Investigating parasite dynamics of migratory ungulates for sustaining healthy populations: Application to critically-endangered saiga antelopes *Saiga tatarica*

Abstract

Contact between wild and domestic ungulates is increasing across rangelands, enabling disease co-transmission. Disease management is difficult given uncertainties in complex system behavior, limited empirical data, and logistical obstacles to interventions. We studied gastrointestinal nematode (GIN) transmission in a rangeland shared by both livestock and the critically-endangered migratory saiga antelope, *Saiga tatarica*, in order to model infection dynamics under current and plausible future scenarios of increasing livestock numbers, climate change and anti-helminth treatments. Our model was parameterised for trichostrongylid GIN – a cause of mortality and morbidity in ungulates globally - using data on observed faecal nematode egg output and host numbers and distribution. Results showed that seasonal saiga migration leads to asymmetry in parasite transmission, with the majority of GIN acquired by saigas in their autumn and winter range through prior pasture contamination from livestock. Consequently, reducing parasite burdens in livestock early in the season in these areas could disproportionately reduce cross-transmission to saigas. Early-season GIN suppression in livestock in the saiga's spring and summer range was predicted to have weaker effect on parasite transmission to saigas but reduces infections during the calving period, potentially increasing population health and resilience at this critical time. Optimally timed treatments could offset the effects of increasing livestock numbers on GIN infection pressure, whilst climate warming had only marginal impacts on GIN transmission under all scenarios. Our findings could support better understanding and mitigation of factors affecting saiga health and rural livelihoods. Our approach is transferable to other systems, particularly those with migratory hosts.

Keywords: parasite, transmission, saiga, ungulate, rangeland, disease, livestock

1.0 Introduction

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 and Fox 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 and 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 and 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. 2021a). 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 and 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.

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. 2010). 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. 2021a). 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. 2020).

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

78 conservation strategies need to consider disease (including MMEs) alongside threats like poaching, to
79 ensure the continued viability of the species (CMS 2021). MMEs are often associated with multiple
80 stressors that can work solely or in combination (Kock et al. 2018). Pasteurellosis-related MMEs in
81 saigas (in 1984, 1988 and 2015) were linked with high humidity and temperature, particularly around
82 the time of mass calving aggregations (Robinson et al. 2019)

83 As well as bacterial and viral pathogens, saigas are infected by various GINs and their migrations
84 have implications for GIN cross-transmission with livestock across their range (Morgan et al. 2007).
85 Major parasitic GINs in saiga antelopes include *Nematodirus gazellae*, *Marshallagia marshalli* and
86 *Teladorsagia circumcincta* to mention a few (Morgan et al. 2005a). Even sub-clinical infections from
87 such GINs are known to reduce growth rates in ruminants (Forbes et al. 2000). Moreover, GINs have
88 been linked to pasteurellosis as a source and trigger in reindeer, *Rangifer tarandus* (Kummeneje

89 1976). A die-off in Chamois *Rupicapra rupicapra* from pasteurellosis was possibly exacerbated by
90 GIN infestation (Posaultz et al. 2014). As mortality from pasteurellosis events is low in other species,
91 it is plausible that the high death rate of saigas due to pasteurellosis MMEs in 1984, 1988 and 2015
92 was associated with the presence of other pathogens, possibly GINs (although Kock et al. 2018 found
93 no evidence of this), or that GINs could exacerbate future MMEs, in combination with other factors,
94 including environmental conditions. Moreover, there is evidence of GIN-induced immune suppression
95 facilitating the invasion of diseases in wild ungulates (Ezenwa et al. 2010). Because the climate
96 anomaly in 2015 involved elevated temperatures, which also tend to favour GIN development, we
97 hypothesise that years in which an anomaly occurs will generate relatively high GIN infection
98 pressure, which could contribute to MME aetiology and/or impair population recovery from such
99 events.

100 Given this background, our primary aim was to understand GIN transmission dynamics in migrating
101 saigas, focusing on the Ural population, which increasingly shares pasture with growing livestock
102 populations. We assessed how GIN parasitism might change for saigas given the anticipated changes
103 in their habitats, using scenario analysis. Lastly, we tested an intervention scenario to reduce GIN
104 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.

2.0 Material 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).

2.1 Study site and populations

We focused on the Ural saiga population in Western Kazakhstan (Fig. 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. 2021a), 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 saiga 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.

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

2.2.1 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. 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 for the 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. To ensure accurate identification between livestock and saiga faeces, we first located the species, observed it until it defecated, and immediately collected the fresh faeces upon deposition. Samples were pooled at

157 the level of the Ural saiga population for saigas and per sheep/goat herd for livestock, following
158 Morgan et al. (2005b). A total of 155 pooled faeces samples were collected: 79 from saigas and 76
159 from livestock. We were interested in the faecal egg count (FEC) of strongyle nematodes as they
160 adversely impact ungulate health and fitness and are inputs for the GLOWORM-FL transmission
161 model (Rose et al. 2015). We used the mini-FLOTAC method (Cringoli et al. 2017) to estimate the
162 abundance of strongyle nematodes, which uses sedimentation-flotation to separate nematode ova from
163 the faecal matter which are then morphologically identified and quantified under a microscope (SM 1
164 – Faecal Egg Count).

