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RESEARCH ARTICLE

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

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Abstract

1. Shared use of rangelands by livestock and wildlife can lead to disease transmission. To align agricultural livelihoods with wildlife conservation, a multipronged and interdisciplinary approach for disease management is needed, particularly in data-limited situations with migratory hosts. Migratory wildlife and livestock can range over vast areas, and opportunities for disease control interventions are limited. Predictive frameworks are needed which can allow for identification of potential sites and timings of interventions.
2. We developed an iterative three-step framework to assess cross-species disease transmission risk between migrating wildlife and livestock in data-limited circumstances and across social-ecological scales. The framework first assesses risk of transmission for potentially important diseases for hosts in a multi-use landscape. Following this, it uses an epidemiological risk function to represent transmission-relevant contact patterns, using density and distribution of the host to map locations and periods of disease risk. Finally, it takes fine-scale data on livestock management and observed wildlife–livestock interactions to provide locally relevant insights on disease risk.
3. We applied the framework to characterize disease transmission between livestock and saiga antelopes *Saiga tatarica* in Central Kazakhstan.
4. At step 1, we identified peste-des-petits-ruminants as posing a high risk of transmission from livestock to saigas, foot-and-mouth disease as low risk, lumpy skin disease as unknown and pasteurellosis as uncertain risk. At step 2, we identified regions of high disease transmission risk at different times of year, indicating where disease management should be focussed. At step 3, we synthesized field

surveys, government data and literature review to assess the role of livestock in the 2015 saiga mass mortality event from pasteurellosis, concluding that it was minimal.

5. *Synthesis and applications*. Our iterative framework has wide applicability in assessing and predicting disease spill-over at management-relevant temporal and spatial scales in areas where livestock share space with migratory species. Our case study demonstrated the value of combining ecological and social information to inform management of targeted interventions to reduce disease risk, which can be used to plan disease surveillance and vaccination programmes.

KEYWORDS

disease transmission, framework, livestock, management, migration, multi-use landscapes, overlap, saiga

1 | INTRODUCTION

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

Although many factors contribute to disease transmission, seasonal distributional overlap between wild and domestic ungulates is particularly significant in the epidemiology of shared pathogens for migratory species. Cross-species disease transmission depends on contact patterns, governed by host distributions and movement (Vosloo et al., 2002), and hence by socio-economic factors and climate-induced changes in resource availability (Robinson & Milner-Gulland, 2003; Weinstein & Lafferty, 2015). Seasonal movements of wild and domestic ungulates, landscape management, and aggregation at various spatial scales, can strongly modify host contact patterns and hence affect disease cross-species transmission risk (Morgan et al., 2006; Pruvot et al., 2020). However, disease management can have negative consequences like compromised immune responses, altered parasite-mediated apparent competition between hosts, and destabilizing the host-parasite arms race (Stringer & Linklater, 2014). Thus, it is important to question what level of contact is detrimental and if control is indeed required, especially in data-poor and logistically challenging systems. Beyond contact patterns, host population size and weather, the presence, life histories, and intensity of pathogens also play important roles in disease transmission (e.g. Redfern et al., 2005).

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

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

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

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

2 | MATERIALS AND METHODS

2.1 | A disease risk prioritization framework

The framework aims to help researchers identify and reduce risk of spill-over from livestock to migratory wild ungulates in resource-limited and logistically challenging landscapes. The outputs can be communicated to decision makers to prioritize further data collection and draft interventions. To do so requires risk assessment of spill-over at various scales, combining ecological and social information to produce management recommendations. The framework has three steps, each at progressively finer spatial, ecological and institutional scales (Figure 1).

2.1.1 | Step 1: Identifying disease risks

Step 1 identifies livestock-wildlife spill-over disease risks at the broadest ecological scale (annual distribution). Firstly, potentially important diseases are identified, based on a literature review. Subsequently, relevant disease-risk information is synthesized into a qualitative risk assessment table, based on: (a) likelihood of occurrence in wild ungulates, (b) likelihood of transmission from livestock, (c) severity (morbidity and mortality once transmitted), (d) existing mitigation strategies in livestock. These criteria are synthesized into one risk indicator: high, low, unknown or uncertain. A disease is categorized as high risk when the likelihood of transmission from livestock to wild ungulate is high; disease severity (morbidity and mortality) is high; and mitigation strategies are currently inadequate or unavailable. A disease is low risk when the likelihood of transmission from livestock to wild ungulates is low; the severity is low; or adequate mitigation strategies are already in place. A disease is of unknown risk when the available information about presence in wild ungulates, probability of transmission, mortality rates and mitigation strategies are not adequate for qualitative risk assessment. For a given disease, if there is a mix of high and low, risk for different criteria, the disease is classified as having uncertain risk.

2.1.2 | Step 2: Identify locations and times of disease risk

Step 2 identifies locations and periods of risk for the diseases attributed high, unknown or uncertain risk in step 1, at the intermediate ecological scale (seasonal distribution). This step involves designing an epidemiological risk function to represent transmission-relevant contact patterns, combining key host (density and distribution) and pathogen traits (transmission pathway, life history). Accessible datasets on host numbers and locations are used as function inputs. The output is seasonal disease risk maps at a resolution determined by the datasets. These maps can be used to focus local surveillance and prioritize disease mitigation strategies at appropriate administrative levels.

Depending on available information, more or less complex and data-informed functions can represent this risk. We propose the following basic Equation 1 that can be refined with improved data:

$$R = \left[\frac{n_l}{m}\right] \times n_w, \tag{1}$$

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

A higher R represents a higher disease risk to wild ungulates based on the density and distribution of livestock and wild ungulates and their proximity. In most countries, disease mitigation (e.g. vaccination) is determined at specific levels of government administration. Hence, calculating risk scores at appropriate administrative levels helps policymakers/practitioners prioritize resource allocation. Regions highlighted as having high disease risk from this step can be prioritized for fine-scale investigation in step 3 (below).

