several bat species in North America and fibropapillomatosis in green turtles (*Chelonia mydas*) (Daszak et al., 1999; Schloegel et al., 2006; Blehert, 2009; Van Houtan et al., 2010). As a result, there has been much research on wildlife disease globally. The recent Covid-19 pandemic serves as a case in point that research on diseases has seen an increase. Comparatively, studies on impact of parasites have been rather limited, primarily because their clinical signs are hard to detect so their impacts may be underestimated (Ndao, 2009). Yet, there is evidence for severe negative impacts of parasite on biodiversity. For instance, Trichomonosis, a disease caused by the protozoan parasite *Trichomonas gallinae,* is known to be the casual factor for rapid decline of the Greenfinch *Carduelis chloris* and chaffinch *Fringilla coelebs* (Lawson et al., 2012). Throughout the thesis, I attempt to remedy the lack of inclusion of the social-ecological context which characterizes most parasitological studies, this goes both ways; very few social and ecological studies consider parasites. Given the potential adverse impacts on host health and fitness, there must be more integration, from both directions.

Hence a "One Health" approach is likely to be a more holistic way of considering issues of host health in a given ecosystem. Figure 8.2 highlights some of the key areas needed to be focused on in order to achieve this. Currently, despite its aspiration to be inclusive and interdisciplinary, One Health is predominantly practiced by veterinary and public health professionals, leading to a focus on disease transmission at the human-animal interface, and less on the environmental and socio-economic aspects (Jenkins et al., 2015). In order to deal with the challenges posed by the environmental and socio-economic determinants of health, which includes biodiversity loss, climate change and loss of ecosystem services to name a few, it is crucial that into the future, veterinary and public health officials collaborate more with environmental and social scientists (Zinsstag, 2012). Table 8.2 illustrates how this collaborative "One Health" approach could be operationalized in our study sites.

Table 8.2 Operationalizing the "One Health" approach in our case study sites.

Overarching theme	***Site***	***Stakeholder***	***Exemplar Objective***	***Example of tasks***
Animal Health	Ural	Veterinary and animal husbandry department	Aligning livestock and saiga health.	Vaccination of livestock against diseases of concern (*chapter two*). Providing anthelmintic for a defined period of time to livestock (*chapter seven*)
	Kibber		Aligning livestock and bharal health	Providing support to herders to conduct five-point-checks in order to conduct targeted anthelmintic treatment (*chapter five*)
	Pin		Aligning livestock health with ibex health	Providing anthelmintic for a defined period of time to livestock (*chapter six*)
Environmental Health	Ural	Conservation NGO - ACBK	Maintain/improve pasture quality	Investigate if pastures are degraded and are leading to resource competition and increased disease transmission between saiga and livestock (*chapter three*)
	Kibber	Conservation NGO - NCF	Promote wildlife-friendly land-use	Investigate if current livestock management regimes are leading to contact patterns with bharal that could lead to disease transmission (*chapter five*)
	Pin	The migratory *Kinnaura* herders	Ensure quality of their summer pastures in Pin	Rotational grazing of leased pastures in Pin every few years to maintain their quality, as degraded pasture can increase disease transmission (*chapter four*)
Public Health	Ural	Local health centers	Reduce disease spill-over to humans	Prioritize vaccination of outlying herders that might be at particular risk to zoonotic spill-over
	Kibber Pin	Village-herder council	Mitigate negative food security impact due to disease in livestock	Setting up a community run, livestock insurance program to offset losses of livestock due to disease (eg. Mishra et al., 2013)

Note: The information provided in the table is illustrative rather than exhaustive and is included based on the experiential learning gained while doing the thesis. For instance some tasks are action based, while others are research based (with the hope of eventually being applied).

8.4 Conclusion

Through the thesis, I have demonstrated that rangelands are intertwined social-ecological systems and therefore host health is also a social-ecological concern (Hruska et al., 2017). Therefore, it is critical that host health be considered with an interdisciplinary lens. Studies are increasingly calling for this paradigm shift, given the paucity of such investigations in the past (Mishra et al., 2021). A step towards achieving this is combining ecological and social information at varying temporal and spatial scales to understand patterns of disease transmission in order to inform management (Khanyari et al. 2021; Chapter 2). Additionally, my thesis demonstrates the power of using predictive modelling to explore potential interventions in a virtual environment. Nestled within my research is the recognition that stakeholders such as herders, who share habitats with wildlife, have first-hand experience of wildlife-livestock interactions, can provide rich information concerning the health of both livestock and wild ungulates, and the potential ways forward – i.e. they can be empowered to produce solutions that work for them (Tomaselli et al., 2018). Following on from this, when considering disease transmission within rangelands, it is crucial to align the goal of wildlife conservation with that of maintaining and improving agricultural livelihoods – if this alignment isn't strived for, it is likely that negative trade-offs between conservation and livelihood aims will create negative human-wildlife interactions (Redpath et al., 2015). This can hamper the sustainability and resilience of rangelands (Hruska et al., 2017). Zooming out, and in conclusion, the thesis teaches me that it is important to view rangelands holistically - putting GINs and diseases in the broader context of considerations about how best to manage human-wildlife coexistence.

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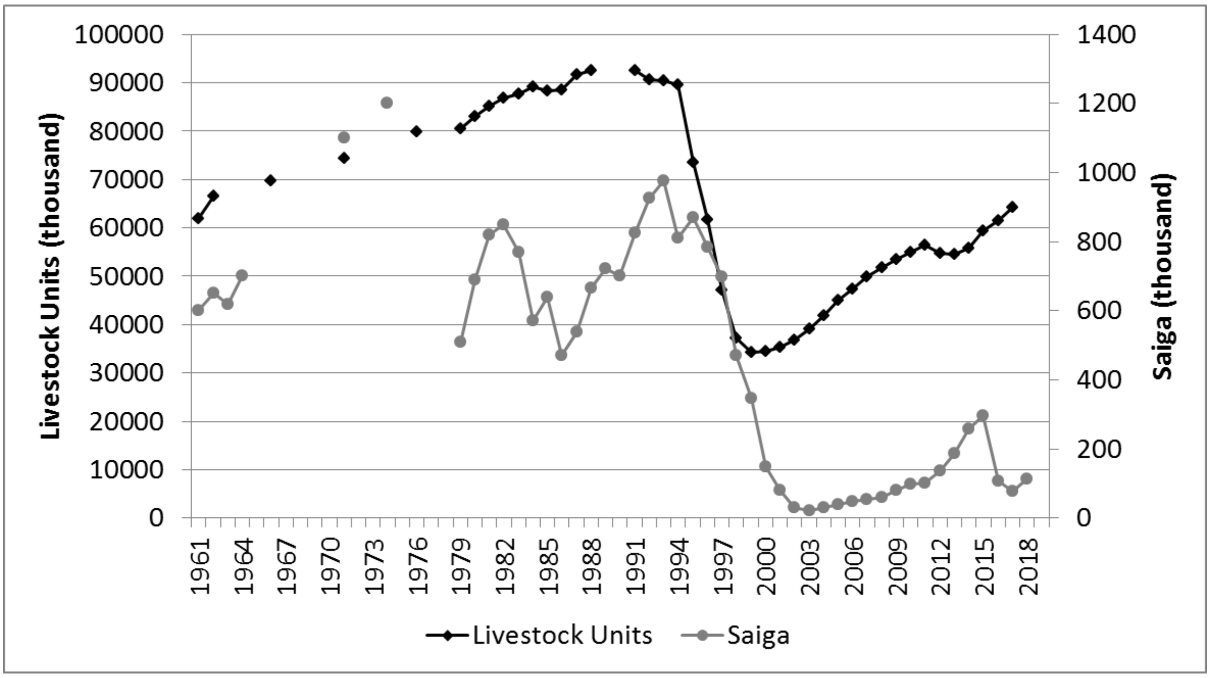
Appendix A – Supplementary material for chapter 2



A - Figure 1. Livestock numbers (in livestock units; 1 head of cattle or horse = 5 sheep or goats) and saiga numbers in Kazakhstan from 1961 to 2017 (sources: Kazakhstan national statistics & FAOSTAT; Bekenov and Milner-Gulland (1998); Kazakhstan national saiga count statistics)

A - Table 1. A qualitative integrated risk assessment, using literature, for potential risk of disease spill-over diseases from livestock to saigas (with a focus on the Betpak-dala region). Green indicates low risk, red indicates high risk and grey indicates uncertain risk. Diseases in Table 1 (main text) are not repeated here.

Disease **(key references)**	**Likelihood**	**Severity**	**Mitigation**	**Uncertainty**
Brucellosis *Lundervold 2001; Beauvais et al. 2018*	Mostly cattle but sheep and goats could also be carriers and sources. Saigas can be carriers too .	Individual deaths in saiga recorded but effects on populations unknown.	Regular vaccination of stock. Testing and slaughtering infected cattle.	Lack of local capacity for diagnosis and testing. Inadequate compensation for affected animals.
Tuberculosis *Lundervold 2001*	Potential presence and transmission from cattle. Could occur in saigas, however, historical very few cases.	Effects on saigas unclear but not known to be severe.	Testing and slaughter of infected individuals.	Lack of local capacity for diagnosis and testing. Lack of knowledge on prevalence and impact. Impact on saiga needs to be understood.
Bluetongue *Lundervold 2001; 2004*	Seroprevalence zero in saigas in previous surveys, but many wild species with similar natural histories to saigas were known to be seropositive. Sheep, goats and cattle could be carriers.	Sheep, goats and cattle were known to be affected. Not known to cause saiga mortalities even when sheep sharing pasture with saigas were infected.	No indication of active mitigation measures against this disease.	Further research into current prevalence of disease in livestock and saigas. Need to test if acquisition of disease results in immediate death of saigas hence no seroprevalence.