165 *2.2.2 Transmission model (GLOWORM-FL) to predict pasture infectivity over time*

166 The GLOWORM-FL model is based on the life cycle of the free-living stages of trichostrongylid
167 GINs (Equations 1-7) (Rose et al. 2015). It estimates parasite development rates from eggs in faeces,
168 once deposited by hosts, to the third-stage infective larvae (L3), and their migration onto pasture,
169 while accounting for simultaneous weather-dependent mortality at each stage. This results in an
170 estimate of the number of L3 that are available for ingestion over time. Host faecal output (f) is
171 multiplied by the host species density (D) and number of eggs per gram of faeces (FEC) to estimate
172 egg output on pasture (E_{new}) on the sampling dates. E_{new} values were interpolated linearly between
173 sampling dates to obtain daily time series, which were used as input for simulations at daily intervals.
174 The development of L3 in faeces ($L3_f$) from eggs (E), via the pre-infective larval stages (L; Equations
175 2-4), is subjected to temperature-dependent stage-specific mortality rates (μ_i, where *i* corresponds to
176 the life cycle stage) and development rate (δ). Upon accounting for a moisture-limited development
177 success correction factor (C), overlapping nematode cohorts are tracked with newly deposited eggs
178 (E_{new}) added to existing eggs.

179 A temperature- and moisture-dependent horizontal migration rate (m_1) is used to estimate the L3
180 migration from faeces onto pasture ($L3_p$). As $L3_p$ can be in either the herbage ($L3_h$) or the soil ($L3_s$),
181 random bi-directional movement between soil and herbage was simulated with substrate-specific
182 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). This was done as transmission to livestock or saiga occurs predominantly from herbage, even though the GINs can be found in both herbage and soil. The biomass of dry herbage per hectare was estimated using the available data in 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. 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) (SM1 - 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 the parasitic GIN *Teladorsagia circumcincta* because this species tends to dominate in cool temperate areas, has similar responses to weather 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 SM2.

$$E_{new} = D(f \times FEC) \quad (1)$$

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

$$\frac{dL}{dt} = -(\mu_2 + 2\delta)L + 2\delta E \quad (3)$$

$$\frac{dL3_f}{dt} = -(\mu_3 + m_1)L3_f + 2\delta L \quad (4)$$

$$\frac{dL3_p}{dt} = -\mu_4((1-m_2)L3_p) - \mu_5(m_2 L3_p) + m_1 L3_f \quad (5)$$

$$L3_s = L3_p(1-m_2) \quad (6)$$

$$L3_h = L3_p m_2 \quad (7)$$

2.2.3 Predicting pasture infectivity across the Ural rangelands

Figure 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 (Khanyari et al. 2021b).

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. 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.

INSERT FIGURE 1

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 the amount of 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 and 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 former date range was to investigate the impact of the intervention on an annual scale, while the latter - a maximum 30 day intervention length - was derived from interviews with herders. It 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.

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 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 1 and SM3 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 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. We did not use the formal test as *p*-values themselves do not provide a good measure of evidence, they are prone to false positives, and often don't tell us about the magnitude or range of an effect (while bootstrapped 95% CI do indeed provide us with such information) (Karpen 2017).

INSERT TABLE 1

3.0 Results

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. 2A) as conditions become favourable for larvae development and survival. Saigas (2B) and livestock (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. 2D). Here, pasture infectivity is almost entirely contributed by livestock that were grazing over the summer period (2F), with saiga contributions being negligible ($AUCL3_h$ <10) and confined to late September/October (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 (SM2 Table 1) and slightly warmer weather (SM3 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 2C,F).

INSERT FIGURE 2

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. 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 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 (SM4, Fig. 1). The autumn/winter compartment had a more pronounced late-season small/secondary peak than the spring/summer compartment (Figure 2A and D), which is probably due to the slightly warmer weather in this compartment (SM3, Fig. 1).

INSERT FIGURE 3

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. 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. 4, SM5 Table 1). 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. 4; SM5 Table 1).

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 (SM6 Table 1).

ESS significantly reduced $AUCL3_h$ for all seasons and scenarios (Fig. 4, SM5 Table 1). 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. 4 and SM5 Table 1). 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 (SM5, Fig. 1).

INSERT FIGURE 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. 2010). 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. The model is well suited to exploring further scenarios, including changes in saiga population size and distribution, and how they might alter infection dynamics and the effectiveness of interventions in livestock. Alongside this, more nuance could be incorporated into the parasite model such as seasonal fluctuations in dung deposition rates that are likely to change depending on forage quality and water availability (Pfeffer et al., 2018). Field observations and experiments would be required to parameterize the model to enable these refinements to be included.

