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Predicting and reducing potential parasite infection between migratory livestock and resident Asiatic ibex of Pin valley, India

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Disease cross-transmission between wild and domestic ungulates can negatively impact livelihoods and wildlife conservation. In Pin valley, migratory sheep and goats share pastures seasonally with the resident Asiatic ibex (*Capra sibirica*), leading to potential disease cross-transmission. Focussing on gastro-intestinal nematodes (GINs) as determinants of health in ungulates, we hypothesized that infection on pastures would increase over summer from contamination by migrating livestock. Consequently, interventions in livestock that are well-timed should reduce infection pressure for ibex. Using a parasite life-cycle model, that predicts infective larval availability, we investigated GIN transmission dynamics and evaluated potential interventions. Migratory livestock were predicted to contribute most infective larvae onto shared pastures due to higher density and parasite levels, driving infections in both livestock and ibex. The model predicted a *c.*30-day anti-parasitic intervention towards the end of the livestock's time in Pin would be most effective at reducing GINs in both hosts. Albeit with the caveats of not being able to provide evidence of interspecific parasite transmission due to the inability to identify parasite species, this case demonstrates the usefulness of our predictive model for investigating parasite transmission in landscapes where domestic and wild ungulates share pastures. Additionally, it suggests management options for further investigation.

Keywords. Disease; epidemiology; gastrointestinal nematode; intervention; parasite; ungulate

1. Introduction

Many pathogens and parasites found in domestic livestock also infect sympatric wildlife, especially ungulates and vice versa. Disease cross-transmission can have negative impacts on agricultural economies and conservation, and is of concern for wildlife and livestock managers alike (Smith *et al.* 2009; Scasta 2015). Among disease-causing agents, gastro-intestinal nematodes (GINs) are particularly of concern as they can determine host health and production in wild and domestic ungulates (Gulland 1992; Perry and Ran-

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dolph 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), while host behaviour, density, and diversity can influence whether and when stages encounter 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 (Malczewski *et al.* 1996; Morgan *et al.* 2004). Human interventions to control GINs in livestock can consequently affect GINs in wildlife through reduction of shared parasite loads (Weinstein and Lafferty 2015).

Investigating parasite transmission between wildlife and livestock is challenging. Data on infection levels in wildlife are often scarce and open to bias, and are not in themselves sufficient for assessment of cross-species transmission potential (Morgan *et al.* 2006, 2007). Investigating impacts of GIN transmission is especially difficult, yet pertinent, in remote rangelands with migratory hosts (Scasta 2015). Seasonal host movement can result in complex contact patterns, affecting disease transmission across species (Khanyari *et al.* 2021a). Predictive disease models offer a way to identify 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 towards livestock. Nevertheless, testing control options in practice is difficult, expensive and can be 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 understudied issue is transhumant livestock herding in mountainous regions, where livestock and wild ungulates co-graze pastures (Mishra *et al.* 2021). These ecosystems are highly seasonal, hosts are often mobile, and areas are remote and understudied (e.g., Ghoshal 2017). Mountain regions are threatened by climate change, with communities often dependent on livestock for their livelihoods and are home to wild ungulate species of conservation concern (e.g. Saberwal 1996; Bagchi *et al.* 2004; Ghoshal 2017). The remoteness of these landscapes, along with logistical challenges such as obtaining sufficient parasite data from wild species that occur in rather low densities in these regions, often makes disentangling the parasite dynamics of this ecosystem especially difficult when using only empirical data. Therefore, these ecosystems are ideal candidates for model-based testing of potential interventions to explore their viability.

Transhumant communities inhabit mountains across the globe (Kuznar 1991; Saberwal 1996; Huntsinger *et al.* 2010; Ayantunde *et al.* 2014). In particular, there are several transhumant communities in the Indian trans-Himalayas, like 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 Pin valley. Here the migratory livestock herders—the Kinnaura—share pasture seasonally (in summer) with Asiatic ibex, *Capra sibirica.* Local sedentary small-bodied ruminant livestock are present in the villages of Pin valley but are low in number and seldom share pasture with the ibex (Khanyari *et al.* 2022a). 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 and 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, 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), which could facilitate spill-over of parasites from migratory livestock to ibex, since GINs have free-living stages in the environment (Khanyari *et al.* 2022a). 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 cross-species GIN transmission in Pin valley (Rose *et al.* 2015).

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. Our primary research aim was to investigate the GIN parasite transmission dynamics between migratory livestock and ibex in Pin valley. We hypothesized that historical pasture use (e.g., egg shedding) over months, along with periods of accumulated larval development will determine the availability of infective larvae on pasture; this is because Pin valley's highly seasonal temperate pastures (Bagchi *et al.* 2004) are characterized by moderate temperatures (hence slow parasite development) and low precipitation, hence a more prolonged impact of precipitation events on parasite transmission (Morgan and van Dijk 2012).

At the same time, we explored what actions taken in livestock herds might limit GIN transmission to wild ungulates. For this, we virtually evaluated the outcomes of possible interventions—various timings and duration of anthelmintic-induced reduction of GIN eggs contributed to pasture by livestock—to attenuate infection pressure for both the Kinnaura flocks and ibex, using a sensitivity analysis. Our approach, illustrated in figure 1, 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.