2.1.3 | Step 3: Fine-scale disease spill-over risk from livestock to wildlife

Step 3 identifies fine-scale (within-season distribution) transmission risk from livestock to wild ungulates, with the granularity informed by maps from step 2. Participatory research techniques like semi-structured interviews and resource mapping (Huntington, 2000) can be used to gather data on aspects including land access mechanisms (political), livestock distribution (social) and health issues in livestock and their mitigation (veterinary) from a representative sample of local stakeholders. This should focus on diseases of concern delimited by step 1, in areas of risk, delimited by step 2. Upon synthesizing social and ecological information on the within-season locations and movements of wildlife and livestock, and livestock health issues and disease mitigation strategies, obtained through participatory research techniques with local stakeholders (e.g. herders), the output is a disease risk statement. The statement considers the likelihood that (a) in case of a disease event, an outbreak originated in

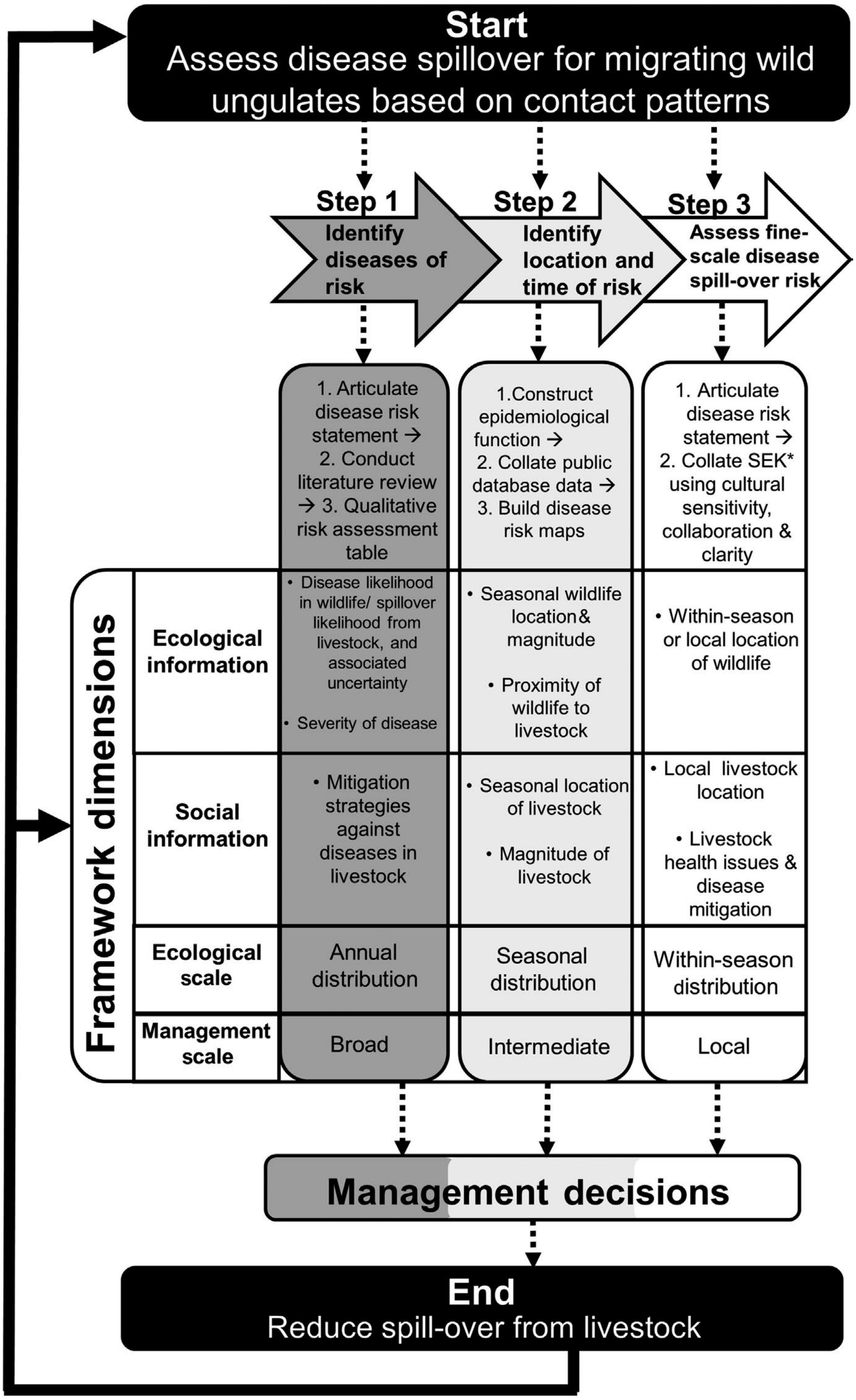

FIGURE 1 A disease risk prioritization framework based on contact patterns, comprising three steps, with components across four dimensions of information and scale. They collectively inform management decisions across various scales, to reduce potential or actual spill-over. *SEK, socio-ecological knowledge

livestock and was transmitted to wild ungulates, or (b) in the absence of a disease event, disease will cross-transmit from livestock to wild ungulates.

2.2 | Case study of framework application: Saiga antelopes

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

Following the collapse of the Soviet Union in 1991, saigas declined by >90% due to overhunting, leading to them being listed as Critically Endangered on the IUCN Red List (Milner-Gulland et al., 2003). Following a partial recovery, another MME killed >200,000 individuals in Betpak-Dala in May 2015, representing 88% of this population and 62% of the global population (Kock et al., 2018). The proximate cause was haemorrhagic septicaemia caused by a normally commensal bacterium, *Pasteurella multocida* serotype B, possibly linked to heightened humidity and temperature in the 10 previous days (Kock et al., 2018). The role of livestock in the 2015 MME remains understudied. Another MME took place in the Mongolian subspecies *S. t. mongolica* in 2016–2017, caused by a livestock-transmitted virus, peste-des-petits-ruminants virus (PPRV), killing a significant proportion of the population (Pruvot, Fine, et al., 2020).

Increasing livestock numbers throughout the saiga range since 2000 (Appendix S1) produces both a threat of disease spill-over to saigas, and opportunities to understand shared drivers of disease emergence. We focused our work on the Betpak-Dala saiga population (Figure 2). We defined the 'maximum potential range' of the population by pooling seasonal saiga locations from 1970 to 2008 (Singh et al., 2010a; see step 2 below). Saigas migrate within this range seasonally, with their migration varying annually, based on population size, climatic conditions, pasture condition, availability of surface water, and the amount of disturbance experienced by the animals (Bekenov et al., 1998; Singh et al., 2010a).

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

2.2.1 | Step 1

We assessed all existing and potential diseases with transmission risk between livestock and Betpak-Dala saigas, to prioritize future investigations. Given the limited literature on saiga disease, we used guided expert opinion to survey all peer-reviewed articles published in English on infectious diseases of saigas and sympatric livestock (Appendix S2). Due to their extensive contributions to, and engagement with, the saiga literature since the early 1990s, the authors EJMG, ERM, SR and RK were able to point to relevant articles. We also used comprehensive reviews of the relevant information in the Russian literature. For instance, Robinson et al. (2019) reviewed Soviet-era literature on MMEs, Lundervold (2001) reviews historical disease events and prevalence in saigas recorded in English and Russian, and Bekenov et al. (1998) reviews the ecology and management of saigas in Kazakhstan, including disease. This literature was used to understand the presence, transmission risk, and severity of diseases that can infect livestock and saigas. We explored potential mitigation options for these diseases using literature and expert judgement of veterinarians and researchers in Kazakhstan. If there was uncertainty about the host range of a disease and its potential spill-over to saigas, we aided our interpretation by scanning the literature on other wild ungulates, with a particular focus on those co-occurring with livestock across temperate regions, as pathogen range often mirrors host phylogeny (Walker et al., 2017). Diseases known to infect both domestic and wild ungulates in other regions, therefore, were considered likely to cross from livestock to saigas. We conducted the search in Google Scholar, and used a snowballing approach until we had gathered relevant information or satisfied ourselves that there was no information available. Hence, the assessment was indicative rather than exhaustive.