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 and 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. 1998), predicted L3 density on herbage (Fig. 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 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. 2020), and undernutrition is known to exacerbate GIN impacts in ungulates (e.g. Gulland and 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). For this reason, we selected mean strongyle egg counts to seed the model: this group includes several species of nematode that are common in both livestock and saigas in Kazakhstan and can cross between them (Morgan et al., 2005a); and which share similar climatic constraints on transmission (Van Dijk et al., 2008). GIN species more distantly related to *Te. circumcincta*, for example *Marshallagia marshalli*,

also share strong similarities in the effects of climate on the development and availability of infective larvae (Aleuy et al. 2019). Results therefore represent a first approximation of likely seasonal and between-host transmission dynamics, that can be revisited as further work reveals nuances of the composition of GIN communities in this system and ecological differences between GIN species.

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. 2). It is likely that GINs further stress individuals nutritionally and immunologically, particularly calving females (Gulland and Fox 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. 2021a). This aligns with the suggestions for migratory species in general that intervening where it matters the most is critical for cost-effective management (Singh and Milner-Gulland 2011; Allen and 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 (Khanyari et al.2021b).

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).

5.0 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.

Author Contributions

This study was conceived by MK, EJMG, NJS, SR and ERM. MK 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. MK analysed the data. All co-authors contributed to the writing of the manuscript.

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Figures

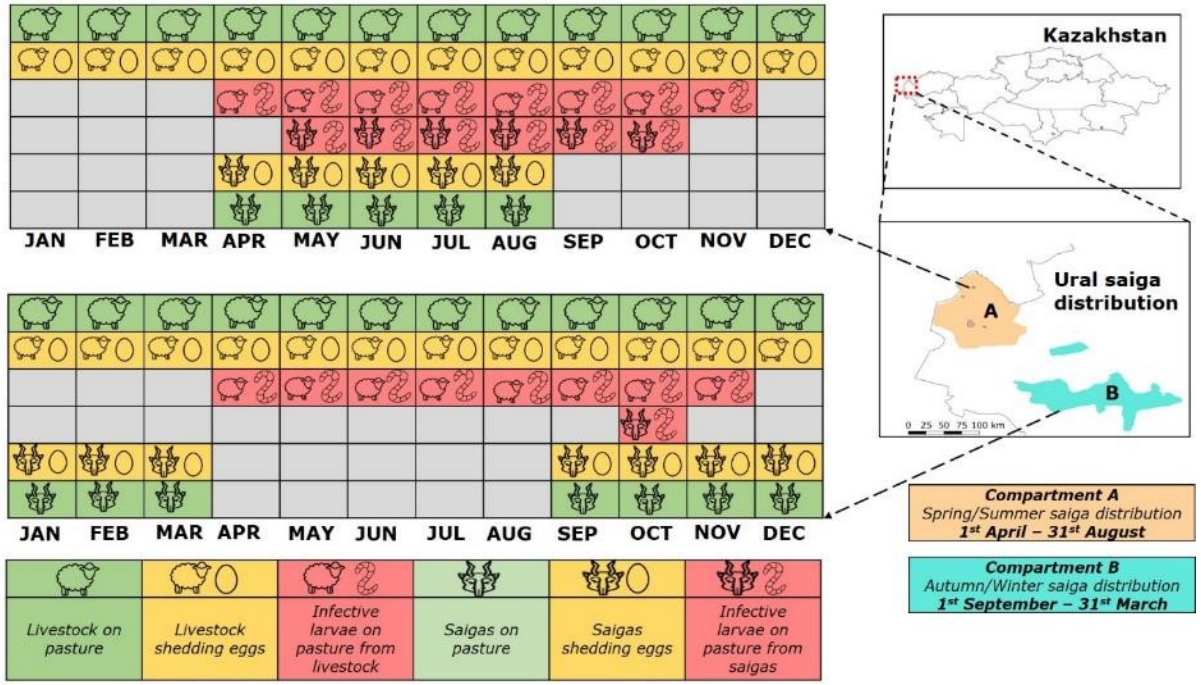


Figure 1. A schematic of the two-host parasite system in Ural, in the absence of intervention against parasites. Top map - location of the Ural saiga population in Kazakhstan, bottom map - seasonal distribution of saigas in Ural. Calving locations (small shaded polygons) are within the spring/summer saiga distribution. See text section 2.2.2 for detailed explanation. Icons courtesy of Noun Project.