2. Material and methods

2.1 *Study area*

The study area centred on the 497 km^2 Pin valley (32° N 78° E), which is within Lahaul-Spiti district, Himachal Pradesh, India (figure 2). Part of the study area is a protected area, the Pin Valley National Park. The region is characterized by low precipitation (<500 mm annually, with most precipitation in the form of snow), a short growing season and low primary productivity (Mishra *et al.* 2001). This high-altitude (average 4420 m) region experiences extreme climate, 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 (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, the number of sheep and goats has drastically declined in Pin (930 in 2003 to 55 in 2019) while large livestock (yaks, dzos, cattle and horses) have slightly increased (1326 in 2003 to 1866 in 2019). The other major land use is agriculture, and local people grow varieties of barley and pea (Mishra 2001). Additionally, migratory herders—the Kinnaura—have traditional rights/leases over a few pastures for seasonal grazing.

The Kinnaura herders undertake a long-distance migration with their sheep and goats. They are native to the Rupi-Bhaba area (31.5° N, 77.9° E), where they spend a large part of the spring season (April–May) and autumn (September–October; figure 2). 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).

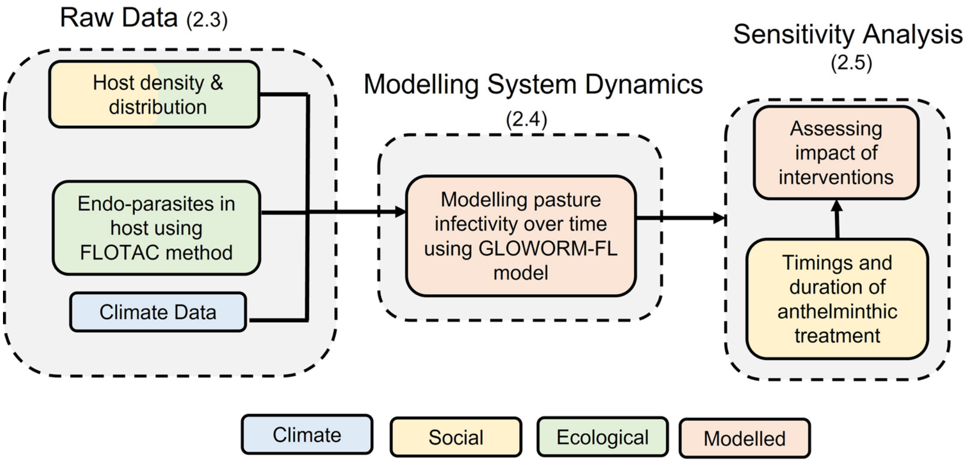

Figure 1. A schematic representation of how various forms of information combine to give an overall understanding of the two hosts (ibex and sheep + goat combined) GIN system to inform control measures. The numbers indicate the sections within the paper.