Necrobacillosis (*Fusobacterium necrophorum*; calf diphtheria) *Petrov 1979; Lundervold 2001*	Spill-over indication from sheep and goat in a saiga outbreak in 1978. However, no indication of occurrence in either in recent decades.	The 1978 outbreak caused 5000-6000 deaths in the Bepak-Dala population.	No indication of vaccination or other mitigation measures.	Lack of knowledge of occurrence in livestock and saiga.
Akabane Disease *Orynbayev et al. 2016*	High seroprevalence in saiga yet lack of outbreak suggests saiga have natural immunity. Sheep and goats known to transmit.	No cases of outbreaks in saigas recorded.	None from our knowledge.	Lack of knowledge on current mitigation (if any). Impact of high seroprevalence on saiga health.
Q Fever *Orynbayev et al. 2016*	Some level of seroprevalence in saigas. Can transmit from sheep, goat and cattle.	No cases of outbreak in saigas recorded.	None from our knowledge.	Lack of knowledge on current mitigation (if any).
Paratuberculosis *Orynbayev et al. 2016*	Low seroprevalence in saigas. Known to affect ruminants in general but rarely outside farmed wildlife.	No cases of outbreak in saigas recorded.	None from our knowledge. Not outbreaks in livestock either.	Lack of knowledge on current mitigation (if any).
GINs* *Bekenov et al. 1998; Morgan et al. 2006*	Present in all species. Sheep and goat were likely to transmit given phylogenetic similarities and pasture sharing.	General levels in saigas were moderate, but at levels thought to affect fitness in other wild ungulates.	Opportunistic and highly variable anthelmintic use for small stock.	Migration results in complex contact patterns. A lack of understanding of spatial and temporal trends in GINs. Climate change can affect GIN infectivity. Cross-transmission can occur through indirect

				contact (sequential pasture sharing). Limited on-ground mitigation strategies.
Chlamydophila abortus Beauvais et al. 2018	No reference in saigas but expert elicitation suggests potential.	Unknown	None from our knowledge	Research into whether this truly occurs in saigas is needed. And if it does, what, if any are the impacts.
Leptospirosis *Beauvais et al. 2018*	No reference in saigas but expert elicitation suggests potential. Cattle seem to be more likely, yet found in sheep and goat too.	Unknown	Testing regimes (especially for cattle) are present in some places	Research into whether this truly occurs in saigas is needed. And if it does, what, if any are the impacts. Efficacy and coverage of the testing regime needs to be validated.
Listeriosis *Beauvais et al. 2018*	No reference in saigas but expert elicitation suggests potential. Sheep/goat and cattle are known to harbour and potentially transmit this.	Unknown	Testing regimes for sheep/goat and cattle are present in some places	Research into whether this truly occurs in saigas is needed. And if it does, what, if any are the impacts. Efficacy and coverage of the testing regime needs to be validated.
Salmonella enterica *Beauvais et al. 2018*	No reference in saigas but expert elicitation suggests potential. Sheep/goat and cattle are known to harbour	Unknown	None from our knowledge	Research into whether this truly occurs in saigas is needed. And if it does, what, if any are the impacts.

	and potentially transmit this.			

Notes: *=Gastro-intestinal Nematodes; Beauvais et al. 2018 list additional diseases that might be of concern to saiga upon eliciting expert opinion.

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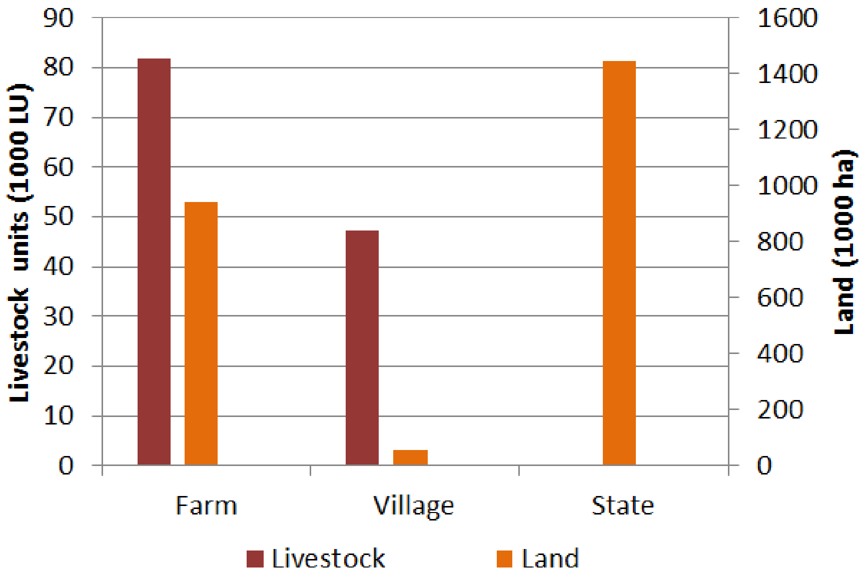
A - Table 2. Land holdings by sub-district (ha) (Source: Amangeldi and Dzhangeldy district land committees, 2016)

Sub-district	**Village land**	**Leased land**	**State Reserve**
Urpek	8,728	171,407	603,911
Kabyrga	3,056	14,090	161,987
Albarboget	20,926	88,810	55,491
Aralbai	4,420	63,607	179,842
Akkol	20,898	603,911	442,452
Total	58,028	941,825	1,443,683



A - Figure 2. Distribution of land area and livestock holdings between the village lands, leased lands and state reserve lands. (source: Amangeldi and Zhangeldi district land committees, 2016)

A - Table 3. Livestock numbers (head) in Amangeldi and Zhangeldi** raions 2016 by sub-district and comparison of totals with those for 2008

Sub-district	**Cattle**		**Sheep**		**Horses**		**Camels**		**Total: sheep equivalents %**	
	Farm	Village	Farm	Village	Farm	Village	Farm	Village	Farm	Village
Urpek	3,004	1,784	6,194	3,618	1,409	725	0	44	64%	36%
Kabyrga	461	757	1,232	1,149	101	312	0	0	38%	62%
Albarboget**	2,486	1,890	8,723	5,350	1,193	240	59	6	63%	37%
Aralbai**	1,703	NA	3,412	NA	1,030	NA	0	NA		
Akkol**	453	775	2,043	2,993	138	282	0	0	38%	62%
Total 2016	13,313		34,714		5,430		109		~58%	~42%
Total 2008 (for comparison)	11,208		20,638		2,596		74			

(sources for 2016 data: village akims and district statistics offices, 2016; sources for 2008 data: Lenk, 2008). **Taken from land cadaster, some households lease in more than one sub-district. NA = not available

Note: Livestock were most mobile in spring and summer, when the largest herds may change location multiple times. During winter, animals were kept mostly in barns, although outdoor grazing is possible in some areas. Owners of large private farms were often absent, leaving management and herding to hired staff.

A - Table 4. Human population statistics by sub-district.

Sub-district	**Population**				**Households**	**Households leasing land***
	1989	1999	2008	2016	2016	2016
Urpek	4,400	2,119	1,815	1,694	270	58
Kabyrga	1,300	646	392	354	46	20
Albarbogeet	1,954	1,044	765	654	143	21
Aralbai	2,168	716	626	658(2009(	113	11
Akkol	1,070	786	595	543	100	6
Totals	10,892	5,311	4,193	3903	672	116

(sources for 2016 data: village akims and district statistics offices, 2016; sources for 2008 data: Lenk, 2008).

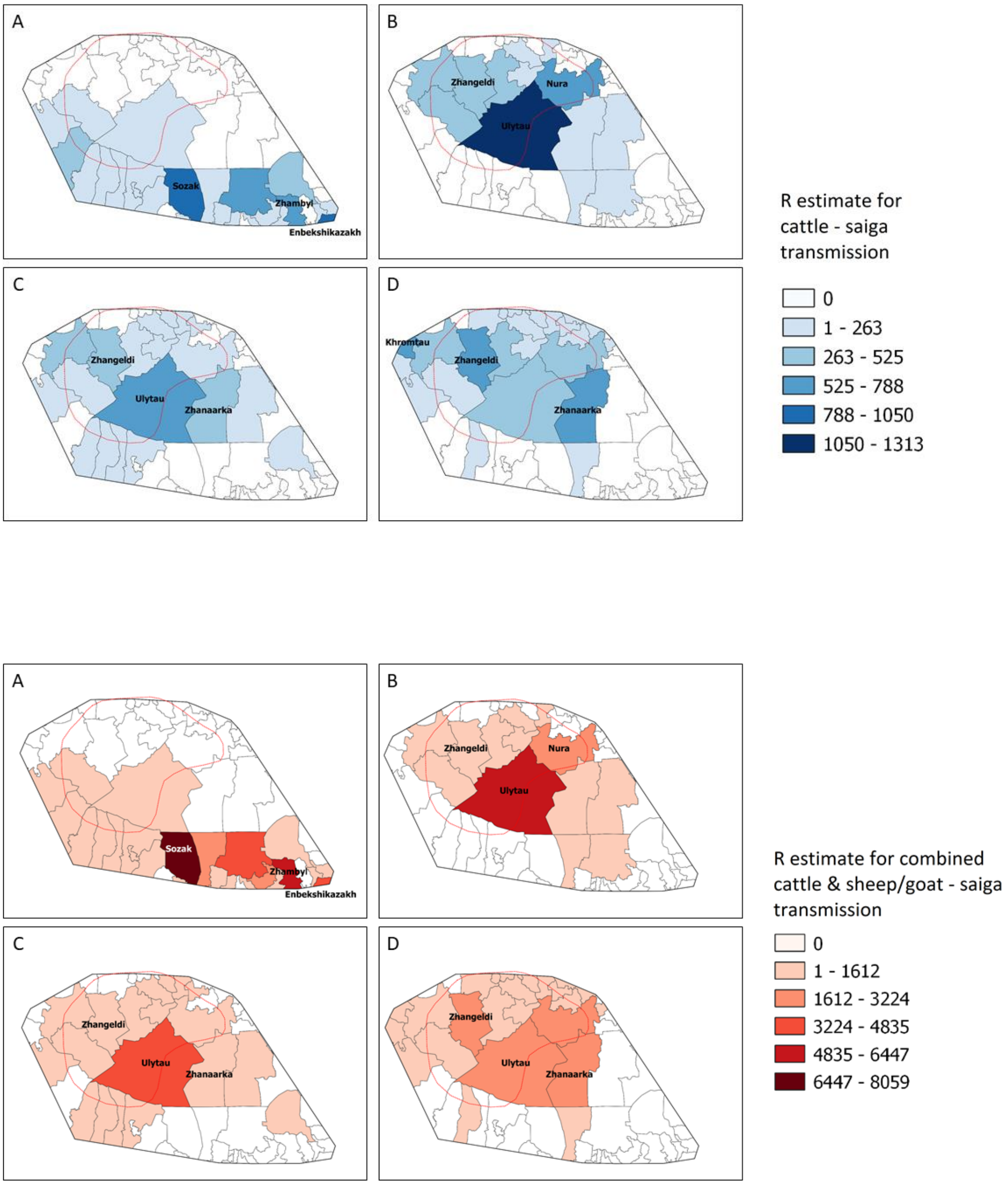
A - Table 5. Livestock numbers, no. of saiga groups, average distance between livestock and saiga and corresponding disease risk score for each raion across seasons