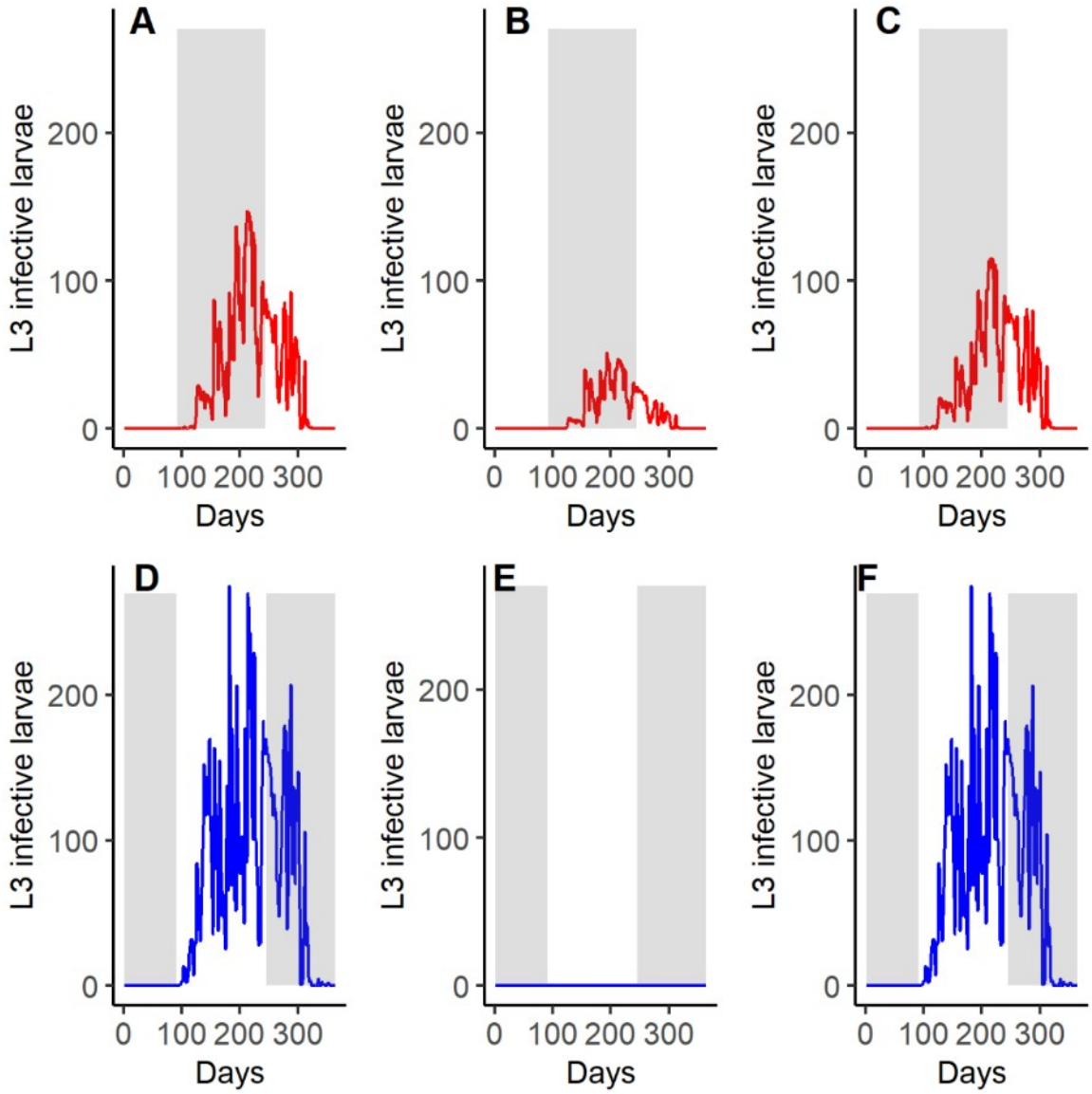
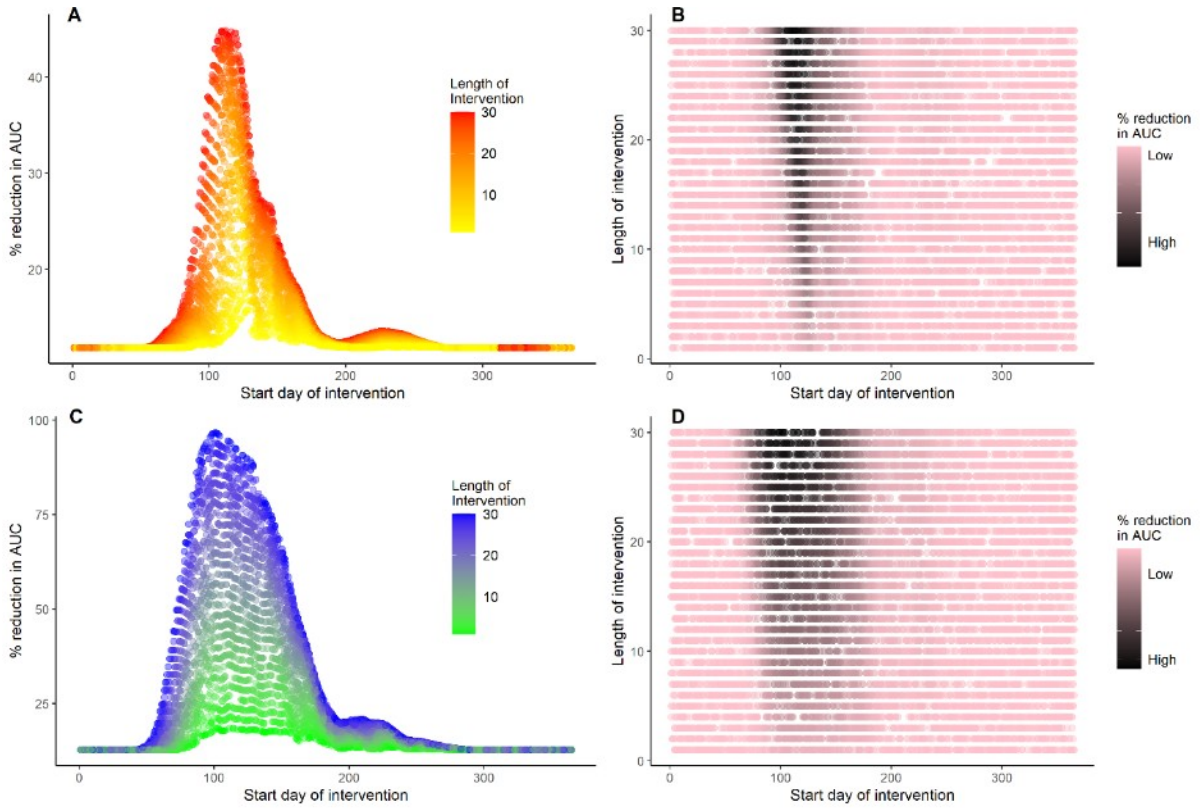