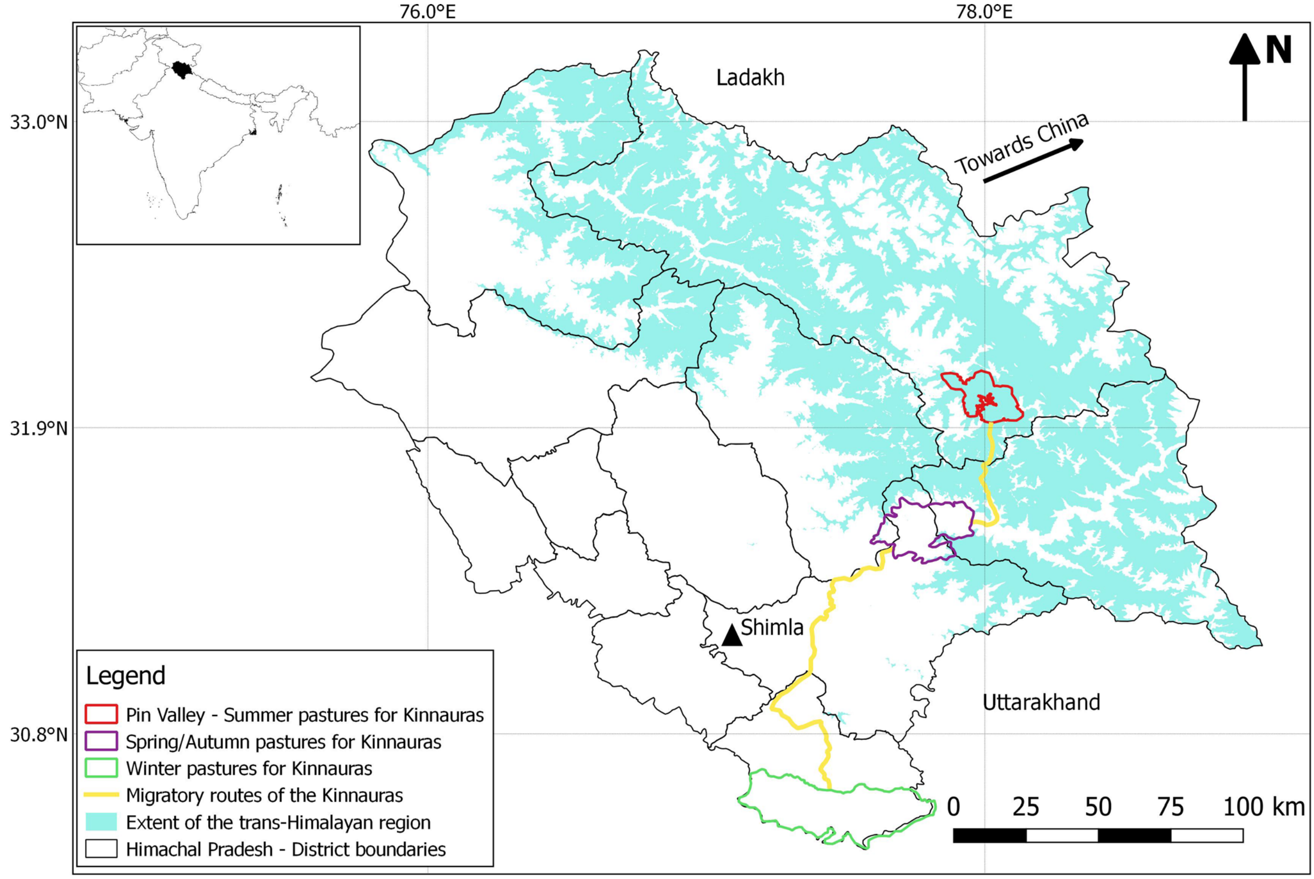

Figure 2. Map displaying the migratory route and seasonal pastures of the Kinnaura herders. The inset map shows the state of Himachal Pradesh within India. Our study area (Pin valley, 497 km^2) is outlined in red and exists entirely within the trans-Himalayan region (*c.* 3200–5200 m). Map boundaries were obtained from *https://hplahaulspiti.nic.in/*.

Our modelling approach is adapted from Khanyari *et al.* (2022b), who applied it to migratory saigas and resident livestock in Kazakhstan. However, while we use the same parasite life-history model and sensitivity analysis, our research questions here differ as does the target system, which has resident wild ungulates and migratory livestock. This difference exemplifies the flexibility of the model framework and its applicability to transhumant systems more globally.

2.2 *Parasite life cycle*

Our model is based on the life cycle of the free-living stage of trichostrongylid GINs (see section 2.4). Figure 3 illustrates the life cycle of trichostrongylid GINs. Figure 3a is a schematic whereas figure 3b displays each component of the life cycle. These parasites have a direct life cycle with no intermediate hosts. Adult parasite females lay eggs in the gut of the host which are subsequently shed with the faeces on pasture. Once in the environment, eggs (E) release the larvae (L) that complete the development to infective third stage (L3) larvae, with a lag that is determined by suitable weather (adequately warm temperature and sufficient evapotranspiration). This lag is longer with colder weather. The L3 then migrate out of faeces into soil ($L3_s$) and onto herbage ($L3_h$).

Hosts get infected after ingesting L3 larvae while grazing. In shared pasture such as in Pin, this process can lead to cross-transmission (figure 3a). After ingestion, the parasitic larvae complete its development to adult worms in the gut. The prepatent period (time between infection and first eggs shed) varies depending on the parasite species and the host (Rose *et al.* 2015).

2.3 *Data collection: Parasites and climate as inputs for the parasite model*

Data from local, sedentary sheep and goats were not collected as they are extremely low in number and do not share pasture with ibex (Khanyari *et al.* 2022a). Fresh faecal pellet samples were collected from

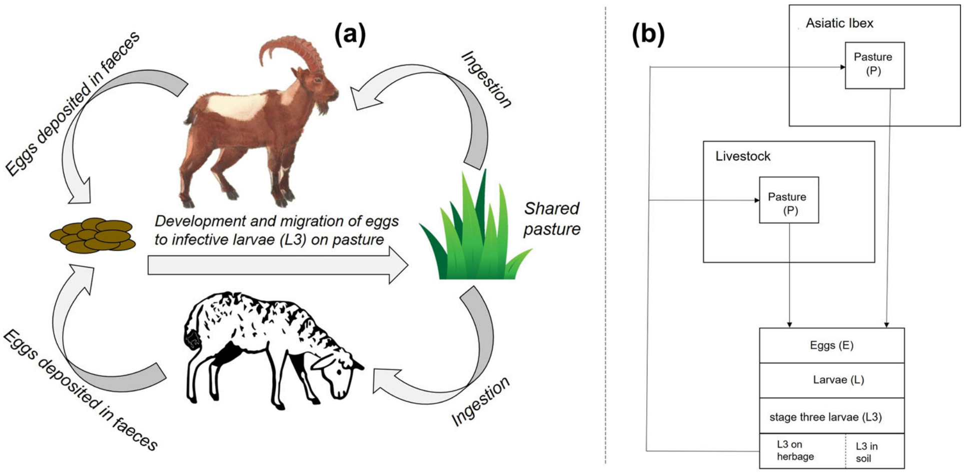

Figure 3. **(a)** A schematic of GIN transmission in our case study site. Above, Asiatic ibex; below, livestock (sheep/goat). Sheep icon courtesy Francesco Cesqo Stefanini (noun project) and ibex courtesy Sartaj Ghuman. **(b)** Conceptual diagram of the GLOWORM-FL model framework.