2.2.2 | Step 2

At step 2, we aimed to highlight areas of Betpak-Dala where surveillance could be particularly focussed, due to the spatio-temporal overlap of saigas and livestock. There is limited information on actual disease transmission between livestock and saiga. We therefore used Equation 1 plugging in number of saiga group for wild ungulates ($n_w = n_s$):

$$R = \left[\frac{n_l}{m}\right] \times n_s, \tag{2}$$

where R = disease risk score, n_l = livestock number in a given area, n_s = number of saiga groups present in that area at a defined time, m = mean observed distance between groups of saigas and livestock farming settlements during periods of co-occurrence. Table 1 gives the data sources for parameter estimation.

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

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

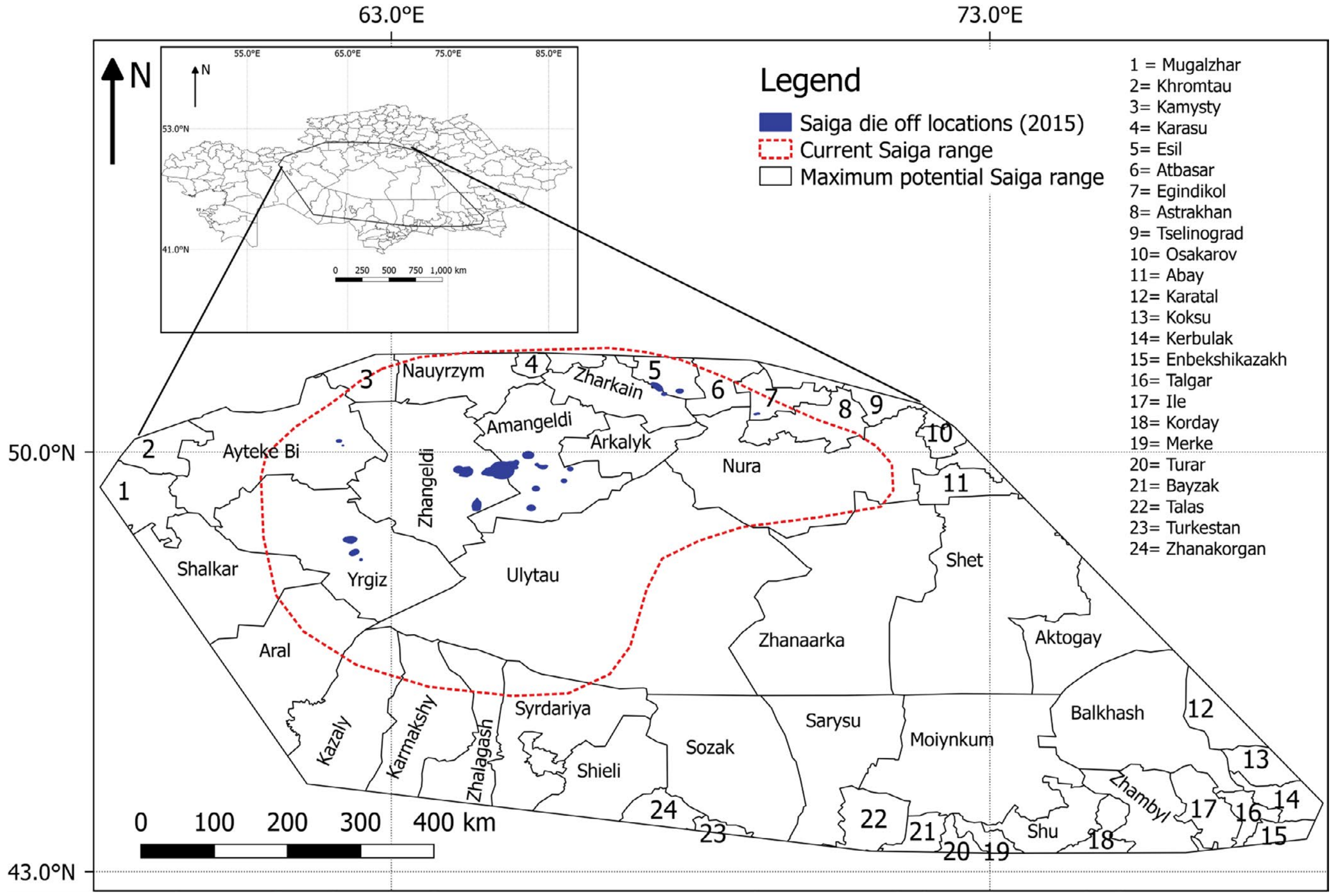

FIGURE 2 Inset: Historic range of the Betpak-Dala saiga population within Kazakhstan. Main map: The individual raions (districts) within the maximum potential Betpak-Dala saiga range. Also mapped is the Betpak-Dala population extent during the MME and the 2015 die-off sites.

2.2.3 | Step 3

In our case study, step 3 involved gathering fine-scale information to assess the likelihood that disease transmission from livestock had contributed to the 2015 MME. Given that no pathogens except *Pasteurella multocida* serotype B were identified in the dead saigas, Kock et al. (2018) had identified pasteurellosis as the cause of death, consistent with the symptoms of haemorrhagic septicaemia (step 1). The 2015 MME occurred across the calving range over the same short time period (Figure 2). Most animals observed at the die-off sites died within a few hours of onset of clinical signs (Kock et al., 2018). Incubation periods for haemorrhagic septicaemia range from 12 hr to a few days (Bastianello & Henton, 1994), suggesting that if transmission from livestock contributed to the pasteurellosis MME, it would have occurred locally—during, or immediately prior to, calving (step 1). This does not exclude the possibility of prior transmission of a predisposing pathogen earlier in the saiga migration, but no such pathogen was found (Fereidouni et al., 2019; Kock et al., 2018). Therefore, we focussed on step 3 of our investigations in areas where die-offs were reported, rather than first using step 2 to identify areas of potential risk. As it happens, these areas are also areas identified at step 2 as of higher-than-average risk. Hence our framework is also useful to potentially traceback places of spill-over.

