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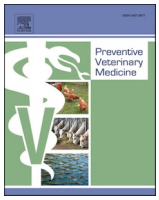

Seroprevalence and risk factors of Peste des petits ruminants in different production systems in Uganda

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ABSTRACT

Peste des petits ruminants (PPR) is a highly contagious and fatal disease of mostly domestic goats and sheep. First reported in Uganda in 2007, the extent of peste des petits ruminants virus (PPRV) exposure, geographical distribution and risk factors of its transmission and spread are not clearly understood. In this study, we used cluster random sampling methodology to select study villages from three districts representing three different production systems along Uganda's "cattle corridor". Between October and December 2022, 2520 goat and sheep serum samples were collected from 252 households with no history of PPR vaccination in the past one year. The household heads were interviewed to assess possible risk factors of PPRV transmission using a structured questionnaire. The serum samples were screened with a commercial competitive enzyme-linked immunosorbent assay (cELISA) for PPRV antibodies. The determined overall true seroprevalence of PPRV was 27.3% [95% CI: 25.4–29.1]. The seroprevalence of PPRV antibodies in different production systems was 44.1% [95% CI: 40.6–47.7], 31.7% [95% CI: 28.4–35.0] and 6.1% [95% CI: 4.4–7.9] for pastoral, agropastoral and mixed crop-livestock production systems respectively. A mixed-effects multivariable logistic regression model revealed strong statistical evidence of association between female animals and PPRV antibody seropositivity compared to males [OR= 2.45, 95% CI: 1.7–3.5, $p < 0.001$]. The likelihood of being PPRV antibody seropositive significantly increased with increasing small ruminant age. Animals older than 3 years were more than three times as likely to be PPRV seropositive compared to animals aged under 1 year [OR= 3.41, 95% CI: 2.39–4.85, $p < 0.001$]. There was no statistical evidence of association between small ruminant species and PPRV antibody seropositivity ($p = 0.423$). Village flocks that interacted with neighboring flocks daily during grazing (IRR = 1.59, 95% CI: 1.19–2.13) and watering around swamps (IRR = 1.59, 95% CI: 1.19–2.13) were highly correlated with increased number of PPRV seropositive animals as compared to flocks that were more restricted in grazing and watered around other water sources other than swamps. Flocks from pastoral and agropastoral production systems were more than 10 times more likely to have seropositive animals than mixed crop-livestock flocks. Targeting PPR control interventions (vaccination and livestock movement control) to pastoral and agro-pastoral small ruminant production systems that are very prone to PPR incursions is recommended to prevent PPRV spread to low-risk smallholder mixed crop-livestock production systems.

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1. Introduction

Peste des petits ruminants (PPR), also known as goat plague, is a highly contagious disease of domestic small ruminants (goats and sheep) caused by Peste des petits ruminants virus (PPRV) which is currently the only member of *Morbillivirus caprinae* species within the *Morbillivirus* genus of the *Paramyxoviridae* family (Postler et al., 2016).

PPR is associated with yearly economic losses of up to 2.1 billion US dollars globally (OIE-FAO, 2015). These losses result from mortalities, morbidities, cost of treatment, lost opportunities for international trade, loss in milk yield and live weight gain (Jones et al., 2016; Parida et al., 2015). Since the 1940s when the disease was first reported in West Africa, it has spread to over 70 countries in the rest of Africa and to Asia (Banyard et al., 2010). The affected countries are home to more than 80% of the global small ruminant population with over 300 million people deriving their animal protein and income from small ruminants (Banda and Tanganyika, 2021; Mazinani and Rude, 2020). Nevertheless, from the available literature, most PPR endemic countries have not sufficiently scaled up their vaccination campaigns using the commercially available effective PPR vaccines to maintain the required 80% protection levels while accounting for flock population dynamics (turnover rate, restocking frequency, movement among others) (OIE--FAO, 2015). Consequently, the disease continues to spread to new areas, causing significant economic losses. To this end, the Food and Agriculture Organisation of the United nations (FAO) and the World Organisation for Animal Health (WOAH, formerly known as OIE) have launched a global campaign to eradicate PPR by the year 2030, using vaccination as the main control measure in high-risk or endemic areas (FAO and WOAH, 2022).

Highly efficacious PPR vaccines that provide life-long protective immunity against all the four known PPRV lineages are available on the market (EFSA AHAW Panel, 2015). Moreover, small ruminants that survive the PPRV infection remain protected from severe clinical disease for at least 3 years (Baron et al., 2016). Female small ruminants that are vaccinated and or survive natural infection pass on maternal antibodies to their kids that usually offer them protection for at least 3 months (Ata et al., 1989; Balamurugan et al., 2012; Markus et al., 2019). However, there is currently no marker vaccine or diagnostic test that differentiates antibodies from vaccinated animals and those from naturally infected animals. This complicates seroprevalence estimation studies (OIE-FAO, 2015).