migratory livestock (sheep and goats), and ibex. Data collection for ibex occurred throughout the year 2019, whereas for the migratory flocks, it occurred in June–August 2019, i.e., during the time they spend in Pin valley. Collection was opportunistic, with fresh faeces collected from the ground. To ensure we were correctly sampling the target species, we observed individuals deposit fresh pellets and subsequently collected them from the ground. Care was taken to ensure that animals were not disturbed while collecting the samples. As ibex in Pin valley live in proximity to humans, they exhibit limited evasive movement (Ghoshal 2017). Also, while there are several precipitous regions across Pin valley, often ibex and livestock use undulating pasture to graze in (Bhatnagar 1997), where pellets would remain and not roll downhill. For ibex, samples were opportunistically collected from all age and sex classes. The date and location of each sample was recorded. We pooled fecal samples within species type (ibex or livestock) to aid with faecal egg counts (Morgan *et al.* 2005). A pooled sample for ibex consisted of individual faeces, mixed thoroughly together, from at least 15 different individuals of varying age-sex classes found in a general area on a specific day. As sheep and goats are herded as one unit, we collected combined fresh faecal samples from them, taking various samples from different individuals of sheep and goats, and collecting as many as possible at a given time (at least 15 different individuals for one pooled sample).

Faecal egg counts (FEC) were conducted on pooled faecal samples to evaluate the number of helminth eggs reaching the pasture to seed onward transmission, and as an indirect indicator of parasite burden. A mini-FLOTAC method (Cringoli *et al.* 2017) was used as a field-friendly 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, which were quantified morphologically under a microscope. From a well-mixed composite (pooled) sample, we took 5 g of faeces and mixed that with 45 ml saturated sodium chloride salt solution (we added about 40–45 g of sodium chloride in 100 ml water), and then examined the suspension under a microscope, following procedures of Cringoli *et al.* (2017). The same was done for ibex and livestock. Livestock samples (n=65) were therefore pooled at the level of each migratory livestock herd, with all 28 herds being sampled, and ibex samples (n=74) were pooled at the level of the study population (Morgan *et al.* 2005; see supplementary table 1). The uneven pooling of samples, i.e., at the population level for ibex and at the herd level for livestock, can bias FEC results as parasite eggs are known to aggregate in faeces (Grenfell *et al.* 1995). Nonetheless, Morgan *et al.* (2005) showed that FECs in a well-mixed composite sample of 10 sheep (3 g of faeces from each) is likely to provide an adequate estimate of a herd or group mean FECs. Moreover, for entry into the parasite model, herd-level counts were averaged, effectively giving a population-level average FEC. Sample hereafter refers to a pooled sample.

The number of eggs of strongyle parasites 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 used the bootstrap t-test to compare the difference in mean abundance of endoparasites between ibex and livestock (Wilcox 2017). We were particularly interested in the FEC of strongyle nematodes as they are used as input into the GLOWORM-FL model (see 2.4).

Primary meteorological data were not available. Therefore, interpolated datasets were used to estimate parasite vital rates within the population dynamic models (below). We attained daily temperatures and precipitation from the POWER Data Access Viewer (DAV) (POWER 2020), which offers access to almost real-time 0.5×0.5 degree datasets by single point (latitude and longitude). This was obtained 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 and 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).

2.4 *Transmission model: predicting pasture infectivity over time*

The aim of the transmission model is to predict infective larvae over time on pasture using the data inputs of GIN counts, climate data (temperature and precipitation) and the life-history parameters of the GINs of interest (figure 1). The predictive model is based on the life cycle of the free-living stages of trichostrongylid GINs (see equations 1–7 below), as described by the GLOWORM-FL model (Rose *et al.* 2015). GLOWORM-FL explicitly includes movement of infective larvae between the herbage and soil, and incorporates moisture related limitations on the movement of larvae between faeces and pasture (both herbage and soil) (Rose *et al.* 2015) (figure 3).

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 host density—which we obtained from Khanyari *et al.* (2022a)—and host faecal output (f) (equation 1; figure 3b). 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) (equations 3 and 4; figure 3b). To predict change in population size, overlapping nematode cohorts are tracked using differential equations, with existing eggs being replenished by newly deposited eggs (E_{new}), after taking into account a moisture-limited development success correction factor (C) (equation 2; figure 3b).