Semi-structured interviews and resource mapping (Huntington, 2000) were conducted between 6 and 24 May 2016. Interview topics included land access mechanisms, livestock distribution and health issues in livestock and their mitigation, focussing on pasteurellosis. The team visited the central 'Torgai' cluster of die-off sites in Zhangeldi and Amalgeldi *raions* of Kostanai *oblast* (Figure 3). We aimed to survey a representative selection of herders, Protected Area rangers and State wildlife rangers; the latter two are mandated to protect saigas. Within each of our five focal study regions (i.e. sub-districts), we first interviewed the mayor and veterinarians and then conducted 19 in-depth interviews using a snowballing approach with livestock owners, as key informants. The selection criterion for interviewees was that they were grazing livestock near areas of observed saiga mortality.

We also visited the land committee and veterinary departments at the administrative centres of Amangeldi and Zhangeldi *raions*. In Zhangeldi, we photographed cadastral maps from 2014, showing village grazing land and parcels leased by registered farms and companies and obtained land statistics (Supplementary Material 3). In Amangeldi, it was not possible to photograph cadastral maps. Instead, committee staff drew the borders of those land parcels located in saiga areas on the topographic maps. The identity and size of those parcels could be inferred based on the land statistics.

TABLE 1 Variables included in the disease risk score, Equation 1

Symbol	What it represents	Database	Reliability of data	Further comments
n_l	Number of livestock in *raion* (district)	Kazakhstan government online livestock identification database (Kazakhstan Government Online Livestock Identification Database, 2018)	Livestock must be registered within 3 months of birth in Kazakhstan. Government collated this information and data are increasingly available as Kazakhstan aims to modernize its veterinary system. Finest scale of comprehensive online data was at the settlement level, but these needed on-ground reconciling of settlement names with GPS locations so aggregated *raion*-level data were used	For further analyses, livestock was split into three categories, 'sheep/goat', 'cattle' and 'combined' (sheep/goat and cattle). Depending on disease type, transmission threat could be from only sheep/goat, only cattle, or both
n_s	Number of saiga groups in *raion* for each season	A database of point location of saiga groups, each with a season attribute, was obtained by contacting the lead author of Singh et al. (2010a), which pooled saiga locations from 1970 to 2008. These were spring, summer, winter and calving. We defined this as the 'maximum potential range'. We used this rather than the contemporary range, as we lacked saiga group location data for this area	Singh et al. (2010a) used group locations from historical field reports to generate historical seasonal ranges by migrating saigas. They collated information from books, published articles and other Russian language sources. The maximum potential range polygon was generated by drawing a Minimum Convex Polygon(MCP) around the plotted locations of saiga groups retrieved from Singh et al. (2010a), in QGIS. Contemporary saiga distribution (i.e. distribution in 2015) was obtained from the Convention on Migratory species report for saigas (CMS, 2015)	Saiga population range has changed considerably over the past 5–6 decades and the contemporary saiga range during the die-off (2015) was more restricted than it was in the 1970s (Singh & Milner-Gulland, 2011) As saigas are a herding species, the group was the appropriate unit of analysis
m	Mean distance between saiga groups and settlement (kms)	A shape file of settlements in Kazakhstan was accessed (Diva-GIS, 2018), collated by the US National Imagery and Mapping Agency (NIMA). We calculated the distance (km) between saiga group locations in winter, summer, spring and calving, using the Nearest hub tool in QGIS. Distances between the closest settlement and each saiga group were calculated and the sum of these distances were divided by the number of saiga groups in a *raion*	The Kazakhstan settlement shapefiles are an open access, freely usable and validated data source	We assumed that settlements were a robust proxy for livestock presence for the Betpak–Dala saiga population as the sub-district administrative statistics declared a large proportion (40%) of livestock in our study area were held by households (SM3). Regardless, logistical constraints dictate that most livestock are kept close to human settlements

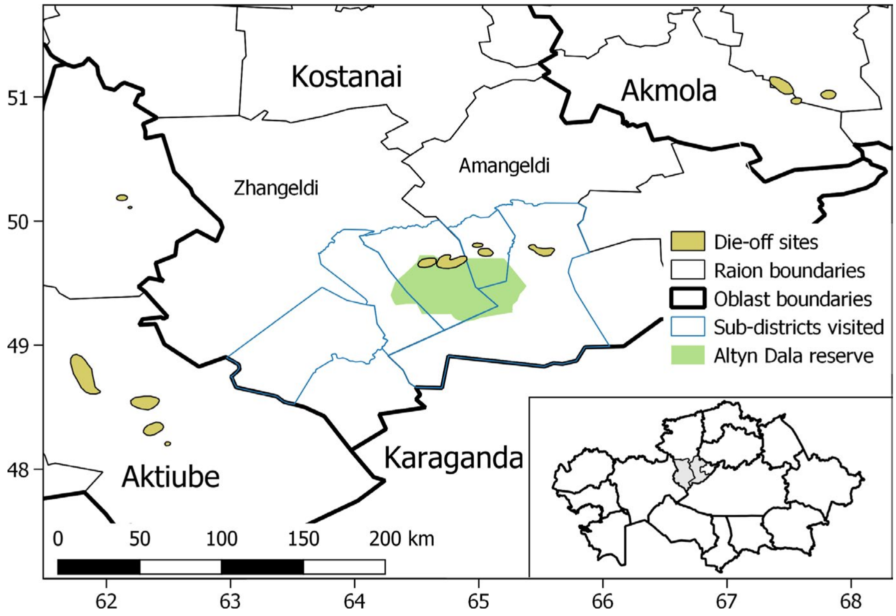

FIGURE 3 Location of 2015 saiga die-off sites including those visited during fieldwork
Note: Source of die-off location data: Association for the Conservation of Biodiversity of Kazakhstan/Committee for Forestry and Wildlife of the Ministry of Ecology, Geology and Natural Resources of Kazakhstan.

3 | RESULTS

3.1 | Step 1: Identifying disease risks

Table 2 is the qualitative integrated assessment of potential risks of disease spill-over from livestock to saigas. Four illustrative diseases are represented here, covering low, high, unknown and uncertain risk. We include pasteurellosis due to its importance for step 3. The remaining diseases are listed in Appendix S2.

3.2 | Step 2: Identifying locations and times of disease risk

Estimated values for *R* were calculated and mapped to highlight the *raions* with highest risk of saiga-livestock contact. We generated separate *R* estimates for saiga using numbers of sheep and goats (Figure 4), cattle and combined ruminants (Appendix S4) because cross-species transmission risk for various diseases was predominantly from cattle (e.g. lumpy skin disease) or sheep and goats (e.g. PPRV), or both (e.g. FMD; Table 1).