Raion	SG pop	Cattle pop	Average Distance(km)	No. saiga groups	Cattle score	SG score	Combined score
SUMMER							
Sarysu	187238	20624	56.17	1	4	33	37
Esil	20965	18865	16.44	3	34	38	73
Egindikol	12388	10885	5.72	2	38	43	81
Karasu	21114	31127	11.23	2	55	38	93
Zhaksy	26684	24589	11.59	3	64	69	133
Arkalyk	23911	16513	13.51	5	61	89	150
Karmakshy	13776	19317	13.51	7	100	71	172
Korgalzhyn	28814	20826	5.51	2	76	105	180
Osakarov	43123	33806	3.78	1	90	114	204
Tselinograd	39276	31051	6.73	2	92	117	209
Zharkain	21154	12484	12.61	9	89	151	240
Astrakhan	43675	31568	10.27	4	123	170	293
Shalkar	111478	45926	14.59	3	94	229	324
Nauyrzym	27518	22052	11.61	10	190	237	427
Atbasar	41719	39537	13.30	7	208	220	428
Yrgiz	125043	38815	17.78	8	175	563	737
Mugalzhar	128235	46499	11.78	5	197	544	742
Khromtau	50134	39722	6.76	9	529	667	1196
Ayteke Bi	82823	40792	26.00	26	408	828	1236
Amangeldi	78011	34108	14.03	20	486	1112	1598
Nura	99592	45328	21.62	25	524	1152	1676
Zhangeldi	69233	32759	12.32	22	585	1236	1821
Zhanaarka	102476	59762	15.60	19	728	1248	1977
Ulytau	195903	52957	27.81	27	514	1902	2416
SPRING							
Sarysu	187238	20624	92.40	1	2	20	22
Moiynkum	133118	32408	60.95	1	5	22	27

Zharkain	21154	12484	14.01	4	36	60	96
Arkalyk	23911	16513	15.01	5	55	80	135
Zhanaarka	102476	59762	31.07	3	58	99	157
Atbasar	41719	39537	13.66	4	116	122	238
Shet	213446	87420	35.43	6	148	362	510
Ayteke Bi	82823	40792	6.83	6	358	728	1086
Yrgiz	125043	38815	21.34	16	291	938	1229
Amangeldi	78011	34108	15.2	17	382	873	1255
Zhangeldi	69233	32759	9.48	14	484	1023	1507
Nura	99592	45328	20.47	28	620	1362	1982
Ulytau	195903	52957	24.59	61	1313	4859	6172
WINTER							
Kyzylorda	19436	20743	24.97	1	8	8	16
Zhalagash	50977	31352	44.47	6	42	69	111
Talas	298834	26441	19.67	1	13	152	165
Shieli	73992	55629	46.83	7	83	111	194
Syrdariya	28503	33848	73.13	28	130	109	239
Karmakshy	57422	27520	24.19	7	80	166	246
Kerbulak	311145	59028	13.63	1	43	228	272
Bayzak	230959	39233	8.27	1	47	279	327
Talgar	114503	42639	4.77	1	89	240	330
Shalkar	111478	45926	18.57	4	99	240	339
Kazaly	88301	34564	26.58	11	143	365	509
Merke	248512	41204	9.57	2	86	519	606
Ulytau	195903	52957	52.16	13	132	488	620
Balkhash	106345	91717	15.81	5	290	336	626
Yrgiz	125043	38815	29.81	12	156	503	660
Turkestan	461731	111160	8.43	1	132	548	680
Korday	363003	69294	10.69	2	130	679	808
Aral	87936	49298	13.11	9	338	604	942
Shu	284465	35941	17.51	9	185	1462	1646
Sarysu	187238	20624	31.84	31	201	1823	2024

Moiynkum	133118	32408	25.77	52	654	2686	3340
Enbekshikazakh	287608	94981	2.09	2	909	2753	3662
Zhambyl	632233	106765	13.22	9	727	4305	5032
Sozak	349109	40538	24.66	51	838	7221	8059
CALVING							
Egindikol	12388	10885	7.9	1	14	16	29
Zhaksy	26684	24589	11.8	1	21	23	43
Atbasar	41719	39537	17.6	1	23	24	46
Shet	213446	87420	52.3	1	17	41	58
Zhalagash	50977	31352	25.8	2	24	39	64
Syrdariya	28503	33848	7.3	1	46	39	85
Kazaly	88301	34564	24.5	2	28	72	100
Shalkar	111478	45926	15.2	1	30	73	103
Karmakshy	57422	27520	22.2	3	37	78	115
Zharkain	21154	12484	5.4	2	47	79	126
Balkhash	106345	91717	17.8	2	103	119	222
Arkalyk	23911	16513	14.0	8	95	137	231
Yrgiz	125043	38815	34.3	5	57	182	239
Amangeldi	78011	34108	15.9	7	150	343	493
Nura	99592	45328	14.3	6	191	419	610
Ayteke Bi	82823	40792	9.5	7	299	608	908
Zhanaarka	102476	59762	27.2	16	352	603	955
Zhangeldi	69233	32759	12.5	16	420	887	1307
Ulytau	195903	52957	35.8	47	696	2575	3272

Pop= population; SG = sheep/goat



A - Figure 3. Above: Disease risk score for saiga from cattle, **Below**: Disease risk score for saiga from combined livestock; A= winter saiga range, B= spring saiga range, C= calving saiga range, D= summer saiga range.

A - Table 6. Diseases against which vaccination and testing is reported in the our two *raions* of interest (within which are the five sub-district where we concentrated our field-work).

Raion **(year)**	**Species (heads)**	**Vaccine**	**Vaccine planned**	**Vaccine Coverage (%)**	**Test**	**Test planned**	**Test Conducted(%)**
Zhangeldi* (2016)	Cattle (27,314)	Emkar *(Clostridium chauvei)*	10,500	9,300 (34.0%)	Leptospirosis	206	78 (0.3%)
					Listeriosis	206	78 (0.3%)
	Sheep/Goat (60,296)	*Clostridium septicum*	500	200 (40.0%)	Listeriosis	530	226 (0.4%)
		Contagious Ecthyma	1,000	1,000 (100%)			
	Horses (8,249)	Pasteurellosis	300	650 (7.9%)	Glanders	2,200	650 (7.9%)
		Rabies	1,000	-			
		Strangles	-	-			
		Anthrax	7,200	4,100 (49.7%)			
Amangeldi** (2016)	Cattle (13,313)	Emkar *(Clostridium chauvei*	20,200	3,000 (22.5%)			
		Hypodermatosis	2,500	-			
	Sheep/Goat (34,714)	*Clostridium septicum*	-	-			
		Contagious Ecthyma	-	-			
	Horses (5,430)	Rabies	700	-	Glanders	3,000	800 (14.7%)
		Pasteurellosis	300	2,163 (39.8%)			
		Anthrax	6,600	5,100 (93.9%)			
		Strangles	3,700	-			

*Additionally there was rabies vaccination for dogs and cats, Anthrax vaccination for camels, Echinococcus treatment for dogs, TB testing for camels and testing for infectious epididymitis (for unknown stock).

** Additionally there was rabies vaccination for dogs and cats, Anthrax vaccination for camels, Echinococcus treatment for dogs, TB testing for camels.

A - Table 7. Pasteurellosis vaccination plan for Zhangeldi and Amangeldi *raion*.

	Cattle (head)	Cattle vaccinated	. Sheep and goats (head)	Sheep and goat vaccinated	Horses (head)	Horses vaccinated
Zhangeldi (Torgai) *raion* total 2016	27314	10500	60296	11200	8249	300
Amangeldi *raion* total 2016	13313	10500	34714	12200	5430	2163
Amangeldi *raion* total 2015		9100		12100		270
Urpek s.o. 2015	4788	900	2227	1500	2134	120
Kabyrga s.o. 2015	1218	500	547	500	413	0

(Source: *raion* veterinary headquarters, 2016). Past = Pasteurellosis; No.=number animals in 2016; C=cattle, S=sheep and goats, H=horses. As seen from table 1, in the Zhangeldi raion c.38% cattle, c. 19% sheep/goat, and c. 4% horses were vaccinated in 2016, while in Amangeldi raion c. 79% cattle, c. 35% sheep/goat and c.40% horses were vaccinated in 2016. Interesting, the total number of vaccines for cattle and sheep/goat were similar for the years 2015 and 2016 for both raions, however the total vaccines for horses was nearly 10 times higher for Amangeldi raion in 2016 compared to 2015.

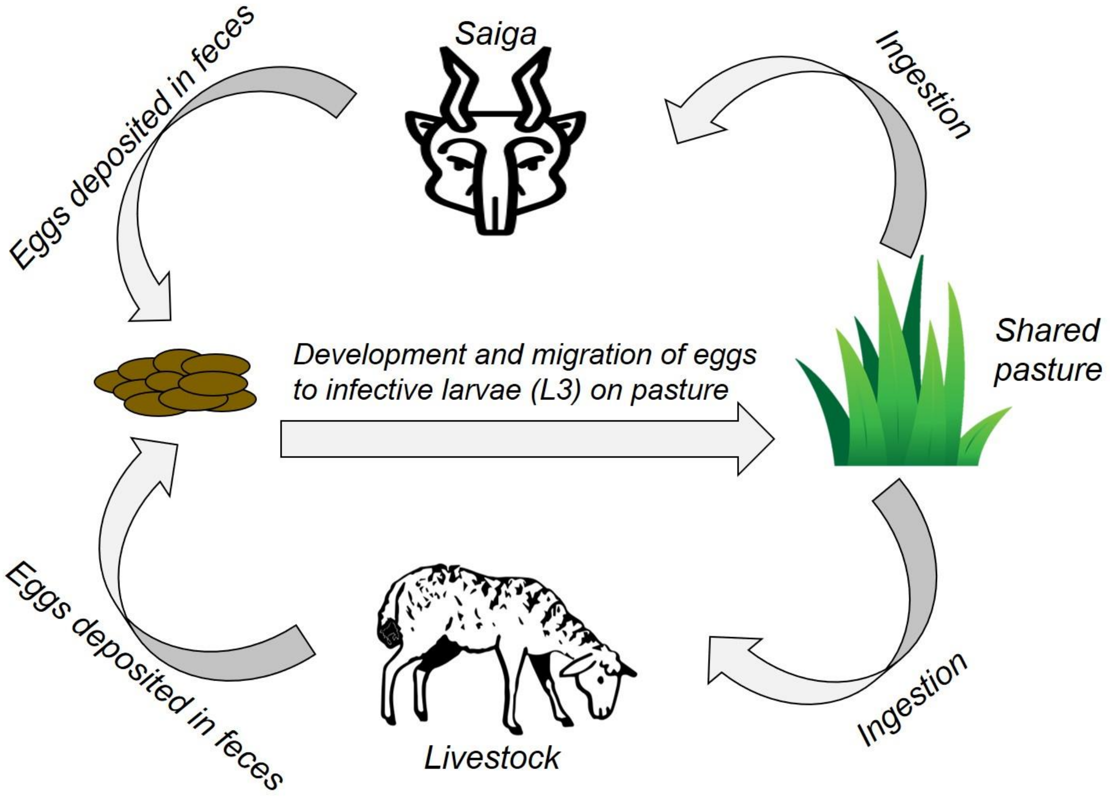
Proportions couldn't be calculated for 2015 as we lacked data from Zhangeldi, and while we had vaccination data from Amangeldi, we lacked livestock numbers. Exact percent coverage is difficult to estimate due to changes to plan and unknown coverage in relation to age-sex characteristics of livestock.