The progress of L3 from faeces onto pasture (L3_{p}), is mediated by a climate-dependent horizontal migration rate (m_1). The horizontal migration rate (m_1) is the instantaneous daily rate of L3 moving from faeces onto pasture (L3_{p}). 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 (equations 5–7; figure 3b). The vertical migration rate (m_2) is the proportion of total pasture L3 (L3_{p}) on herbage (L3_{h}). The state variables and parameters are defined in

Table 1. State variable and parameter definitions*

State variable/parameter	Definition	Units
E	Eggs	Count
L	First stage (L1) and second stage (L2) larvae	Count
L3_{f}	Third stage infective larvae (L3) in faeces	Count
L3_{p}	Total L3 on pasture (soil and herbage combined)	Count
L3_{s}	L3 in soil	Count
L3_{h}	L3 in herbage	Count
δ	Development rate from egg to L3	Instantaneous daily rate
μ_1	Egg mortality rate	Instantaneous daily rate
μ_2	L1 and L2 mortality	Instantaneous daily rate
μ_3	L3 mortality rate in faeces	Instantaneous daily rate
μ_4	L3 mortality rate in soil	Instantaneous daily rate
μ_5	L3 mortality rate on herbage	Instantaneous daily rate
m_1	Horizontal migration of L3 onto pasture	Instantaneous daily rate
m_2	Proportion of total pasture L3 on herbage	Proportion
C	Development success correction factor	Proportion

*Obtained from Rose *et al.* (2015).

table 1, while the estimates of model parameters are displayed in table 2.

We ran the model in R version 3.6.3 (R Core team 2020), using the *lsoda* function ('deSolve' package) (Soetaert *et al.* 2010). The model output is the daily number of individual GINs per hectare for each life-stage. We calculated $L3_h$ per kg dry matter of herbage (L3/kg DM) by dividing $L3_h$ (equation 7; figure 3b) by the biomass of dry herbage per hectare (parameterized from Bagchi and Mishra 2006). Henceforth, pasture infection denotes $L3_h$ per kg dry herbage (L3/kg DM). Annual infection pressure was estimated by summing daily L3/kg DM for the whole year, i.e., area under the curve ($AUCL3_h$). FECs were fed in (see 2.3) to seed the model. Total egg output per hectare was estimated based on the host weight obtained from the literature and averaged across sexes (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 the relative contribution of each host to pasture infectivity, the model was run for ibex separately, livestock separately, and ibex and livestock combined together, in the manner of Morgan *et al.* (2007) and Khanyari *et al.* (2021b) for 30 years of climate data (see 2.3). 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 valley, 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.

Table 2. Model parameters for *Te. circumcincta* for the GLOWORM-FL model

Parameter	Estimate*
δ	−0.02085 + 0.00467T (F1,10 = 76.57, p < 0.001, R2 = 0.88, R2adj = 0.87)
μ_1	exp(−1.62026−0.17771T + 0.00629T2) (F2,2 = 6.27, p = 0.27, R2 = 0.93, R2adj = 0.78)
μ_2	Same as above
μ_3	$10 \times \mu_4$
μ_4	exp(−4.58817−0.13996T + 0.00461T2) (F2,12 = 43.55, p < 0.001, R2 = 0.88, R2adj = 0.86)
μ_5	Same as μ_3
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 $\sum_{i=-7}^{t} \frac{P_i}{E_i} \geq 1$
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). Data source obtained from several published studies. The exact list can be seen in Rose *et al.* (2015).

We used parameters for the GIN *Teladorsagia circumcincta*, because this species tends to dominate in cool temperate areas, and has similar responses to climate outside the host as other common genera like *Trichostrongylus* (O'Connor *et al.* 2006). Studies from the western Himalayan regions (similar to Pin valley) have found *Trichostrongylus* species to be common in ruminants (Dhar *et al.* 1982; Jithendran and Bhat 1999). Additional details about the model, including parameters used, are in Rose *et al.* (2015).

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

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

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

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

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

$$L3_s = L3_p(1 - m_2) \tag{6}$$

$$L3_h = L3_p m_2 \tag{7}$$

2.5 *Simulation model: identifying optimum times and duration of intervention*

We concentrate on livestock-centred interventions, since doing health interventions in ibex is logistically challenging and 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 $L3_h$

Table 3. Endo-parasite prevalence, range (eggs per gram) and mean (± standard error) across migratory livestock and ibex in Pin valley

		*Strongyloides**	*Strongyle* GINs[2]*	*Nematodirus**	*Trichuris**	*Moniezia*
Migratory livestock (*n*=65)	Prevalence[1]	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)
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)

[1] Prevalence is expressed at the level of the pooled sample and not the individual animal. Livestock comprise mixed groups of sheep and goats.

[2] *Strongyle* includes eggs morphologically characteristic of the Trichostrongyloidea.

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

per kg of herbage, integrated over the defined time period ($AUCL3_h$), which evaluated 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.* (2022). Here, we assessed the combination of intervention attributes, start date and length, that resulted in the highest reduction in $AUCL3_h$. For the sensitivity analysis, we varied the intervention features by altering the start date of the intervention 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 one month in length was unlikely to be feasible due to issues of cost and anthelmintic availability. Also, longer treatments 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 in the simulation were recorded for post-hoc visualization.