In Uganda, majority of livestock are kept in the "cattle corridor", a region that runs from South-Western to North-Eastern (Fatumah et al., 2023; UBOS, 2021). These animals are generally managed under three traditional production systems that include pastoral, agropastoral and mixed crop-livestock production systems (Kambarage and Kusiluka, 1996). These production systems are defined based on the level of family dependency on livestock or livestock products for sustenance, degree of movement involved, and the type of agriculture practiced alongside livestock (Ibrahim, 1998).

Pastoral production system dominates most of northern Uganda districts, most especially the north-eastern part (Karamoja subregion). In the Karamoja subregion, more than 50% of household income is derived from livestock or livestock products with very little or no crop agriculture. Livestock are kept on a large expanse of communal land where livestock owners move animals over long distances within the region and sometimes across international borders in search of fresh pasture and water during dry periods. Pastoral systems account for more than 16% and ~50% of goat and sheep populations in Uganda respectively (Akwongo et al., 2022; UBOS, 2017).

Agropastoral production systems dominate districts in central and south-western Uganda such as Isingiro, Rakai, Sembabule, Nakasongola, Kiruhura among others. In this system, between 10% and 50% of households depend on livestock or livestock products for their livelihood (Ibrahim, 1998). Crop agriculture is practiced alongside livestock production. Livestock are often kept in fenced farms or openly grazed on fairly large expanses of land with the likelihood of periodic migration to greener areas in search of pasture and water during drought spells (Kambarage and Kusiluka, 1996).

Mixed crop-livestock production system is the commonest management system practiced in majority of the districts in Uganda. In this system, livestock production is secondary to crop agriculture with less than 10% of household income derived from livestock (Ibrahim, 1998). Small ruminants are often kept in relatively small flocks tethered on ropes or closely herded by mostly family labour (women and children) to prevent the animals from encroaching on the crop gardens (Kambarage and Kusiluka, 1996). In such communities, animals are often moved for relatively short distances with a reduced chance for direct contact between flocks.

Previous PPR studies in Uganda reported seroprevalences ranging from 60% to 85%. However, nearly all this PPRV seroprevalence literature available constitute very small studies done in the pastoral production systems (Akwongo et al., 2022; Luka et al., 2011; Mulindwa et al., 2011; Ruhweza et al., 2010). With the rather very high seroprevalence estimates, it is understood that majority of these studies mentioned that they were done following vaccination campaigns whereas the rest, although not explicitly stated, were likely conducted around PPR outbreak periods (during or after) as previously reported (Nkamwesiga et al., 2022). This is likely true because of the need to estimate extent of virus spread or to evaluate the effect of vaccination post PPR outbreaks. Additionally, several PPR outbreaks have been reported in over 50 out of 135 districts of Uganda over the past 5 years with significant uptrend PPR clustering in central and south-western Uganda (Nkamwesiga et al., 2022). These outbreaks have devastated the livelihoods of affected households, in some instances wiping out entire small ruminant flocks or forced sale / salvage slaughter of affected animals (MAAIF, 2022). With limited capacity to conduct mass vaccination and other relevant control measures, the Ministry of Agriculture Animal Industry and Fisheries (MAAIF) has distributed vaccines for field veterinarians to conduct ring vaccination around affected areas to prevent further spread (Ayebazibwe et al., 2022).

Past and recent spatio-temporal cluster analyses of PPR outbreaks, socioeconomic human activities, bioclimatic, topographic, and environmental datasets have identified small ruminant density, extensive road network, animal movement, and draught among others as key factors that drive transmission of infectious diseases such PPR (Fèvre et al., 2006; Nkamwesiga et al., 2022). However, there is still paucity of data about production system-based risk factors of PPRV spread and PPR outbreaks within the endemic districts. This makes it difficult to design production system-based control programs (such as vaccination, movement control, biosecurity and biosafety and improving restocking programs) which partly contribute to the persistence and spread of PPRV in Uganda. We undertook this study to determine the seroprevalence of PPRV across three main small ruminant production systems in Uganda [all with previous reports of PPR outbreaks except the mixed crop-livestock production system], and identify production system- and-animal-level risk factors. The results herein described will help to design production system-based PPR control programs in Uganda and other endemic countries, in line with the national and global PPR eradication campaign by 2030.