A - Table 8. Livestock disease events reported in May 2015 in the steppe area, far from villages and with potential contact with saigas.

Case no.	Description of the event
1	steppe southwest of Urpek. 10 of 100 cattle died. Foaming at the mouth, bloat, no diarrhoea, in poor physical condition and lethargic for 2-3 days before death. Whole sub-group died. Grass was mixed; weather nothing special. Cattle had been vaccinated in April. Vet lab tested the cattle. Local veterinary opinion was toxicosis from 'ran' (*Poa bulbosa*), a type of grass known to cause such disease in cattle. Lab results excluded pasteurellosis, which in any case would, according to the vet, have killed the whole herd and not only 10%.
2	steppe 10km south of Urpek. Four cattle died even though in good condition. Diagnosis was 'Karasan' disease and no compensation was given.
3	east of Kokalat along Kabirga river. 40 of 600 cattle died, 2-3 days after saiga deaths in the area. Haematomas observed over the head, legs and body, then death within one day. No diagnosis was made. At the same time, 10 of 400 horses died on the steppe near the die-off sites, with similar signs.

Appendix B – Supplementary material for chapter 3

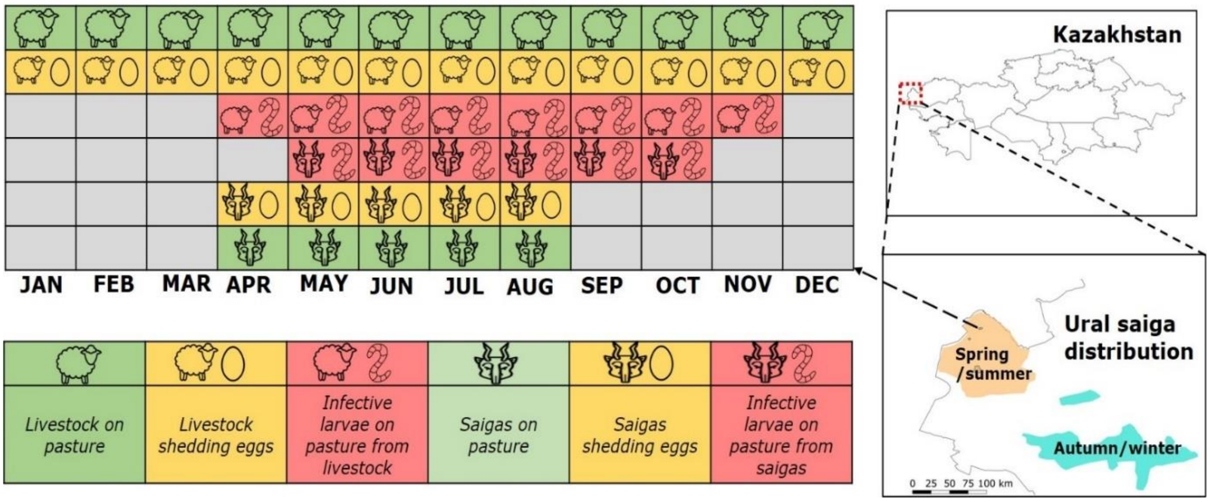
Gastro-Intestinal Nematodes (GINs) life cycle



B- Figure 1. A schematic for GIN transmission in our case study site. Above: Saiga, Below : Livestock (sheep/goat). Icons courtesy noun project.

Figure 2 visualizes the potential dynamics of GINs in our study area. Saigas are in their spring/summer distribution approximately between April-August, and spend September-March in their autumn/winter range – We don't focus on the latter for this paper . Livestock are sedentary. Saigas shed eggs via faeces onto pastures in their spring/summer distribution (April-August). Given temperatures above the development threshold (Rose et al. 2015), these eggs develop into infective larvae on pasture (Fig. 1), subject to a lag between faeces deposition and appearance of infective larvae on pasture. Parasite eggs shed by saigas as they leave their spring/summer distribution are likely to infect pastures for some time following their departure, given the lag between egg shedding and pasture infectivity (Rose et al. 2015).

Livestock occupy and shed eggs onto pasture via faeces in the spring/summer compartment year-round, assuming no housing in winter. Eggs shed in the winter months are unlikely to become infective larvae on pasture due to extreme temperatures. Livestock eggs in this compartment are therefore likely to become infective larvae in the same months as eggs from saigas; albeit for an extended period of time given their continual pasture occupation (Fig. 2).



B- Figure 2. A schematic of the two-host (saiga and livestock – sheep/goat) parasite system in Ural. Icons courtesy of Noun Project.

Reference

Rose, H., T. Wang, J. van Dijk, and E.R. Morgan. 2015. GLOWORM-FL: a simulation model of the effects of climate and climate change on the free-living stages of gastro-intestinal nematode parasites of ruminants. *Ecological Modelling* 297: 232-245.

Questionnaire

Preamble

Before starting the interviews, each respondents was told that the survey's aim was to understand the inter-relations between factors affecting host health in multi-use Western Kazakh rangelands.

Each respondent was told that their identity will be kept anonymous and will not be identified by name or specific location in any publications and communication. They were also told that this study is part of Munib Khanyari's PhD thesis that aims to understand how species movement along-with environmental factors (like weather) affect disease transmission between wild and domestic ungulates. They were also told that the results will be published in internal reports, publicly available peer-reviewed, scientific journals. Publications will solely refer to the areas where the survey was conducted, not individuals, unless requested not to do so by the respondents. After all this, we asked each respondent for permission to conduct the interview. Consent was orally recorded. We also explained that they can withdraw at any time. Interviews were conducted in Kazakh/Russian and translated into English.

Key-informant survey questions:

Q1. How many livestock (sheep and goat) are in your herd? How are they herded?

Q2. Can you describe your livestock movement over the past 12 months?

Q3. Do your livestock have health issues, particularly GINs? Do they occur at the given time of the year? Can you score their impact? 5 animal dies – 4 alive but useless(in term of what they define productivity to be) – 3 severely impacted – 2 impacted but not so severely – 1 little impact – 0 barely noticeable.

Q4. What types of treatment do you employ for these health issues, particularly for GINs?

Q5. What is the demand of livestock produce from your farm? How has that changed since the break-up of the Soviet union?

Q6. How has answers of Q5. in turn impacted livestock management strategies and what (if any) are the implications for host health?

Q7. What are the laws regarding land-use on your farm? What are their implications for host health?

Additional questions particularly for the Focus group discussions:

- In your experience how has herding changed in this area since just after the break-up of the Soviet Union?
- In your opinion, how has the climate changed since just after the break-up of the Soviet Union? How has it affected herding and host health in general?
- What for you is a productive animal?
- What currently limits livestock productivity?

After these directed questions, key-informants and participants of FGDs were allowed to speak freely on any aspects around factors affecting their livestock's health and that of saigas and the rangelands itself.

We asked them to particularly touch upon topics of ecological, social, economic, political and climatic factors affecting host health in their rangelands.

B - Table 1. A table representing the various health problems, their potential causes, impact on the productivity of the animal, treatment, impact and timing of treatment, and additional comments. 46 (35 outlying herders and 11 village-based herders) interviews worth of key-informant data is condensed into this table

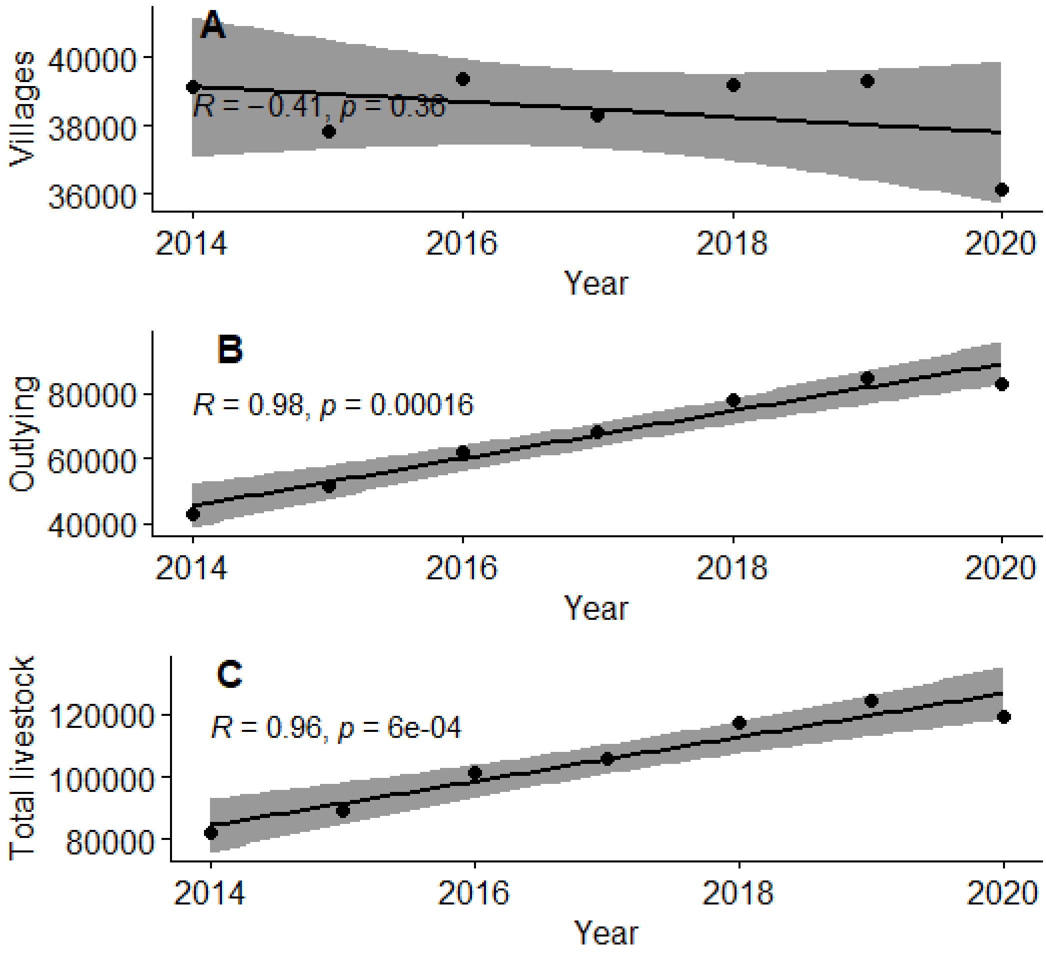
Health Problem	**Potential Cause**	**Symptoms and their impacts**	**Time of problem**	**Level of Impact***	**Interventions**	**Impact of intervention**	**Livestock information****	**Comments**
Oestrus ovis (Tenfek)	Worm in the nose lay eggs	Makes them go in circles. They become thin	Mostly spring/summer	5	Pills	Variably effective	Random; happens to few individuals, across species	Present in village and outlying livestock
Rabies (Behshentvo/ Sibirica)	Unknown	They become violent and scared of water	Anytime	5	Vaccination	Complete cure	Random, happens to few individuals	Present in village and outlying livestock
Black-leg (Karasan)	Something on the ground or grass	Their legs get swollen and weak	Random	5	Vaccination Medicines (like antibiotics)	Complete cure	All types	Present in village and outlying livestock
Bruscellosis	Unknown	Vet takes blood and tells them	Anytime	4-5	Slaughtered and compensated	Animal is killed	Random, happens to few individuals Mostly cows	Compensation isn't enough.