3. Results

3.1 *Predicting pasture infectivity over time*

We analysed 65 pooled fresh faecal samples from migratory livestock, and 74 samples from ibex. Endoparasites present in these samples and their prevalence are presented in table 3 (Khanyari *et al.* 2022a). Shared GINs between both types of livestock and ibex were *Strongyloides* sp., *strongyle* GINs and *Nematodirus* sp. They also shared the platyhelminth *Moniezia* sp. Overall endoparasite loads were significantly higher in migratory livestock than ibex (t=5.94, df=76.71, $p < 0.0001$). This was also true when considering *strongyle* GINs alone (table 3). We 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 valley (supplementary 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 pasture contamination peaks throughout their time in Pin valley (*c.* day 152 – day 243, i.e., 1st June – 31st August; figure 4a). 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 valley. The total number of infective larvae on pasture ($L3_h$) contributed by migratory livestock is magnitudes higher than that contributed by ibex ($AUCL3_h$ ibex = *c.*1100, $AUCL3_h$ livestock = *c.*92,000). Using climate data for each year between 1990 and 2019, and parameterizing GLOWORM-FL model egg inputs using the field data from 2019, we found that parasite transmission seasonality in Pin valley has remained relatively similar across a 30-year time period (figure 4d), with infective larvae

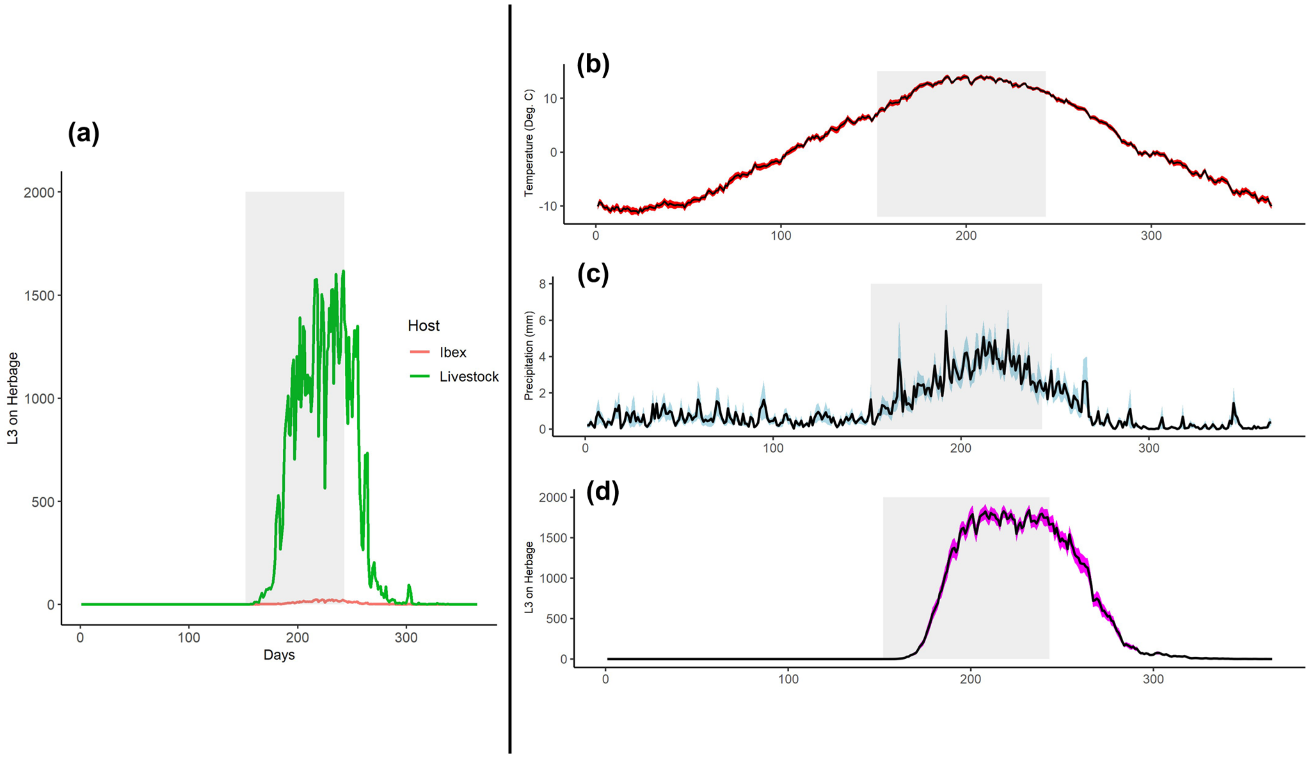

Figure 4. Panel graph for disease transmission dynamics in Pin. The *x*-axis for each graph is day with 1 = 1st January and 365 = 31st December; day 200 is late July. **(a)** GLOWORM-FL model output arising from eggs shed by infections in Asiatic ibex (pink) and migratory livestock (green). Shaded area (grey) indicates when the migratory livestock are present in Pin. **(b)** Average daily temperature (°C). **(c)** Daily precipitation (mm). **(d)** GLOWORM-FL model output (number of $L3_h$ per kg 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 dataset, and black line is the bootstrap mean. The grey shaded polygon indicates the time migratory livestock are present in Pin (days 152–243, 1st June – 31st August).