2. Materials and methods

2.1. Sampling strategy

This cross-sectional study was conducted in three Uganda districts between October and December 2022 (Fig. 1). A list of all districts along the cattle corridor was first grouped into three categories, namely, pastoral, agropastoral and mixed crop-livestock production systems based on available literature and expert opinion (Fatumah et al., 2023; UBOS, 2021). One district was selected from each category using simple random sampling methodology. The selected districts were Nakapiripirit

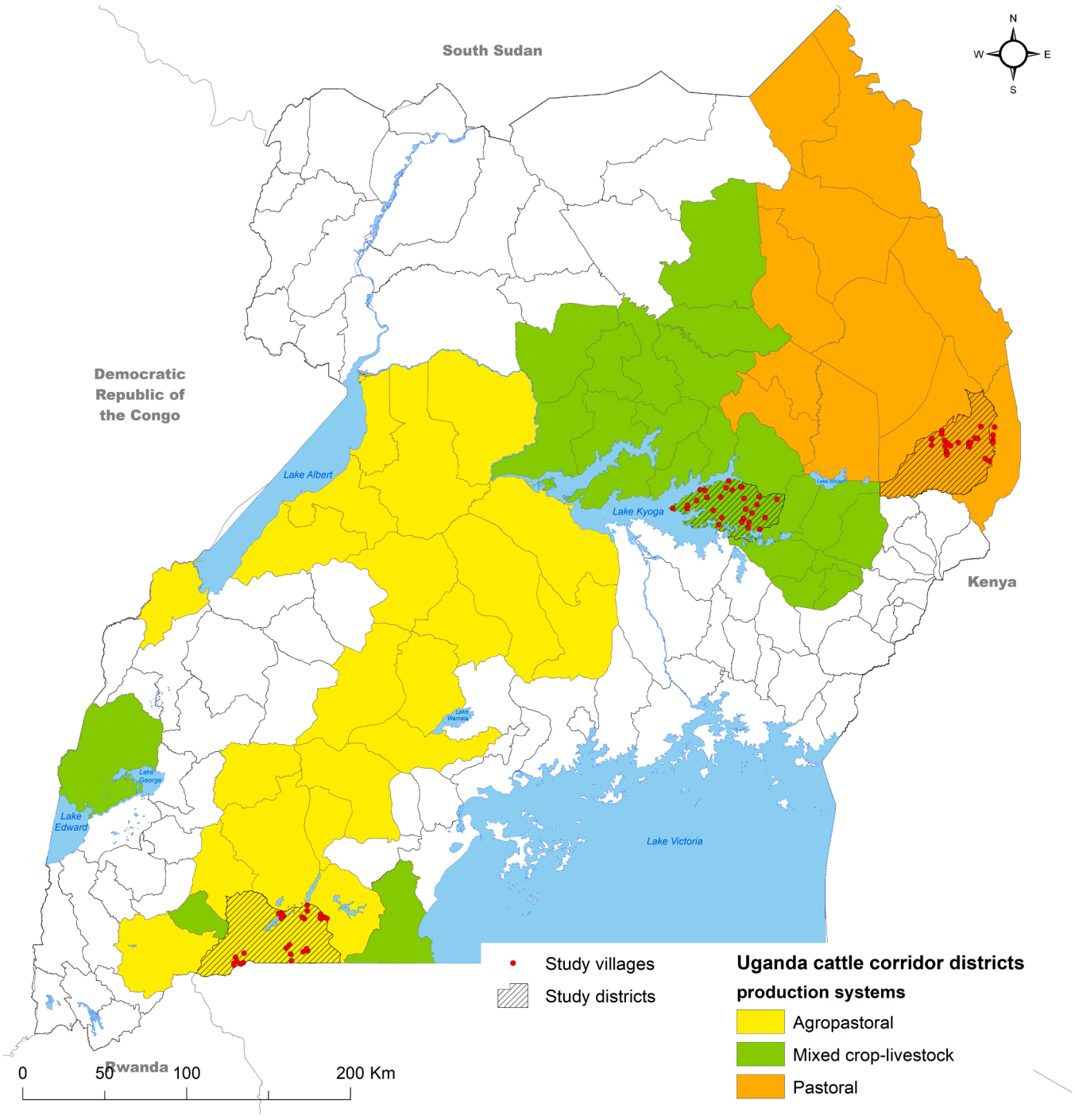

Fig. 1. Map of Uganda showing the study area. Highlighted are the major production systems that characterize districts that span the cattle corridor as demarcated based on current data. The map was generated using ArcMap 10.7 software using open-source datasets from the Uganda Bureau of Statistics.