								Present mostly in outlying cattle.
Dermatitis (Dermatit)	-	Back legs swell and don't work Skin wounds with puss Weakness	Anytime	3-5	Vaccination	Complete cure if timely	Random, happens to few individuals Mostly cows but other species too	Vaccination started in recent times. Present in village and outlying livestock
Gut parasites	Worms New grass Tall grass Dry/ dusty areas Dirty water	Diarrhea Weight loss Eyes are lighter Liquid from nose Loss of appetite Worms in faeces Loss of meat	Spring & Summer	1-4	Anthelmintics Consume individuals Plant preparation Glucose Nothing	Anthelmintics generally cure them and glucose aids recovery. Many recover themselves.	Mostly babies and female sheep.	Anthelmintics need to be purchased from Uralsk. Present in village and outlying livestock
Ticks	Long grass Increased spring temperature Dry spring	Bleeding of the skin Flies lay eggs in it Weaker	Mostly spring	2-3	Vitamins supplement Ivermectin dipping Creams/skin disinfectant	Complete cure	Generally all individuals get	Supplements need to be bought from Uralsk .

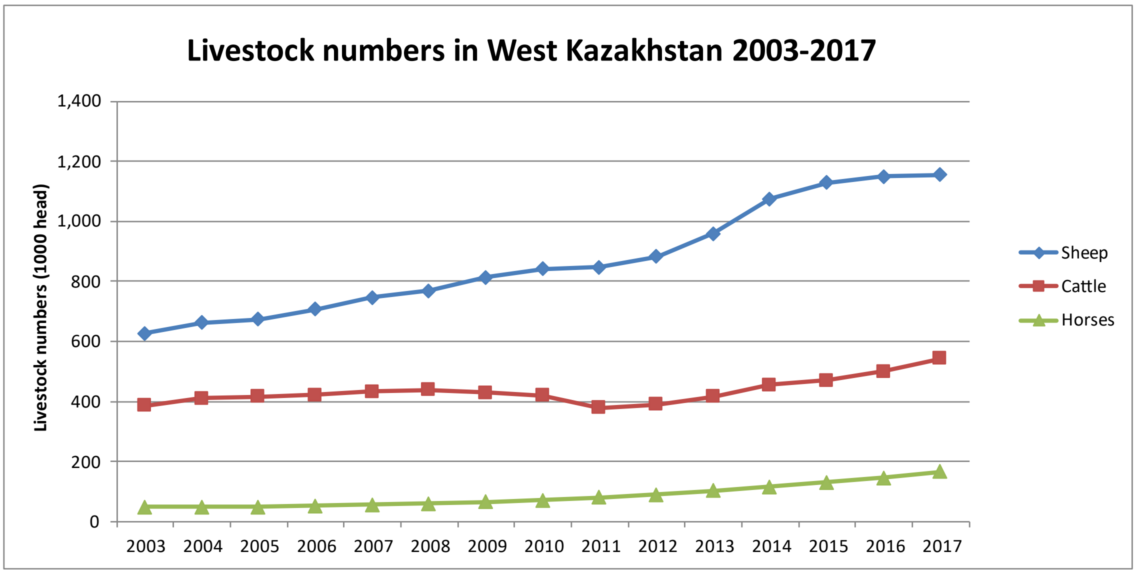
					“*Aldaraspan*” (a shrub) smoke gets the insect out		affected across all species	Mostly present in outlying livestock
Kotyr	When livestock are bought outside after being stall fed for winter	Weight loss Puss on skin	Spring	2	Pills	Complete cure	Random individuals, especially the ones that are weaker in the winter	Pills are available in most villages Present in village and outlying livestock

*this is on a scale of 0-5 with 5 animal dies – 4 alive but useless(in term of what they define productivity to be) – 3 severely impacted – 2 impacted but not so severely – 1 little impact – 0 barely noticeable . We don’t know the frequency of the disease events but these are all diseases that have occurred in the past 5 years in the region. Red = high impact, yellow = medium impact and green = low impact.

**Livestock information head refers to if the health problem is tied to certain kind of livestock. For instance if certain age-sex class or certain species of livestock is more susceptible to it. Unless species is mentioned, we are referring to shoats

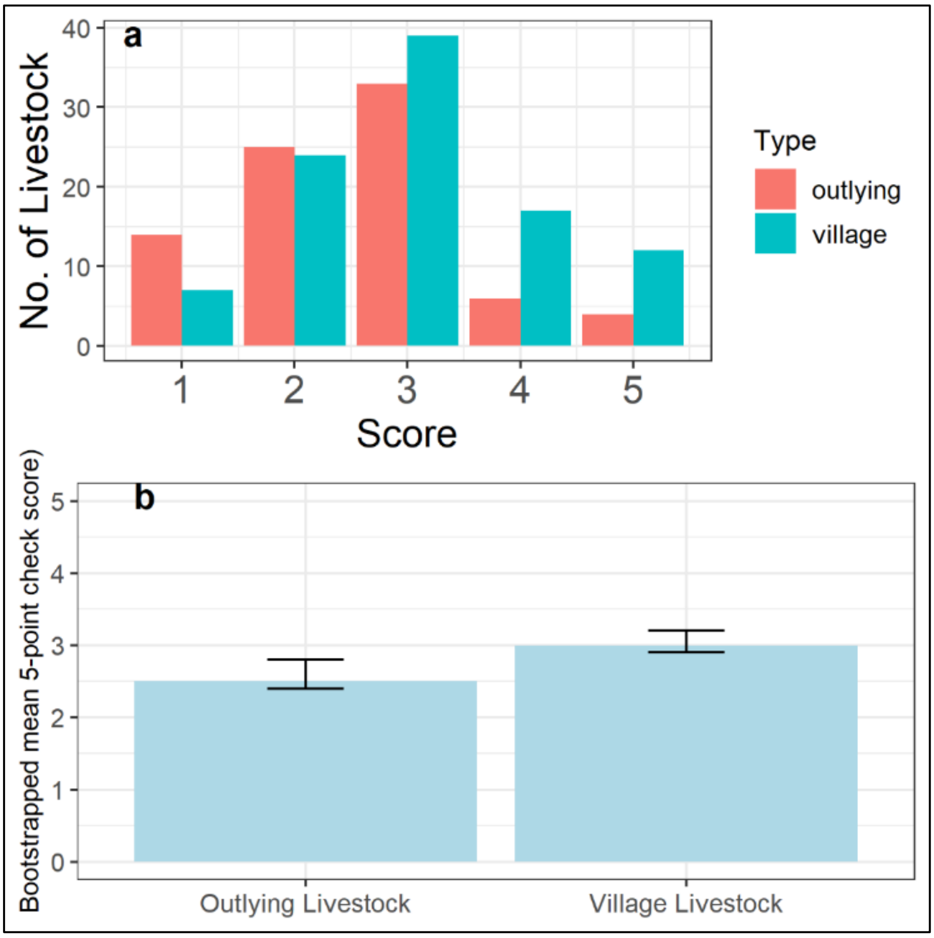


B - Figure 3. A panel graph showing all livestock numbers in A) villages, b) Outlying farms and c) total – over time (2014-2020). Displayed also is the correlation co-efficient (R) and its related p-value. P <0.05 is considered significant. This is for Zhanybek district.



B - Figure 4. Line graphs displaying number of livestock (sheep/goat), cattle and horses in Western Kazakhstan from 2003-2017.

Using 5-point checks (Bath & Van Wyk 2009) health of village-based livestock was worse than outlying livestock (p= 0.0003). Outlying livestock (n=82) had a mean five-point check score of 2.5 (2.4-2.8) while village livestock (n=99) had a mean five-point check score of 3.0 (2.8 – 3.2).



B - Figure 5. Panel bar graphs showing a) number of livestock and their five-point check scores and b) the bootstrapped mean 5-point check score with 95% CI for outlying and village livestock. Scores 1-2=normal, 3=borderline, 4=clinically anaemic, 5=profoundly anaemic.

Bath, G.F. and Van Wyk, J.A., 2009. The Five Point Check© for targeted selective treatment of internal parasites in small ruminants. Small Ruminant Research, 86(1-3), pp.6-13.

Appendix C – Supplementary material for chapter 4

Questionnaire

Preamble

Before starting the interviews, each respondents was told that the survey's aim was to understand contemporary pastoral practices, changes in them and implications for disease transmission between livestock and wildlife (Asiatic Ibex) in Pin valley.