($L3_h$) peaks occurring in late summer–autumn. This follows the summer period which is warm (average daily temperature between 6°C and 11°C; figure 4b), and has relatively high levels of precipitation (figure 4c).

3.2 *Identifying optimal timing and duration of an intervention*

The modelled GIN-control interventions in migratory livestock while they co-grazed pastures in Pin valley with ibex resulted in reductions in predicted infection pressure ($AUCL3_h$; figure 5). 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 ($AUCL3_h$) compared to a no-intervention scenario, during the time livestock are present in Pin valley.

4. Discussion

We investigated disease transmission risk in an Indian trans-Himalayan rangeland, where migratory livestock share pasture seasonally with sedentary Asiatic ibex. We had the dual aim of understanding the system characteristics with respect to parasite transmission and evaluating the effectiveness of potential interventions to improve livestock and wild ungulate health. Only those parasite eggs contributed by ibex affected pasture infectivity in the summer. Migratory livestock were predicted to contribute most infective larvae onto shared pastures due to higher density and parasite levels, driving infections in both livestock and ibex. The model predicted that a *c.*30-day anti-parasitic intervention towards the end of the livestock's time in Pin valley would be most effective at reducing GINs in both hosts. While these results allow for delimiting preliminary management options, it is important to acknowledge a few key caveats in our study. The caveats are (i) we could only identify the GINs to a

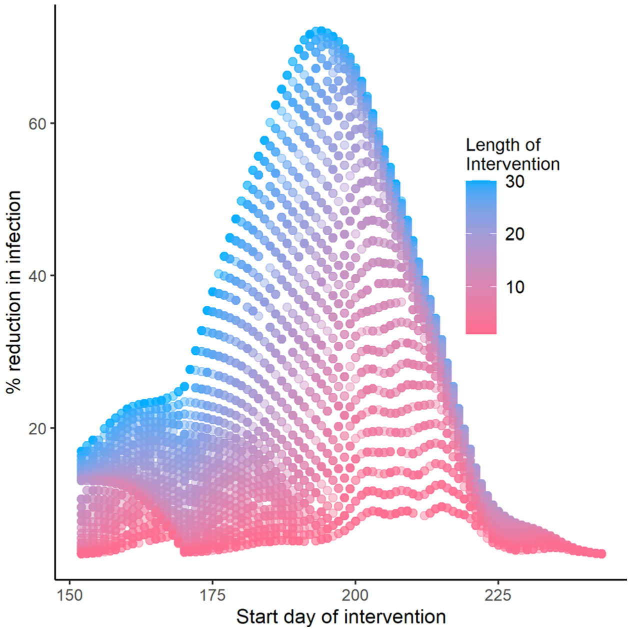

Figure 5. Simulation output showing the effect of start day of intervention in migratory livestock (*x*-axis), and length of intervention (legend) on % reduction in infection (measured as change in AUCL3_h), upon intervention, for the time period migratory livestock graze pastures in Pin (days 152–243; 1st June until 31st August). Peak reduction in AUCL3_h are obtained for a 30-day treatment in the final month of the livestock's presence in Pin.

group rather than a species for which we use model parameters; (ii) parasite cross-transmission is predicted rather than shown through evidence, based on shared pasture use and common groups of GINs between hosts; and (iii) the accuracy of the predictions of the models are not tested with real data (although see Rose *et al.* 2015 for a lab-based validation of the model). These caveats were present as investigating impact and transmission of GINs is especially difficult is remote and harsh landscapes such as Pin valley, which offer limited access to veterinary facilities and advice (Chatterjee *et al.* 2016). Nevertheless, it is important to note that comparison of the GLOWORM-FL model output with examples of preceding models, including GIN species-specific models, suggest improved model predictive performance for the former (Rose *et al.* 2015).

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. However, impacts, if any, on the seasonality and intensity of this infection peak due to increased nematode mortality induced by higher UV irradiation in the high altitude needs investigation (van Dijk *et al.* 2009). 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 higher parasite burdens. Interaction between migration and parasitism are complex. Escape from parasites is a proposed 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) parasitism than year-round residents. Nevertheless, during peak pasture infectivity which is contributed primarily by livestock, since pastures are shared, suggests the potential magnitude of parasite transmission from livestock to ibex is significantly higher than vice versa. However, this does not preclude some transmission from ibex to livestock. Micro-scale pasture sharing between ibex and livestock could influence the direction and magnitude of parasite transmission either by increasing (e.g., through more intense co-grazing of more nutritious vegetation) or decreasing (through avoidance of pasture previously grazed) overlap. This warrants further research.

Using climate data for each year between 1990 and 2019 and parameterizing GLOWORM-FL model egg inputs using the field data from 2019, the model suggests that infection seasonality in Pin valley has remained similar for the last 30 years. Nonetheless, it is likely that the magnitude of infection pressure has increased, as migratory livestock numbers have increased in Pin valley since the 21st century, while ibex numbers have remained relatively stable (Ghoshal 2017; Khanyari *et al.* 2022a, b). We were not able to model these trends as we do not have accurate time series information on both livestock and ibex numbers. Additionally, climate change is projected to result in a hotter and drier climate across the Indian trans-Himalaya (e.g., Norris *et al.* 2020). Although warm temperatures can result in faster infective larval development and continued development into the autumn, drier periods can compensate for this by restricting development, particularly in the summer (van Dijk *et al.* 2008).