Figure 2. GLOWORM-FL output ($L3_h$ per kilogram of herbage) contributed by hosts in Ural in 2019. The x-axis: 1= 1st Jan. 2019 and 365 = 31st Dec. 2019. **A:** combined hosts in the spring/summer saiga distribution, **B:** saigas in the spring/summer saiga distribution, **C:** livestock in the spring/summer 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.



721

722 **Figure 3.** The simulation output for anthelmintic treatment in spring/summer **(A and B)** and autumn/
723 winter (**C and D**) compartments of the Ural saiga distribution. For plots **A** and **C** the x-axis is the start
724 day of intervention on a one year scale (day 1 to day 365), while the y-axis is the % reduction in
725 $AUCL3_h$ for a given combination of intervention length and start date. The colour of the points
726 represents the length of intervention (days). Note that the y-axes are different for the two
727 compartments, with a far higher $AUCL3_h$ reduction attained in the autumn/winter compartment. For
728 plots **B** and **D** the x-axis is the start day of intervention on a one year scale (day 1 to day 365), while
729 the y-axis is the length of intervention (1-30 days). The colour of the circles represents % reduction in
730 $AUCL3_h$, with high (black) corresponding to >40% reduction in **B** and >90% reduction in **D.**

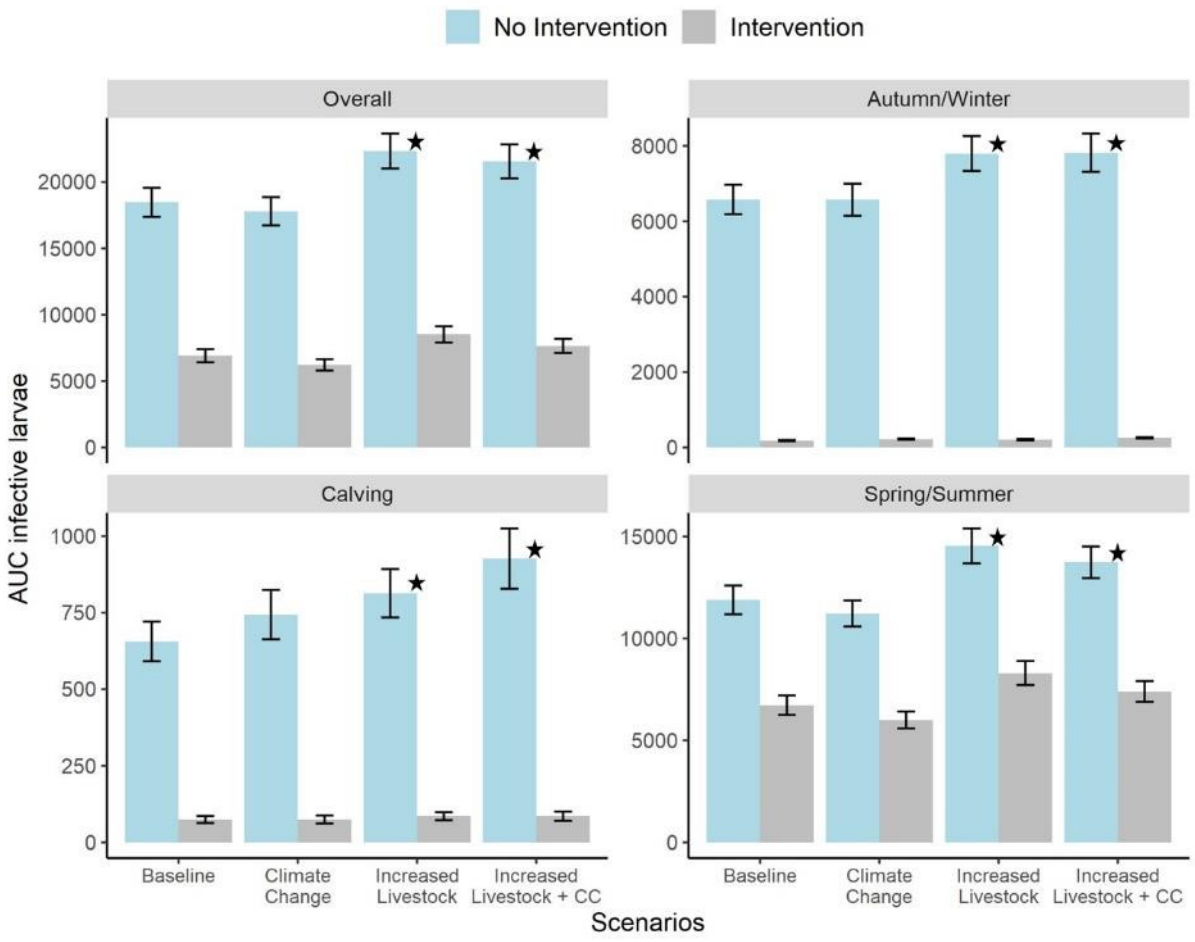


Figure 4. Panel graph displaying the mean $AUCL3_h$ (i.e., area under the curve of L3 density, an index of infection pressure, see text) experienced by saigas (with simulated 95% confidence intervals) for four different scenarios: baseline (current conditions), climate change, increased livestock, and 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.

742 **Table**

743 **Table 1.** Future scenarios for host numbers and climate in Ural, Kazakhstan, explored in the