(pastoral), Serere (mixed crop-livestock) and Isingiro (agropastoral). Study villages were selected from the complete list of villages (sampling frame) for each district provided by MAAIF (UBoS, 2009), using the cluster random sampling method as previously described (Bennett et al., 1991; Sullivan, 2007). Assuming an animal-level PPRV antibody seroprevalence of 50%, interclass correlation coefficient (ICC) of 0.029 (Waret-Szkuta et al., 2008) and design effect of 1.84, a total of 28 villages with a minimum of 30 small ruminants were required to be sampled per village. Consequently, a total of 840 small ruminants were required from each of the three districts to achieve the set precision and be able to detect risk factors if they existed. We then conducted a scoping visit to the study areas where we randomly replaced all villages where PPR vaccination had been conducted in the past 12 months with the help of district veterinary officials.

For the agropastoral and mixed crop-livestock production systems, at least three farms / households were randomly selected from a list of livestock-keeping households in the district (obtained during a scoping visit). However, in pastoral production system (Nakapiripirt district) where animals from the same village graze together, it was not necessary to select flocks as emphasis was on selection of 30 study animals from the communal village flock.

Individual animals were selected using systematic random sampling. We quickly estimated flock size and divided that number by the required animals per flock to obtain the position of the next animal to sample as

small ruminants exited the holding ground in a single file. Ten animals (5 sheep and 5 goats whenever possible) were randomly selected from each selected farm, flock or household. In case a selected household had less than 10 eligible small ruminants, we sampled all eligible animals they owned and sampled additional animals from the nearest household to make a total of 30 animals per village. Sampled animals were aged by the veterinarian taking samples based on their dentition as previously recommended (Dyce et al., 2002; Uhart et al., 2016). All the data was then aggregated at village level.

By the time of this study, no PPR outbreak had been reported from Serere district. However, from 2007 to 2020, between 10 and 12 and 1–2 laboratory confirmed PPR outbreaks had been reported in Nakapiripirit and Isingiro districts, respectively, prompting dispatch of vaccine doses sufficient for ring vaccination strategy (Ayebazibwe et al., 2022; Nkamwesiga et al., 2022).

2.2. Study population

Small ruminants (sheep and goats) of 4 months and above from flocks with no history of PPRV vaccination in the year before the study were included. All pregnant animals and clinically sick animals were excluded from the study for ethical and animal welfare reasons. All household heads (and/or caretakers of the small ruminants) of the sampled flocks were interviewed to gain insight of the epidemiological drivers of PPRV transmission.

2.3. Blood sample collection and serum extraction

In order to allow for easy access to the jugular vein, the animal handling assistant restrained the sheep/goat's body by holding the animal under its jaw and turned the head to the side, at a 30-degree angle as previously recommended (Uhart et al., 2016). Blood samples were drawn from small ruminants as previously described (Uhart et al., 2016) by Uganda Veterinary Board-licensed veterinarians. About 6 mL of jugular blood were obtained from sheep and goats into serum separator vacutainer tubes (SST) that contained a clot activator gel which allowed rapid blood clotting and serum separation. The SST tubes were serially labeled and the extra meta-data on each sample such as date, geographical position system coordinates, sex, age and species of animal recorded using Open Data Kit (ODK) on a tablet (Hartung et al., 2010). Upon separation of serum from whole blood, usually 12 h after blood sample collection, two 1.5 mL aliquots of serum were pipetted off from each blood sample into pre-barcoded cryogenic tubes. These were packed into cryoboxes and temporarily stored at − 20 °C at the district or regional laboratory before transporting them to the National Animal Disease Diagnostics and Epidemiology Centre (NADDEC) laboratory in Entebbe within one week for long term storage at − 80 °C until required for further analysis.

2.4. Household interviews

Structured farmer interview guides were used to collect data on the possible epidemiological drivers of PPRV transmission (Supplementary Table 4). These drivers included potential risk factors, production systems, water sources, possibility and frequency of contact with other flocks and wildlife, source of the animals (for restocking), distance from livestock markets, shared water sources, and vaccination status of the animals among others. The structured questionnaires were translated into respective local languages and pretested in a non-target district before implementation of this study.

2.5. Detection of PPRV antibodies

The PPRV specific IgG antibodies in serum were detected using the ID Screen® PPR (IDVet, 310 rue Louis Pasteur, 34790 Grabels, France) commercial competitive ELISA kits following the manufacturer's instructions (Libeau et al., 1995).