Depending on diseases of concern highlighted in step 1, the assessment of spatio-temporal contact in step 2 could be used to refine priorities for data gathering and intervention. For example, for a disease to which saigas were especially vulnerable during calving, and for which sheep and goats were the main hosts, it would be logical to prioritize Ulytau, Zhangeldi and Ayteke Bi *raions* (Figure 4c), for further risk investigation in step 3, and for resource allocation like vaccines.

3.3 | Step 3: Assess the actual disease spill-over from livestock to wildlife

In the five regions where pasteurellosis was found in saigas in 2015, *c*.40% of pasture land was leased parcels away from the village, containing 60% of the livestock. The remaining grazing was village land, which represented just 2% of pasture (Appendix S3). Most livestock was located along the Torgai and Kabyrga rivers, distant from the saiga calving areas (Figure 5). However, a number of large holdings were located further south, some reportedly having over 1,000 small stock and many hundreds of cows and horses. The sites closest to the die-off areas were summer camps used for short periods. Horses were not herded, even if owned by village-based farmers, ranged farther than other livestock (*c*. 25 km from farms), and were therefore likely to share grazing with saigas.

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

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

Very few farmers reported grazing livestock on the steppe in spring 2015. Those who did reported negligible livestock mortalities (Appendix S5), and none related to pasteurellosis. Veterinary teams concurred and indicated no notable increase in any disease or diagnosis in livestock throughout 2015 in the area. In 2015 and 2016, most vets agreed that livestock pasteurellosis vaccine coverage was partial (Table 3). Respondents stated that emergency pasteurellosis vaccination was conducted for livestock in the steppe after the MME. Respondents also suggested that planned 2016 coverage for

TABLE 2 A qualitative integrated risk assessment for potential risk of disease spill-over from livestock to saigas, with a focus on the Betpak–Dala population in Kazakhstan (four exemplar diseases). Green = low risk, red = high risk, dark grey = unknown and grey = uncertain risk

Disease (key references)	Likelihood	Severity	Current Mitigation	Uncertainty
🟩 Foot and Mouth Disease (FMD) Bekenov et al. (1998), Fadeev and Sludskii (1982) and Morgan et al. (2006)	Cattle, sheep and goats are known to be carriers and transmit to saigas. Cattle are more readily infected by airborne virus	Historically, spill-over caused MMEs, especially affecting saiga calves	Kazakhstan is FMD-free due to past livestock vaccination; could be re-instituted if FMD arrives again. Saigas seem to need re-infection from livestock to be affected	Kazakhstan retains capacity to ensure that FMD remains eliminated. Especially, prevention of re-introduction of FMDV through cross border livestock movement
🟥 Petit Peste des Ruminants (PPR) Kock et al. (2015) and Pruvot, Musiani, et al. (2020)	Sheep and goats are known to suffer epidemics and can vector virus to wildlife (including saigas) through environment. Novel disease in Kazakhstan, but occurs in neighbouring countries. Unless mitigation is proactive, saigas will remain defenceless	Caused a devastating MME in Mongolian saiga sub-species in 2016	Nearly all susceptible animals are vaccinated in oblasts along the southern border region of Kazakhstan. Coverage in other regions is likely low or non-existent	Lack of knowledge and expertise to deal with PPRV. Vaccination coverage limited to preventing disease entering from Kyrgyzstan, but PPR has also been recorded in China and Mongolia and there does not seem to be vaccination in the areas bordering these two countries. PPR outbreaks in Kazakh saigas (the nominate sub-species) not recorded yet, though seroprevalence has been determined
⬛ Lumpy Skin Disease EFSA (2020) and Taylor et al. (2019)	Outbreak in cattle in Kazakhstan has been recorded. No published outbreaks in saigas, but there is published evidence of spill-over to wildlife in other regions of Eurasia	*c*. 10% of infections resulted in mortality in cattle	Nearly all susceptible animals are vaccinated in oblasts along the Russian border. Coverage in other region is likely low or non-existent	An emerging disease in Kazakhstan with only one confirmed report from 2016. Current extent and spread in future remains highly uncertain. Efficacy of vaccines remains uncertain. Evidence of susceptibility and severity of infection in saigas needed
▨ Pasteurellosis* Kock et al. (2018) and Robinson et al. (2019)	Livestock and saiga are both known to be affected, and transmission between domestic and wild ungulates was known to occur (e.g. exposure to Chamois *Rupicapra rupicapra* and Alpine Ibex *Capra ibex* in France, Richomme et al., 2006)	Lives as a harmless commensal in saigas but can cause MMEs on occasions. Saiga MMEs have been linked to temperature and humidity anomalies, suggesting potential climatic drivers	Livestock is partially vaccinated in parts of Kazakhstan	Transmission from livestock to saigas has not been demonstrated but there is evidence of cross-transmission from livestock to other wild ungulate species, especially when livestock herds are not guarded or enclosed. Additionally, coverage of vaccination was unclear. Lack of local capacity for diagnosis

*Pasteurellosis covers several syndromes and pathogens. The information in this table refers to haemorrhagic septicaemia as that was what caused the death of saigas in the 2015 and 1988 MMEs (Kock et al., 2018). But other MMEs may have involved different syndromes caused by related pathogens, as in the Russian literature all syndromes were described as 'pasteurellosis' without specification of the disease or pathogens (Robinson et al., 2019). See Appendix S2 for the list of remaining diseases.