744 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).

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

746

Supplementary Material 1 – Method details

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). 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 morphologically identified and quantified under a microscope. All samples were processed on the day of collection. The number of eggs found for strongyle nematodes was recorded for each pooled sample and multiplied by five to obtain FEC in eggs per gram (EPG) of faeces (see Cringoli et al., 2017 for details of the method). 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).

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 (500 in each compartment) within the two seasonal compartments – spring/summer (A) and fall/winter (B; Fig. 1) for the years 2000-2020. This was done by first randomly generating 500 points in each compartment. Daily values of temperature and precipitation were obtained for each point for the year 2000-2020, from the online interface of the POWER Single Point Data Access widget. For each compartment's 500 points per year, we obtained averaged daily temperature and precipitation values.

Supplementary Material 2 – Model Parameters

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. Aerial surveys occur usually annually in April (see Singh et al. 2010 for detail about the survey) while the livestock data is collected by Kazakh Statistical Bureau once at the end of each year.

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

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).

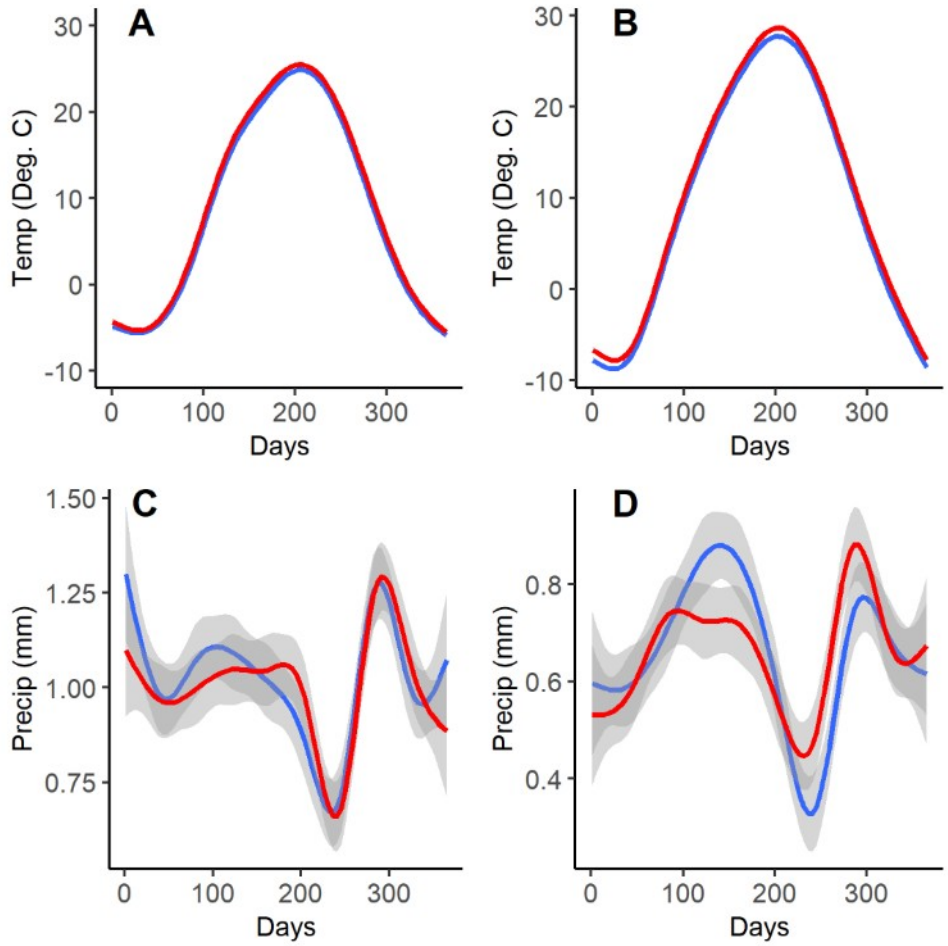
** Rose et al. (2015) obtained these parameters from several published studies. The exact list can be seen in Rose et al. (2015).