Moreover, pasture infectivity peaking in late summer suggests maximal potential transmission of GINs at this point, i.e., mature infections are likely carried over into winter. This has the potential to compromise host health in the harsh winter months (Kohli *et al.* 2014). In Svalbard reindeer, *Rangifer tarandus*, GIN infection was associated with poor body condition in winter and a low fecundity the following year (Stien *et al.* 2002). However, more research is needed to understand the impact of GINs on body condition of ibex and livestock.

4.2 *Model assumptions and considerations*

Nonetheless, we need to consider our results with some caution given certain model assumptions. As exposure to UV irradiation increases mortality of L3 in water (van Dijk *et al.* 2009) and estimates of mortality in soil are much lower than estimates of mortality on pastures (Grenfell *et al.* 1987), the model assumes the mortality rates of L3 on herbage to be higher than in soil. In fact, the model uses the mortality rate of L3 in faeces (μ_3) as a proxy for L3 mortality on herbage (μ_5). This is an approximation; however, experimental research is needed to accurately parameterize the instantaneous daily rate for L3 mortality on herbage, especially at high altitudes with higher levels of ultraviolet irradiation. Additionally, the model assumes that L3 on pasture ($L3_p$) either reside in soil ($L3_s$) or on herbage ($L3_h$). However, parasite species-specific life-history experiments are needed to accurately parameterize the transition of $L3_p$ to $L3_h$ on herbage, and on montane pasture compared with the relatively uniform lowland temperate grass sward.

Finally, since we lack information on GIN species composition, the transmission model was calibrated to *Te. circumcincta* as this species has a climate envelope broadly similar to other species that are also common in small ruminants in temperate and montane environments, such as *Trichostrongylus* spp. (e.g., Jithendran and Bhat 1999). 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 (Walker and Morgan 2014), this simplifying assumption probably ignores some degree of host specificity within a mixed species parasite fauna. More information on species composition in the Pin valley multi-host GIN system is needed, and could be generated using techniques such as faecal cultures to allow for identification of the actual GINs infecting the ibex and livestock. Wherever possible more sophisticated molecular approaches like ‘nemabiome’ deep amplicon sequencing can be used as well (Avramenko *et al.* 2015; Beaumelle *et al.* 2021).

Furthermore, longitudinal pasture larval counts of ibex and livestock at large scale (at least the entire co-grazed region of >400 km^{-2}), would be needed to effectively validate model output. With the currently limited veterinary expertise and infrastructure in the region, this is unrealistic. In their absence, the model, which has been successfully applied to manage parasite infection in other systems (Rose *et al.* 2015; Walker *et al.* 2018), is well grounded in the available data, makes intuitive sense, and allows us to explore scenarios quantitatively—particularly as relative levels of infection, and not just occurrence, is important.

4.3 *Identifying optimum time and duration of interventions: Lessons learnt and future avenues*

The simulation suggested that a *c.*30-day treatment of migratory livestock in the last 30 days of their time in Pin valley is the most effective time 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 but also to lower GIN burdens in livestock as they undertake the strenuous migration back from Pin valley into Rupi.

The months spent by migratory herders in Pin valley are often the most productive in terms of their livestock gaining body condition (e.g., increased weight and size; Ghoshal 2017). Upon returning to Rupi in autumn (*c.* September–October), the herders sell several livestock. The price of an individual is 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 valley. This has the dual potential of ameliorating people’s food security while improving their income. 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) and residues may be found in food for human consumption (Delatour and Parish 1986). 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 reducing the selection pressure for anthelmintic resistance and reducing the cost of intervention.

Our model output identifies critical periods during which treating livestock is likely to have significant benefits for ibex health and body condition. However, understanding impact of parasitism on ibex health is difficult as cross-sectional correlations between GIN burden and body condition are notoriously limited in wildlife (Irvine 2006). Reducing infection during late summer into autumn has the potential not only to attenuate parasite-related negative health impacts during ibex rutting—usually in winter (Bhatnagar 1997) but also can potentially reduce over-winter parasite burdens, leading to improved fecundity (Albon *et al.* 2002). 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 (Stringer and 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 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. 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 could be widely implemented.

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 domestic and wild hosts, with a range of benefits for both herder livelihoods and conservation. Beyond Pin valley, our study provides a transferable multi-pronged approach to investigate 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 herders' livelihoods.

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Author contributions

This study was conceptualized by MK, EM, EJM and KS. RO adapted and conducted the sensitivity analysis. HRV built and provided the GLOWORM-FL model. MK conducted the field work and analysed the data. AK helped with the analysis. MS provided critical inputs during the writing of the manuscript. MK and EM lead the writing of the manuscript and all authors commented on subsequent drafts.

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