Each respondent was told that their identity will be kept anonymous and will not be identified by name or specific location in any publications and communication. They were also told that this study is part of Munib Khanyari's PhD thesis that aims to understand how species movement along-with environmental factors (like weather) affect disease transmission between wild and domestic ungulates. They were also told that the results will be published in internal reports, publicly available peer-reviewed, scientific journals. Publications will solely refer to the village/area where the survey was conducted, not individuals, unless requested not to do so by the respondents. After all this, we asked each respondent for permission to conduct the interview. Consent was orally recorded. We also explained that they can withdraw at any time. Interviews were conducted in Hindi as that is a language all respondents and interviewers were mutually comfortable in.

Key-informant survey questions:

Q1. *For both herder types:* How many livestock (sheep and goat) are in your herd? How has this number and its proportions changed since the turn of the 21st century? Can you shed some light of why these changes occurred?

Q2. *For both herder types:* Can you describe your livestock movement over the past 12 months? Do your livestock share pasture with Asiatic ibex in Pin?

Q3. *Only for the Kinnaura herders* – what are the reasons for undertaking the migration?

Q4. *Only for the Pin villagers* – what are the reason you allow for the migratory livestock to access your pastures?

Q5. *For both herder types:* Do your livestock have health issues, particularly GINs? Do they occur at a given time of the year? Can you score their impact? 5 animal dies – 4 alive but useless(in term of what they define productivity to be) – 3 severely impacted – 2 impacted but not so severely – 1 little impact – 0 barely noticeable.

Q6. *For both herder types:* What types of treatment do you employ for these health issues, particularly for GINs?

Q7. *For the Kinnaura herders* : What is the current state of pasture quality that you access in summer (in Pin)? What are its indicators? How and why has pasture quality changed since the turn of the 21st century, and what might the implication of this be for your livestock and the rangelands at large?

Supporting questions:

- In your opinion how has climate changed since the turn of the 21st century and what are its implications for your livestock and the pastures they graze?
- In your personal experience and knowledge, how has herding changed since the turn of the 21st century?

After these directed questions, key-informant were allowed to speak freely on any aspects around contemporary herding practices and changes in them since the turn of the 21st century in order to understand potential impacts on domestic and wild host health and disease transmission to wild ungulates in Pin valley.

We asked them to particularly touch upon topics of host contact patterns, endo-parasite impacts and treatments, livestock holding and composition, reasons for engaging in pastoralism and state of the pasture quality and its implication for host health/disease transmission in Pin valley.

Appendix D – Supplementary material for chapter 5

Questionnaire

Preamble

Before starting the interviews, each respondents was told that the survey's aim was to understand livestock health and management practices in Kibber.

Each respondent was told that their identity will be kept anonymous and will not be identified by name in any publications and communication. They were also told that this study is part of Munib Khanyari's PhD thesis that aims to understand how species movement along-with environmental factors (like weather) affect disease transmission between wild and domestic ungulates. They were also told that the results will be published in internal reports, publicly available peer-reviewed, scientific journals. Publications will solely refer to the village/area where the survey was conducted, not individuals, unless requested not to do so by the respondents. After all this, we asked each respondent for permission to conduct the interview. Consent was orally recorded. We also explained that they can withdraw at any time. We referred to shoats when saying livestock.

Semi-structured interview questions:

Q1. How do you rate your livestock's health? Satisfactory, good, bad, other?

Q2. Do your livestock have health issues?

Q3. What kind of health issues do your livestock have? What causes them?

Q4. What kind of treatment/management do you employ against health issues?

Q5. Do your livestock have ectoparasites? When do they occur? What is their impact?

Q6. Do your livestock have endoparasites? When do they occur? What is their impact?

Q7. Across the year, where are bharal? Can you help us make a map of this?

Q8. How are your livestock distributed across the year around Kibber? Can you help us make a map of this?

After these directed questions, interviewees were allowed to speak freely on any aspects around livestock health and management practices.

D – Table 1. Fecal Egg Count raw data for Kibber livestock and Bharal

https://doi.org/10.5061/dryad.cc2fqz669

D – Ungulate Analysis

To estimate the number of groups ($\hat{G}$) of blue sheep, we fit the 'mt' model using the function BBRecap with a 'uniform prior' for each species. We used the 'mt' model because detection probability was expected to be different across the two surveys (Suryawanshi et al. 2012). We used uninformed uniform priors because this is the first effort to use this method in this landscape for blue sheep. We did 10,000 mcmc iterations with 1000 burn-in. Further details on model fitting are available in Fegatelli and Tardella (2013).

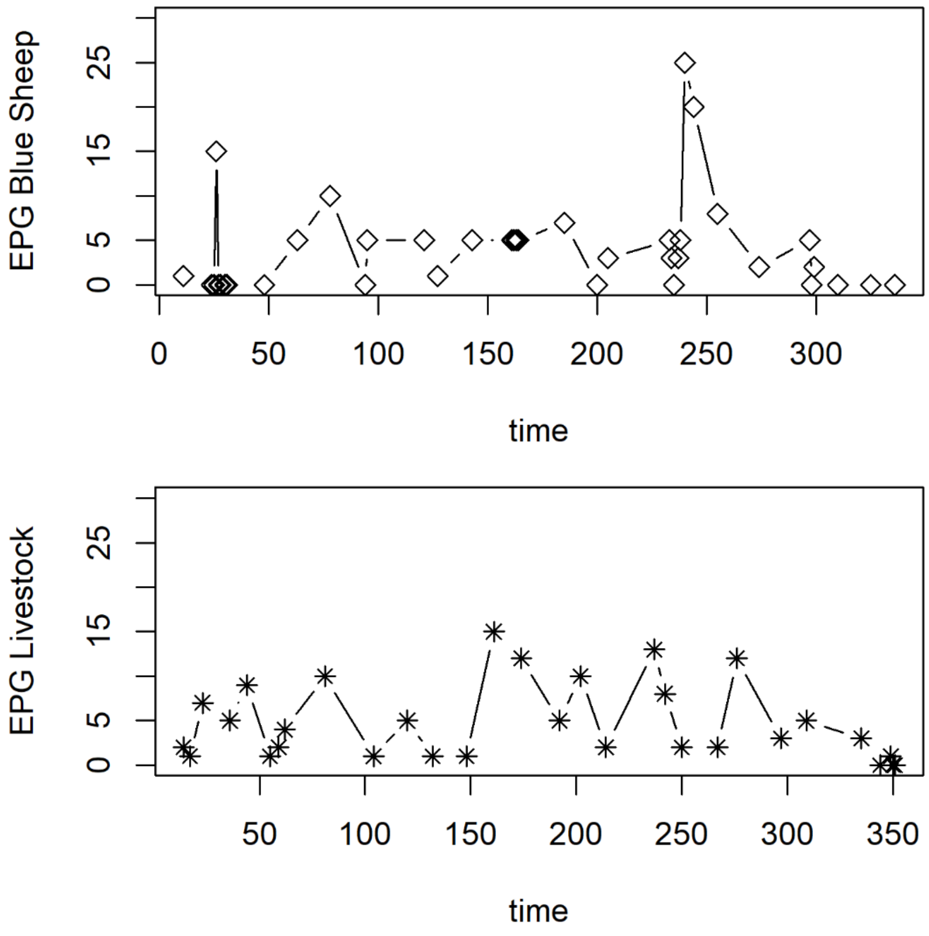
The estimated detection probability by model 'mt' for occasion one and two was interpreted as the detection probability for observer teams one and two. We estimated the total population of each ungulate species (N_{est}), as a product of the estimated number of groups ($\hat{G}$) and the estimated mean group size (μ). To estimate the confidence intervals of their population using the variance in estimated number of groups and the mean group size, we generated a distribution of estimated group size by bootstrapping it 10,000 times with replacement. A distribution of estimated population for each ungulate species(N_{est}) was generated by multiplying 10,000 random draws of estimated number of groups ($\hat{G}$) weighted by the posterior probability and draws of mean group size (μ). The median of the resultant distribution was the estimated ungulate population (N_{est}) and the 2.5 and 97.5 percentiles were used as the confidence intervals. The survey area was calculated by delineated the entire survey area of Google Earth Pro.

D - Table 2. Model parameters for *Teladorsagia Circumcinta* for the GLOWORM-FL Model

Parameter	Estimate*
$\boldsymbol{\delta}$	−0.02085 +0.00467T (F1,10 = 76.57, p < 0.001, R2 = 0.88, R2 adj = 0.87)
$\boldsymbol{\mu_1}$	exp(−1.62026−0.17771T + 0.00629T2) (F2,2 = 6.27, p = 0.27, R2 = 0.93, R2adj = 0.78)
$\boldsymbol{\mu_2}$	Same as above
$\boldsymbol{\mu_3}$	10 x μ_4
$\boldsymbol{\mu_4}$	exp(−4.58817−0.13996T + 0.00461T2) (F2,12 = 43.55, p < 0.001, R2 = 0.88, R2adj = 0.86)
$\boldsymbol{\mu_5}$	Same as μ_3
$\boldsymbol{m_1}$	0.21, P≥ 2 0, P < 2 and $\sum_{i=-7}^{t} \frac{P_i}{E_i} < 1$ 0.025, P < 2 and $\sum_{i=-7}^{t} \frac{P_i}{E_i} \geq 1$
$\boldsymbol{m_2}$	exp(−5.48240 +0.45392T−0.01252T2) (F2,1 = 442.9, p = 0.034, R2 > 0.99, R2 adj > 0.99)
C	0.1, $\sum_{i=7}^{t} \frac{P_i}{E_i} < 1$ 0, $\sum_{i=7}^{t} \frac{P_i}{E_i} \geq 1$

*T, temperature(◦C); P, total daily precipitation(mm); E , total daily evapotranspiration (mm).

** Rose et al. (2015) obtained these parameters from several published studies. The exact list can be seen in Rose et al. (2015).



D - Figure 1. Line graphs showing the FEC (faecal egg count) EPG (eggs per gram) of strongyle sp. in Blue sheep and Livestock. These were used as inputs to the GLOWORM-FL model. The X-axis refers to days with 0 = 1st January 2018 and 365 = 31st December 2018.

D – Table 3. GLOWORM-FL and Q0 model outputs and climate data for 1985-2018.

https://doi.org/10.5061/dryad.cc2fqz669

Appendix E – Supplementary material for chapter 6

E – Table 1. Faecal Egg Count Raw data for migratory livestock and Asiatic ibex in Pin

https://doi.org/10.5061/dryad.gmsbcc2nt

Appendix F – Supplementary material for chapter 7

F- Faecal Egg Count – Mini FLOTAC

For the sheep and goats, as they are herded as a unit, we collected fresh faecal samples, collating samples from as many different individuals as possible. Subsequently, we placed all the individual samples, each of similar volume, into a bag and mashed and mixed them thoroughly using digital pressure. From the mixed composite (pooled) sample, we measured 5 g faeces and mixed that thoroughly with 45 ml saturated sodium chloride salt solution. We then examined the suspension under a microscope at medium power, following the mini-FLOTAC method (Cringoli et al., 2017; see below). The same procedure was followed for saigas. Sample hereafter refers to a pooled sample (i.e. representing a group or herd). A total of 155 pooled faeces samples were collected: 79 from saigas and 76 from livestock.