Parameter	Estimate*	Data Source**
δ	$-0.02085 + 0.00467T$	Rose et al. (2015)
μ_1	$\exp(-1.62026 - 0.17771T + 0.00629T^2)$	
μ_2	Same as above	
μ_3	10 x μ_4	
μ_4	$\exp(-4.58817 - 0.13996T + 0.00461T^2)$	
μ_5	Same as μ_3	
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 $\sum_{i=-7}^{t} \frac{P_i}{E_i} \geq 1$	

m_2	$\exp(-5.48240 + 0.45392T - 0.01252T^2)$	
C	$0.1, \sum_{i=7}^{t} \frac{P_i}{E_i} < 1$ $0, \sum_{i=7}^{t} \frac{P_i}{E_i} \geq 1$	

795

796 ***Supplementary Material 3- Simulated climate data***



797

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

803

Supplementary Material 4 – Early-season suppression

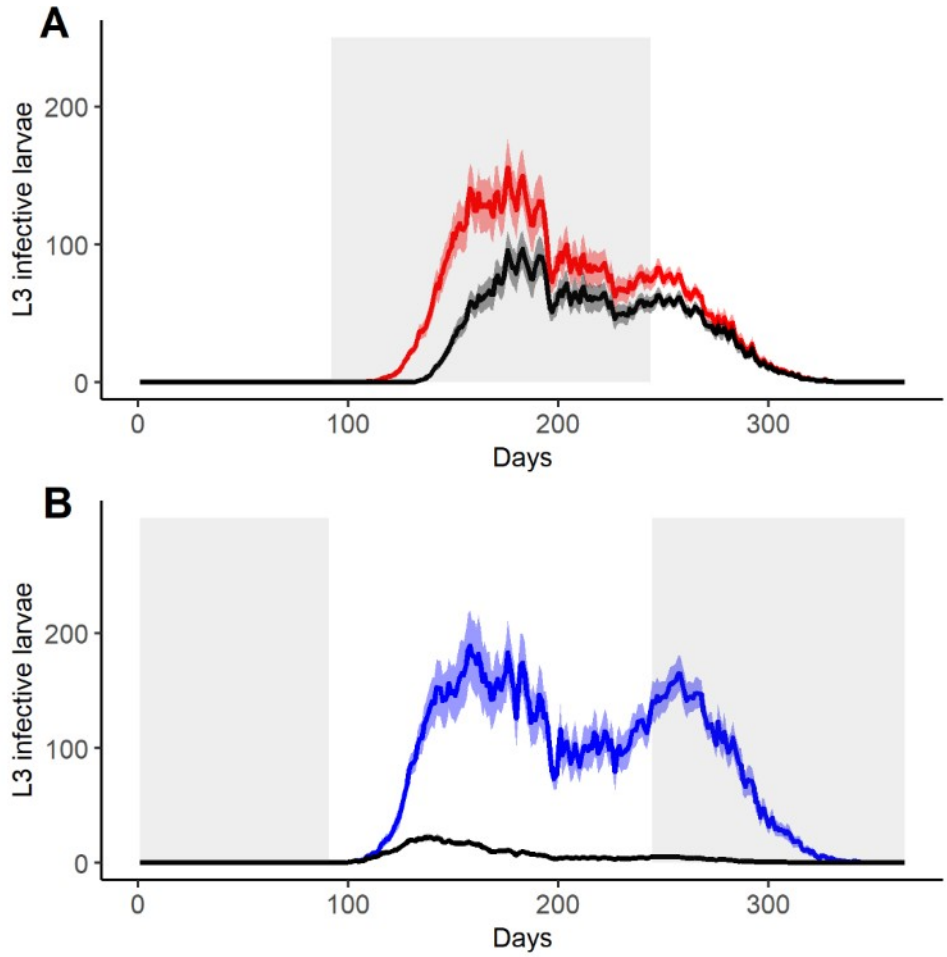


Figure 1. Infective larval load on pasture in the two-host Ural compartments for the period 2000-2020. Model output was generated for each year, from which the mean and the 95% confidence intervals of the outputs was generated. The red, blue and black shaded areas are the 95% confidence intervals of the no intervention (red and blue) and intervention (black) scenarios respectively. **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 grey shaded areas are when saigas are present in either compartment.