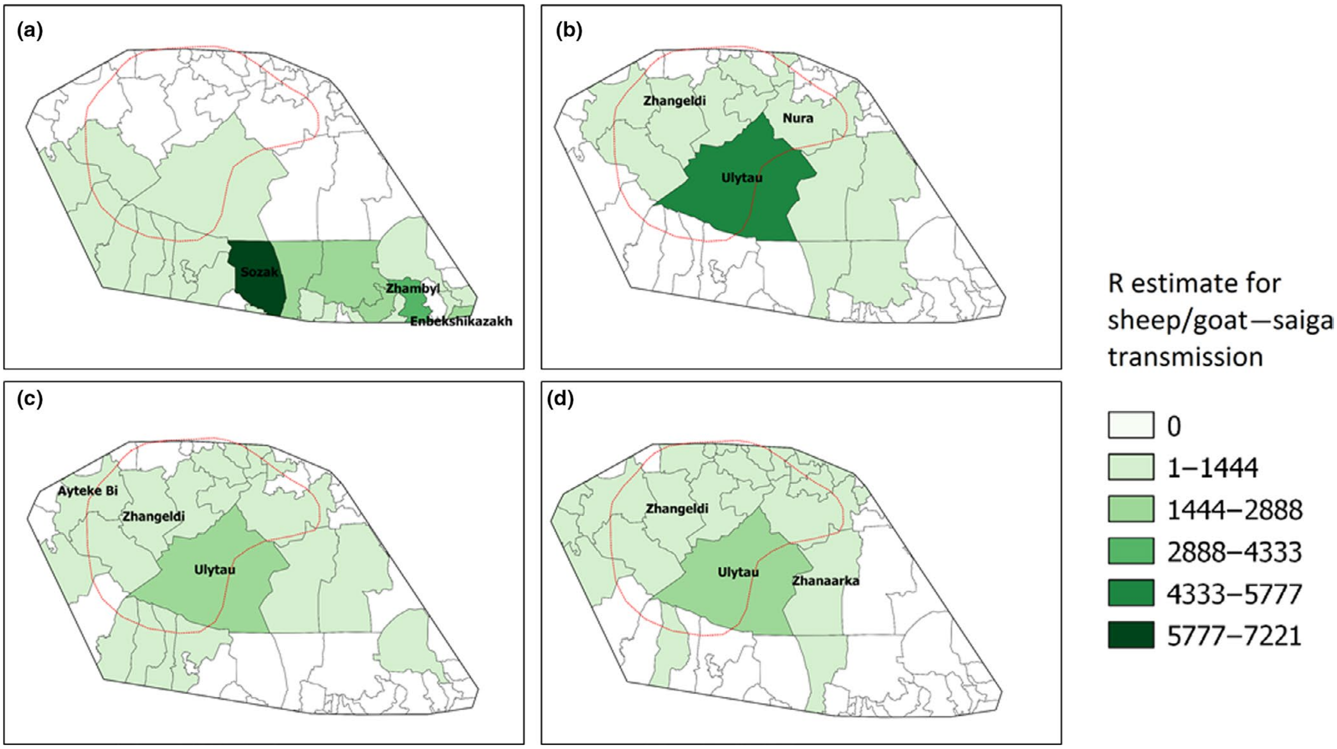

FIGURE 4 Maps showing the disease risk score across the maximum potential saiga range using only sheep/goat distribution data
Notes: Darkness of shading represents magnitude of risk. White regions = saigas absent, hence no risk. Saiga ranges: A = winter; B = spring; C = calving; D = summer. For each season the three raions with the highest scores are labelled. Actual values are given in SM4.

pasteurellosis was directed preferentially towards livestock grazing in steppe areas, rather than those more accessible in the villages as previously, citing the 2015 MME. Pasteurellosis vaccination of horses appeared to increase substantially in 2016 (Appendix S5). This could be in response to the MME as horses are free-ranging; despite lack of evidence for cross-species transmission of pasteurellosis between saigas and horses (Table 1). No cases of pasteurellosis in livestock had been reported in the area for *c*.10–15 years, although this is a long-standing endemic infection with some level of ongoing vaccination (Robinson et al., 2019).

4 | DISCUSSION

The framework highlights the importance of coordination between stakeholders (e.g. conservationists, veterinarians and land managers) to co-manage potential spill-over from livestock to saigas (Figure 6) Several diseases present a risk of cross-transmission to saigas from livestock. These need mitigating, additionally to threats like poaching, to ensure populations remain large enough to survive potential future MMEs (Kock et al., 2018). Uncertainties remain around aspects of cross-species transmission and mitigation, which require careful examination to determine effective solutions (step 1). For a given disease (identified from step 1), practitioners can use the disease risk maps to identify *raions* and seasons of highest risk depending on the livestock species most likely to be an infection source (step 2). This can inform targeted interventions and prioritize detailed field data collection. For saigas, step 2 identified Zhangeldi *raion*, a site which saw die-offs within the 2015 MME, as high risk for cross-species transmission from sheep and goats to saigas in spring, along with two other *raions*. If our investigation at step 3 had not been post-hoc, these *raions* would anyhow have been prioritized for further attention.

Finally, we found no evidence that livestock in the die-off region was a source of infection for the 2015 saiga MME. It is possible that disease incidence could be under-reported as sick livestock are often consumed. Also, livestock were protected by partial vaccination, but we lack data to determine if coverage was adequate for effective protection. However, we would expect even the limited veterinary services in the area, or the herders themselves, to detect and document outbreaks of pasteurellosis as this region has a history of this disease (Robinson et al., 2019; Table 3). Moreover, how contact with livestock in the weeks preceding the die-off (not in the die-off areas) might have affected any cross-species transmission needs investigation. Separation of saigas and livestock at fine scales might not persist in future, as across Kazakhstan livestock are recolonizing the steppe (Dara et al., 2020). Farm locations, size, movement patterns and livestock holdings will all interact to determine future risk.

The applicability of our framework was dependent on the amount and quality of data available. Knowledge gaps exist for all diseases of