The mini-FLOTAC technique (Cringoli et al. 2017) was used to evaluate the density of nematode eggs (Faecal Egg Counts – FECs). If multiple samples from the same host type were analysed on a given date, an average EPG was taken as input into the GIN transmission model (see below). We were specifically interested in the FEC of strongyle nematodes as they adversely impact wild and domestic ungulate health and fitness and are used as inputs for the GLOWORM-FL transmission model (Rose et al. 2015).

F- Climate data

To estimate onward development and survival rates of free-living GIN stages on pasture, we obtained daily temperature and precipitation from the POWER Data Access Viewer (DAV) provided by the National Aeronautics and Space Administration (NASA) (POWER 2020). We used the POWER Single Point Data Access widget, which provides access to near real-time 0.5 x 0.5 degree datasets for specific lat/long points. As we lacked exact point location of saigas, we calculated means of the mean daily temperature and precipitation values of 1000 randomly selected points within the two seasonal compartments – spring/summer (A) and fall/winter (B; Fig. 1) for the years 2000-2020.

F- Table 1. Host densities as inputs into the GLOWORM-FL model. Saiga density data were obtained from ACBK aerial surveys (Association for the Conservation of Biodiversity of Kazakhstan, unpublished data) while the livestock data was obtained by the Kazakh Statistical Bureau.

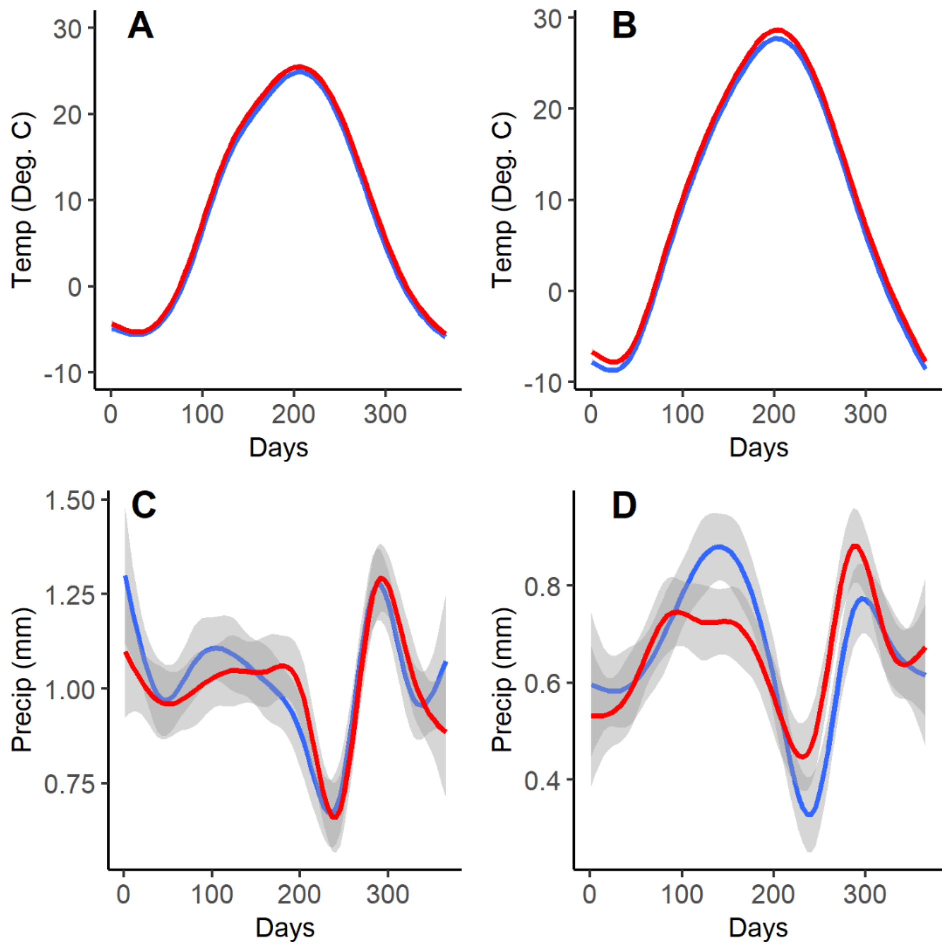
Hosts	Compartment A	Compartment B
Saiga (individuals km^{-1})	16.7	19.5
Livestock (individuals km^{-1})	5.25	8.34

F- Table 2. Model parameters for *Teladorsagia circumcinta* for the GLOWORM-FL Model.

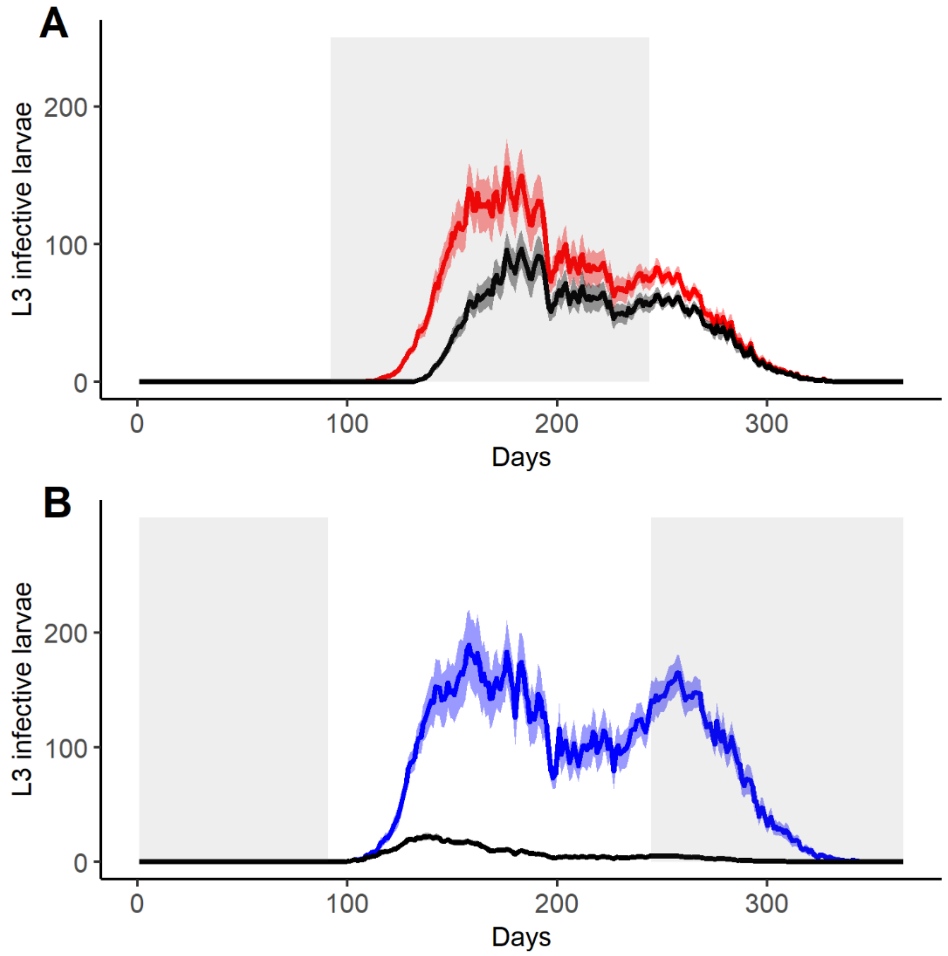
*T, temperature(◦C); P, total daily precipitation(mm); E , total daily evapotranspiration (mm).

** Rose et al. (2015) obtained these parameters from several published studies. The exact list can be seen in Rose et al. (2015).

Parameter	Estimate*	Data Source**
$\boldsymbol{\delta}$	$-0.02085 + 0.00467T$	Rose et al. (2015)
$\boldsymbol{\mu_1}$	$\exp(-1.62026 - 0.17771T + 0.00629T^2)$	
$\boldsymbol{\mu_2}$	Same as above	
$\boldsymbol{\mu_3}$	10 x μ_4	
$\boldsymbol{\mu_4}$	$\exp(-4.58817 - 0.13996T + 0.00461T^2)$	
$\boldsymbol{\mu_5}$	Same as μ_3	
$\boldsymbol{m_1}$	0.21, $P \geq 2$ 0, $P < 2$ and $\sum_{i=-7}^{t} \frac{P_i}{E_i} < 1$ 0.025, $P < 2$ and $\sum_{i=-7}^{t} \frac{P_i}{E_i} \geq 1$	
$\boldsymbol{m_2}$	$\exp(-5.48240 + 0.45392T - 0.01252T^2)$	
C	0.1, $\sum_{i=7}^{t} \frac{P_i}{E_i} < 1$ 0, $\sum_{i=7}^{t} \frac{P_i}{E_i} \geq 1$	



F- Figure 1. Simulated climate data for our case study site. Blue line represents the mean of the "baseline" climate simulation, while the red line represents the means of future climate simulations. The grey regions are the 95% confidence interval. **A**)= Temperature (ºC) in the spring/summer compartment, **B)** Temperature (ºC) in the autumn/winter compartment, **C)** Precipitation (mm) in the spring/summer compartment and **D)** Precipitation (mm) in the autumn/winter compartment.