817 _

818 ***Supplementary Material 5– Future scenarios and changes in infection***

819 ***pressure to saigas***

820 **Table 1.** Future scenario table. Values represented are $AUCL3_h$ experience by the saiga. Grey = early-
821 season suppression. % change values with 95% confidence interval (CI) crossing zero represent no
822 discernible change. Unless stated otherwise "Intervention -Yes" refers to early-season suppression in
823 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]**	
Annual	*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 (%)	-	**-3.6 [-14.4**	**+20.9 [+7.4 -**	**+16.7 [+3.6 -**	

	[95% CI]		**- +8.6]**	**+36.1]**	**+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	
	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]**	

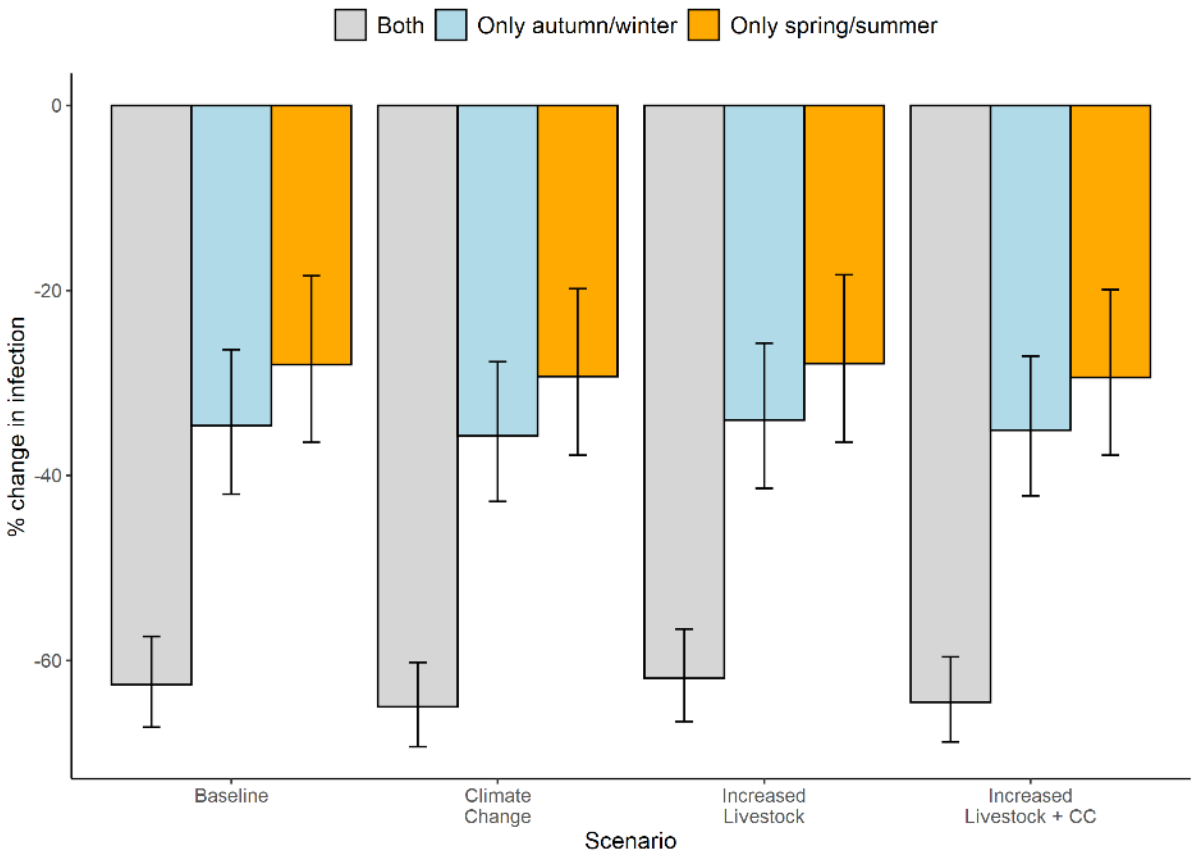


Figure 1. Bar-graph displaying the simulated % change (i.e. attenuation) in infection pressure (measured by $AUCL3_h$, the area under the curve of L3 density experienced by saigas) when early-season suppression is applied to livestock in both autumn/winter and spring/summer compartments together (grey), 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.

Supplementary Material 6 – How does infection pressure changes across scenarios with or without climate anomaly

Table 1. $AUCL3_h$ 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.

	NO CLIMATE ANOMALY			
CLIMATE ANOMALY	***Baseline*** $\bar{x}$ = 646 [38 - 1087]	***Climate change*** $\bar{x}$ = 743 [120 - 1401]	***Increased livestock*** $\bar{x}$ = 815 [49 - 1332]	***Increased livestock and climate change*** $\bar{x}$ = 930 [159 - 1716]
Baseline **$\bar{x}$ = 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 **$\bar{x}$ = 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 and climate change **$\bar{x}$ = 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