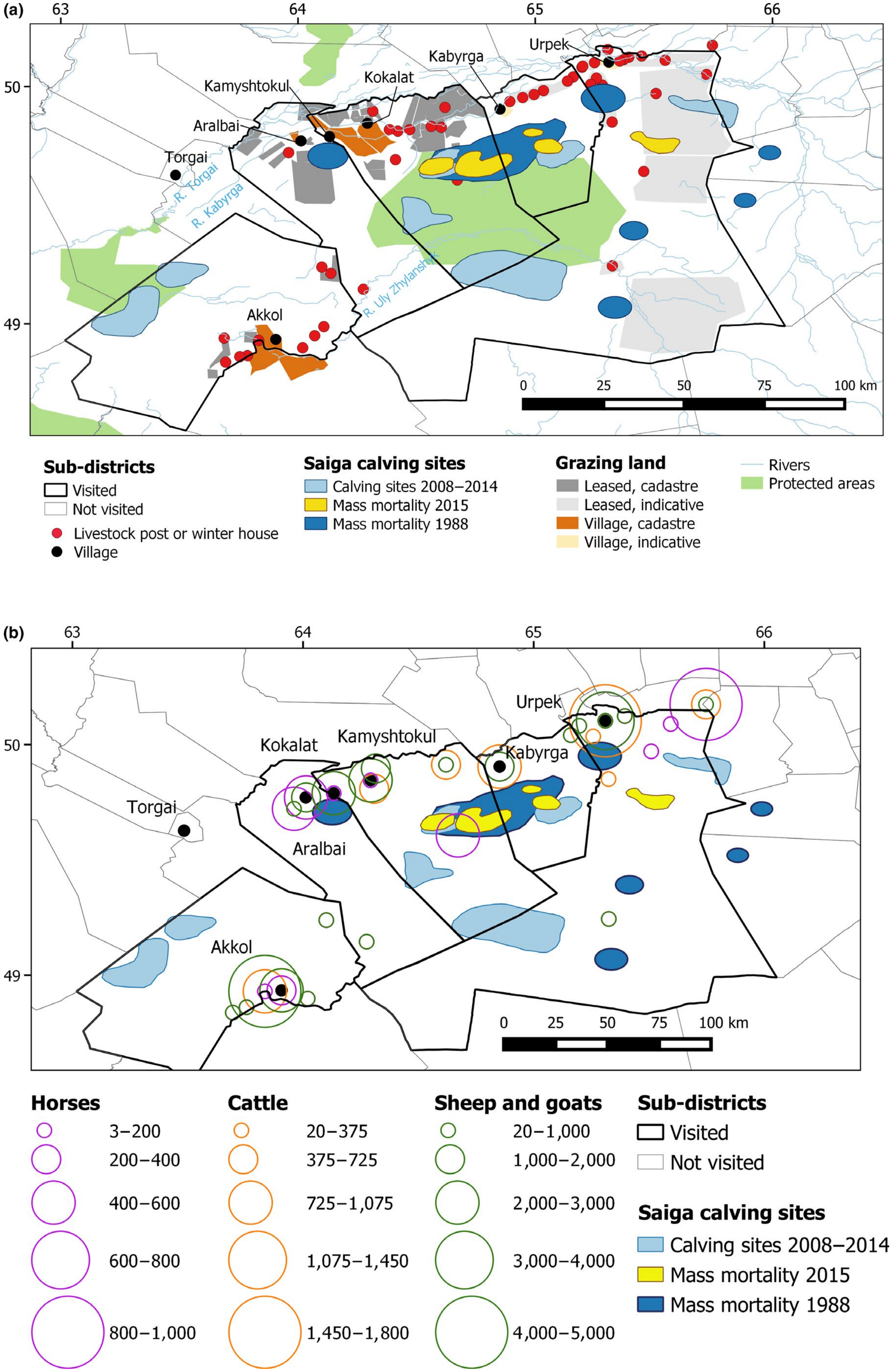
(a)
63
64
65
66
50
49
Urpek
Kabyrga
Kokalat
Kamyshtokul
Aralbai
Torgai
R. Torgai
R. Kabyrga
R. Uly Zhylanshyk
Akkol
0 25 50 75 100 km
Sub-districts
Visited
Not visited
Livestock post or winter house
Village
Saiga calving sites
Calving sites 2008–2014
Mass mortality 2015
Mass mortality 1988
Grazing land
Leased, cadastre
Leased, indicative
Village, cadastre
Village, indicative
Rivers
Protected areas
(b)
63
64
65
66
50
49
Urpek
Kokalat
Kamyshtokul
Kabyrga
Torgai
Aralbai
Akkol
0 25 50 75 100 km
Horses
3–200
200–400
400–600
600–800
800–1,000
Cattle
20–375
375–725
725–1,075
1,075–1,450
1,450–1,800
Sheep and goats
20–1,000
1,000–2,000
2,000–3,000
3,000–4,000
4,000–5,000
Sub-districts
Visited
Not visited
Saiga calving sites
Calving sites 2008–2014
Mass mortality 2015
Mass mortality 1988

FIGURE 5 Left: Study area, livestock locations, protected areas and designated common and leased grazing areas. Right: Livestock locations and numbers in May 2015
Notes: circle sizes represent numbers of animals only, and not the distances they travel. In reality sheep and goats are likely to travel up to 6km from a central point; cattle move similar distances but may go further if not herded. Horses are not herded [source sub-district boundaries: Lenk (2008)]

concern ('uncertainty' in Table 1). Our epidemiological function was highly simplified (step 2). For instance, it did not capture diseases like helminthoses, where indirect contact through contamination of the environment facilitates transmission (Morgan et al., 2006), nor did it capture diseases transmitted through non-livestock alternative hosts or long-lived vectors, enabling persistence of infection in the environment. The function for calculating the disease risk score also has caveats.

Firstly, it assumed risk had a linear relationship with livestock number and saiga group number. As saigas are known to avoid livestock (Singh et al., 2010b), the relationship between saiga density, seasonality and group number/size is likely to be nonlinear, resulting in disproportionately higher risk when many saigas are concentrated in small areas (e.g. calving). Susceptibility of saigas to cross-transmitted pathogens could also vary spatially and seasonally due to nutritional limitations, stress and other factors, and be amplified through disturbance and habitat degradation, introducing additional nonlinearities. Currently the criteria for categorizing risk (low, medium or high) are crude and best interpreted qualitatively. Secondly, we assumed the risk score was transferable spatially (e.g. from a *raion* to a particular pasture), but livestock husbandry and saiga grouping patterns at the local scale are likely to be important drivers of cross-species transmission (Craft, 2015). Hence, step 3 is important. Thirdly, with increasing infrastructural barriers, poaching, and climate change, saiga migration is being constrained. This may in future increase livestock-saiga contact, and hence risk of disease transmission. Fourthly, due to data limitations, saiga locations were historical. To identify actual priority *raions*, updated saiga distribution data is needed. Lastly, we assume that *raion* livestock numbers (n_l) adequately reflect potential sources of livestock disease for saigas.

For step 3, we were limited by the knowledge local stakeholders held and were willing to share. Inadequate archiving of data (e.g. 2015 records from Amangeldi, Table 3) was a hindrance in understanding changes in pasteurellosis vaccination between 2015 and 2016. A major constraint on prioritization in general is the lack of epidemiological studies and knowledge of infection in wild populations.

Going beyond saigas, stakeholders can use the framework to inform disease management at relevant scales. Step 1 could be used by national governments to identify diseases to prioritize mitigation at subsequent steps. Step 2 could be used by regional governments to prioritize locations and times to implement the mitigation. Step 3 could be used to plan local-scale livestock management like restricting pasture use at certain times or reactive vaccination. Although developed for Betpak-Dala saigas, our framework is widely applicable, with some adjustments:

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

A strength of our framework is its iterative nature (Figure 2, thick black lines). With new information, the risk assessments, predictions and consequent management actions are updated across all dimensions and components. Our knowledge of biological systems is often inadequate and costly field surveys are generally required to generate the data necessary to inform management (Margules & Pressey, 2000). Hence, indirect methods of characterizing ecological patterns are of value for decision-making. Despite efforts to deal with imperfect datasets, little is known about how data uncertainty translates into management errors (Hermoso et al., 2013). Being explicit about uncertainties allows future work to account for them. Our iterative framework encourages the use of new information to update aims, assessments and predictions.