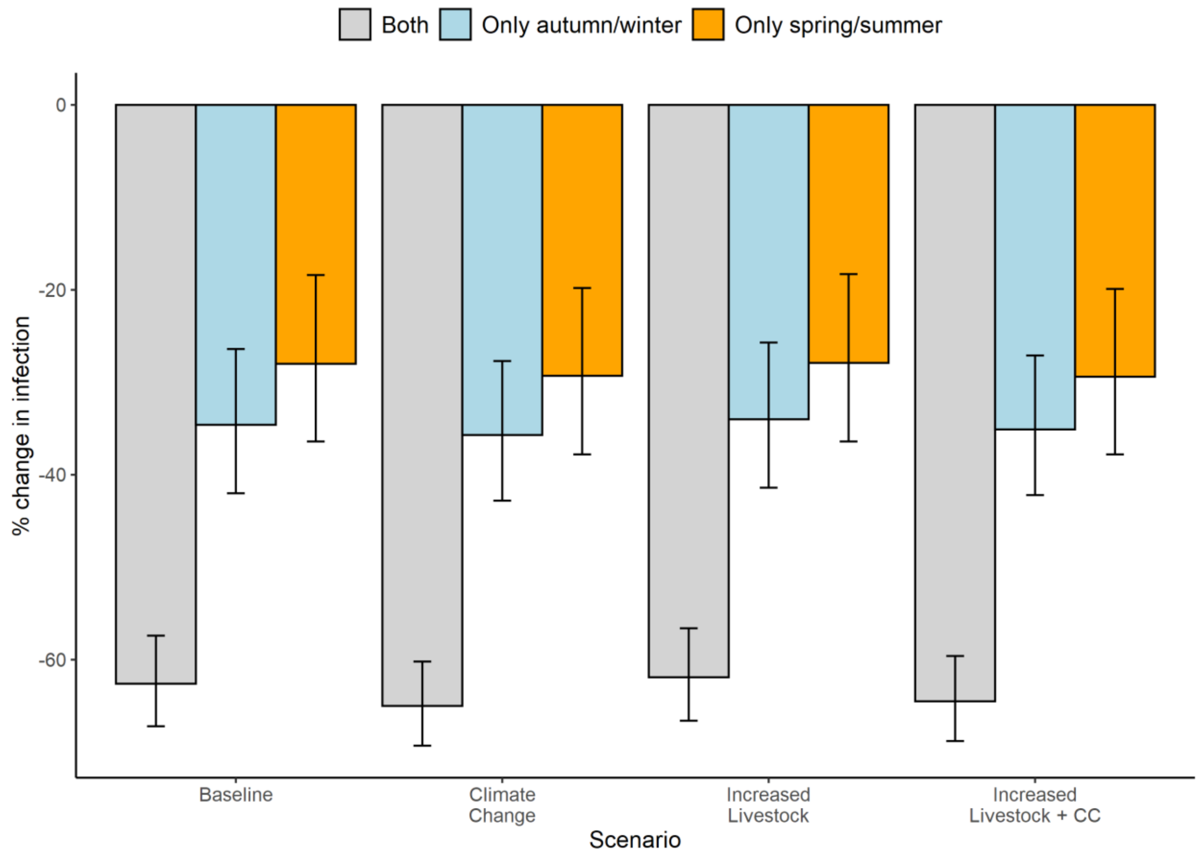


F- Figure 2. Infective larval load on pasture in the two-host Ural compartments for the period 2000-2020. **A:** spring/summer (red = no intervention, black = intervention), **B:** autumn/winter (blue = no intervention, black = intervention). The x-axis for each graph is day with 1 = 1st January and 365 = 31st December. The y-axis is the mean GLOWORM-FL output (number of $L3_h$ per kilogram of herbage) contributed by combined hosts (sheep/goat and saigas). The red, blue and black shaded areas are the 95% confidence intervals of the no intervention (red and blue) and intervention (black) scenarios respectively. The grey shaded areas are when saigas are present in either compartment.

F- Table 3. Future scenario table. Values represented are *AUCL3$_h$* experience by the saiga. Grey = early-season suppression. % change values with 95% confidence interval (CI) crossing zero represent no discernible change. Unless stated otherwise "Intervention -Yes" refers to early-season suppression in both seasonal compartments.

		Baseline	**Climate Change**	**Increased livestock**	**Increased livestock and Climate Change**	**Intervention**
Calving	*Mean [95% CI]*	656 [592 -721]	743 [663 - 824]	813 [734 - 892]	926 [827 - 1024]	**NO**
	Range	38 - 1087	120 - 1400	49 - 1332	159 - 1715	
	Change (%) [95% CI]	-	**+13.3 [-8.0 - + 39.1]**	**+23.9 [+1.8 - +50.7]**	**+41.2 [+14.7 - +73.0]**	
	Mean [95% CI]	75 [63 - 86]	75 [62 - 88]	85 [72 - 99]	85 [70 - 101]	**YES**
	Range	0.02 - 189	0.5 - 213	0.02 - 216	0.6 - 243	
	Attenuation (%) [95% CI]	**-88.5 [-85.4 - -91.3]**	**-89.9 [-86.7 - -92.3]**	**-89.5 [-86.5 - -91.2]**	**-90.8 [-87.8 - -93.2]**	
Spring/Summer	*Mean [95% CI]*	11889 [11184 - 12593]	11225 [10586 - 11863]	14532 [13676 - 15388]	13733 [12958 - 14508]	**NO**
	Range	5693 – 17897	5069 - 16088	7073 - 21822	6473 - 19657	
	Change (%) [95% CI]	-	**-5.6 [-15.9 - +6.1]**	**+22.2 [+8.6 - +37.6]**	**+15.5 [+2.9 - +29.7]**	
	Mean [95% CI]	6727 [6250 - 7203]	6004 [5592 - 6417]	8306 [7715 - 8896]	7399 [6889 - 7910]	**YES**
	Range	2511 - 10435	2082 - 9095	3135 – 12890	2488 - 11147	
	Attenuation (%) [95% CI]	**-43.4 [-35.6 - -50.4]**	**-46.5 [-39.4 - -52.9]**	**-42.8 [-35.0 - -49.9]**	**-46.1 [-39.0 – -52.5]**	
Autumn/Winter	*Mean [95% CI]*	6578 [6187 - 6969]	6573 [6148 - 6997]	7798 [7335 - 8261]	7820 [7312 - 8326]	**NO**
	Range	3449 - 10873	3246 - 10801	4071 - 12900	3865 - 12877	
	Change (%) [95% CI]	-	**0 [-11.8 - +13.1]**	**+18.5 [+5.3 - +33.5]**	**+18.9 [+4.9 - +34.6]**	
	Mean [95% CI]	183 [168 - 200]	222 [207 - 237]	211 [193 - 229]	255 [238 - 272]	**YES**
	Range	70 - 331	121 - 335	81 - 378	139 - 386	
	Attenuation % [95% CI]	**-97.2 [-96.8 - -97.6]**	**-96.6 [-96.1 - -97.0]**	**-97.3 [-96.9 - -97.7]**	**-96.7 [-96.3 - -97.1]**	
	Mean [95% CI]	18467 [17371 - 19559]	17798 [16734 - 18861]	22331 [21012 - 23649]	21553 [20270 - 22835]	**NO**
	Range	9124 - 28770	8315 - 26889	11144 - 34722	10338 – 32534	
	Change (%) [95% CI]	-	**-3.6 [-14.4 - +8.6]**	**+20.9 [+7.4 - +36.1]**	**+16.7 [+3.6 - +31.5]**	
	Mean [95% CI]	6911 [6418 - 7403]	6227 [5799 - 6654]	8517 [7908 - 9125]	7655 [7128 - 8183]	**YES**
	Range	2581 - 10766	2203 - 9430	3216 - 13268	2627 - 11533	

Annual	*Attenuation*	**-62.6 [-57.4 – 67.2]**	**-65.0 [-60.2 - -69.3]**	**-61.9 [-56.6 - -66.6]**	**-64.5 [-59.6 - -68.8]**	
	Mean [95% CI]	13305 [12438 - 14172]	12577 [11740 - 13414]	16104 [15051 - 17158]	15219 [14202 - 16237]	**SUMMER/SPRING ONLY**
	Range	5960 - 21308	5328 - 19896	7206 - 25790	6353 - 24024	
	Attenuation	**-28.0 [-18.4 - -36.4]**	**-29.3 [-19.8 - -37.8]**	**-27.9 [-18.3 - -36.4]**	**-29.4 [-19.9 - -37.8]**	
	Mean [95% CI]	12073 [11353 - 12793]	11447 [10794 - 12101]	14743 [13869 - 15617]	13989 [13197 - 14781]	**AUTUMN/WINTER ONLY**
	Range	5763 - 18228	5190 - 16423	7154 - 22200	6612 - 20043	
	Attenuation	**-34.6 [-26.4 - -42.0]**	**-35.7 [-27.7 - -42.8]**	**-34.0 [-25.7 - -41.4]**	**-35.1 [-27.1 - -42.2]**	



F- Figure 3. Bar-graph displaying the simulated % change (i.e. attenuation) in infection pressure (measured by *AUCL3*$_h$, the area under the curve of L3 density experienced by saigas) when early-season suppression is applied to livestock in both autumn/winter and spring/summer compartments together (grey), only autumn/winter compartment (blue), and only spring/summer (orange). The attenuation % is with respect to the *AUCL3*$_h$ of the corresponding scenario without the intervention (see SM4 Table 1). The bars represent simulated 95% confidence intervals. Overlapping 95% confidence interval are interpreted as not being statistically significantly different.

F- Table 4. $AUCL3_h$ values during calving experienced by saigas across different scenarios and split by years with (red) or without (green) a climate anomaly. Difference in mean $AUCL3_h$ between years with or without climate anomaly for each scenario combination is evaluated using a t-test. *p*-value of <0.05 is considered significant. Values within [ ] represent the range. Significant and near-significant results are shaded with grey.

CLIMATE ANOMALY	***NO CLIMATE ANOMALY***			
	Baseline x̄ = 646 [38 - 1087]	***Climate change*** x̄ = 743 [120 - 1401]	***Increased livestock*** x̄ = 815 [49 - 1332]	***Increased livestock and climate change*** x̄ = 930 [159 - 1716]
Baseline **x̄ = 621 [475 - 708]**	t = 0.296; df = 3.03; *p* = 0.786	t = 1.43; df = 3.50; *p* = 0.234	t = 2.30; df = 3.47; *p* = 0.092	t = 3.45; df = 4.33; *p* = 0.023
Climate change **x̄ = 751 [559-1199]**	t = -0.680; df = 3.34; *p* = 0.541	t = -0.051; df = 3.48; *p* = 0.962	t = 0.412; df = 3.47; *p* = 0.701	t = 1.12; df = 3.72; *p* = 0.328
Increased livestock **x̄ = 775 [589 - 898]**	t =-1.29; df = 2.61; *p* = 0.301	t = -0.314; df = 2.87; *p* = 0.775	t = 0.390; df = 2.848; *p* = 0.724	t = 1.44; df = 3.32; *p* = 0.236
Increased livestock and climate change **x̄ = 880 [610-1484]**	t =--1.13; df = 3.19; *p* = 0.335	t =-0.659; df = 3.26; *p* = 0.553	t =-0.310; df = 3.26; *p* = 0.775	t = 0.239; df = 3.39; *p* = 0.825