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

TABLE 3 Diseases of main concern, for which vaccination and testing is reported in our *raions* of interest. Diseases in red are of transmission concern for saigas from livestock (Table 1)

Raion (year)	Species (heads)	Vaccine	Vaccine planned	Vaccine Coverage (%)	Test	Test planned	Test Conducted(%)
Zhangeldi (2016)	Cattle (27,314)	Rabies	7,800	—	TB	45,420	15,800 (57.8%)
		Pasteurellosis	10,500	9,300 (34.0%)	Brucellosis	33,156	13,275 (48.6%)
		Anthrax	35,000	35,000 (89.3%)			
	Sheep/Goat (60,296)	Rabies	4,600	—	Brucellosis	162,248	26,801 (44.4%)*
		Pasteurellosis	11,200	7,900 (13.1%)*			
		Anthrax	53,300	32,600 (54.1%)			
Amangeldi (2016)	Cattle (13,313)	Rabies	8,000	—	TB	40,140	20,200 (151.7%)
		Pasteurellosis	10,500	10,655 (80.0%)	Brucellosis	38,451	17,546 (131.8%)
		Anthrax	30,900	24,100 (181.0%)			
	Sheep/Goat (34,714)	Rabies	4,700	—	Brucellosis	134,369	50,919 (146.7%)
		Pasteurellosis	12,200	12,670 (36.5%)*			
		Anthrax	41,800	29,000 (83.5%)			
Amangeldi (2015)	Cattle (—)	Rabies	—	—	TB	39,700	—
		Pasteurellosis	9,100	—**	Brucellosis	—	—
		Anthrax	24,600	—			
	Sheep/Goat (—)	Rabies	—	—	Brucellosis	—	—
		Pasteurellosis	12,100	—**			
		Anthrax	41,600	—			
Urpek and Kabyrga S.O.*** (2015)	Cattle (6,006)	Pasteurellosis	1,400	—**			
	Sheep/Goat (2,774)	Pasteurellosis	2,000	—**			

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

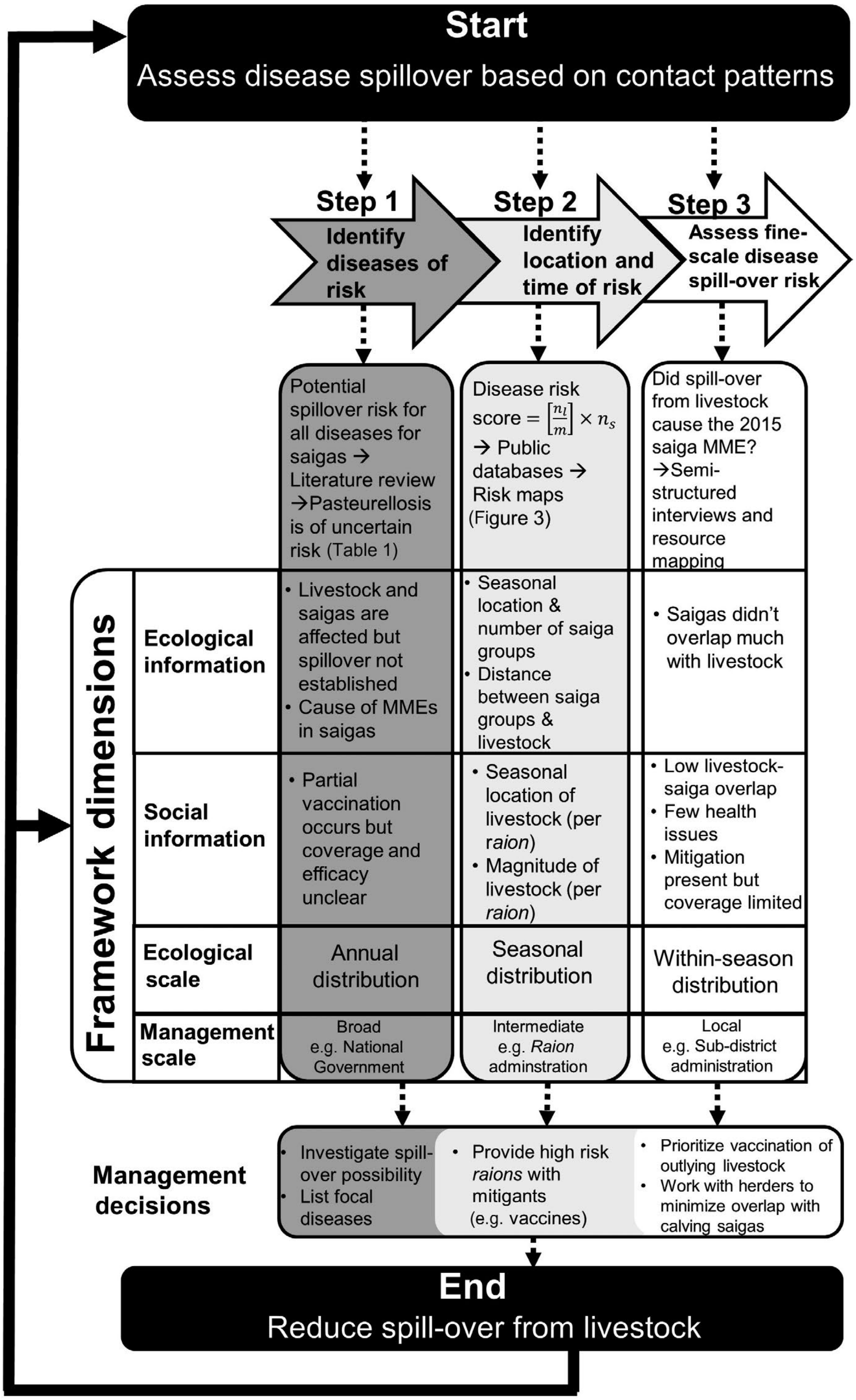

FIGURE 6 Lessons from the application of our disease risk prioritization framework to disease risks from livestock spill-over related to pasteurellosis in the Betpak-Dala saiga population. Information presented here is not exhaustive; see text for more details

5 | CONCLUSIONS

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

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

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AUTHORS' CONTRIBUTIONS

E.J.M.-G. conceptualized the framework which was further refined by her, S.R., E.R.M., N.J.S. and M.K. They also led the writing of the manuscript; S.R., E.R.M., M.K., R.K. and S.Z. conducted the on-ground surveys; T.B. and M.K. analysed the data; N.J.S. provided data. All authors provided critical inputs, contributed to the writing and revising of the manuscript.

DATA AVAILABILITY STATEMENT

Data available from Dryad Digital Repository https://doi.org/10.5061/dryad.jm63xsjb4 (Khanyari et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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