The cut-offs were calculated as;

$$\frac{S}{N}(\%) = \frac{OD_{sample}}{OD_{Negative\ \ control}} * 100.$$

The samples with percentage inhibition (S/N) less than or equal to 50% were considered positive, S/N % between 50 and 60 were considered doubtful whereas samples with an S/N value above 60% were considered negative. During the analysis, we considered all doubtful results as negative in the analysis since these samples were drawn from apparently healthy flocks as previously suggested (Fernandez Aguilar et al., 2020; Shyaka et al., 2021).

2.6. Estimation of true prevalence

True prevalence is traditionally estimated from the apparent prevalence using the Rogan–Gladen estimator as follows:

$$True\ prevalence = \frac{(Apparent\ prevalence + Sp - 1)}{(Se + Sp - 1)},$$

where *Se* denotes test sensitivity and *Sp* denotes test specificity (Rogan and Gladen, 1978). However, if the apparent prevalence is lower than the probability of observing a false positive (1- test specificity), the standard Rogan–Gladen estimator formular returns negative values. Also, if the apparent prevalence is greater than the diagnostic test sensitivity, the percentage true prevalence estimates will be greater than 100%. In both scenarios, the true prevalence estimates returned are not epidemiologically plausible (Reiczigel et al., 2010; Speybroeck et al., 2013). To overcome this problem, we used the fixed values of specificity (99.4%) and sensitivity (94.5%) as provided by the ELISA test manufacturers to estimate the true prevalence using Bayesian approach implemented in the R software package "prevalence" (Devleesschauwer et al., 2022).

2.7. Data analyses

All statistical analyses were done using R software, version 4.3.1 (R Core Team, 2023). We cleaned the data, determined animal-level and village-level seroprevalence and all relevant descriptive statistics. To test for animal-level risk factors, we included all the five captured animal-level factors (i.e., species, sex, age, village, and district) in a mixed effects logistic regression model using the *lme4* package in R software (Bates et al., 2015). To account for clustering and minimize the potential effects of confounding, a small ruminant "village" was set as the random effect in this model since observations were done at village level.

However, for the village level risk factors, data on a range of potential risk factors were collected, curated and screened for multicollinearity based on the variance inflation factor (VIF) to remove all the perfectly correlated variables. Variable selection for the village-level Poisson regression model was done using an automated backward model selection procedure (*stepAIC* function in the 'MASS' package in R). The precision level was set at 95% and p values < 0.05 were considered statistically significant and only the metrics in the final (best fit) model were presented.

To explore the association between incidence and the potential risk factors in a district, we tested the potential risk factors from farm/village interviews such as restocking, communal water source, frequency of contact with other flocks among others. A generalized linear Poisson regression model with log link was fit to these data using the number of positive animals per village as the dependent variable. To account for the spatial dependency of observations as a result of some villages or districts being close to each other, we conducted a spatial autocorrelation test on the residuals of the final regression model the Moran's I test (Chen, 2016).

The spatial scan statistic was computed using the Bernoulli model (Kulldorff, 1997) implemented in the SaTScan software (http://www.

satscan.org/) with default settings. To determine whether any of such clusters is statistically significant, the Bernoulli model takes binary data (positive or negative) in the form of cases and controls and identifies locations (space) where the number of observed cases tends to be more than expected (Chhetri et al., 2010). Statistically significant clusters ($p < 0.05$) were identified and visualized using ArcMap 10.7 software (ArcGIS v. 10.7, ESRI Inc. Redlands, CA, USA).

2.8. Ethical considerations

All study personnel involved in this study were protocol trained. The protocol that generated results described in this study was approved [Reference number: SVAR_IACUC/58/2020] by the School of Veterinary Medicine and Animal Resources Institutional Animal Care and Use Committee SVAR(SVAR-IACUC), Makerere University and the Uganda National Council of Science and Technology (UNCST) (reference number: A103ES). This work was also approved by the Institutional Animal Care & Use Committee (Reference number: ILRI-IACUC2021-08) and the Institutional Research Ethics Committee (Reference number: ILRI-IREC2021-07) at the International Livestock Research Institute. Additionally, the study was administratively approved by all participating district authorities (Prior Informed Consent). Animal sampling was completed by licenced veterinarians in Uganda. Written informed consent was obtained fromall participating farmers to bleed their animals, store their animal blood samples and serum therefrom as well as to interview them. All participating farmers' animals were dewormed as compensation for their time to participate inthe study.

3. Results

3.1. Village-level seroprevalence of PPRV antibodies

The village-level apparent prevalence of antibodies against PPRV ranged from 0.0% to 100.0% across the study area. All the 28 sampled flocks in Nakapiripirit district contained at least one animal positive for PPRV antibodies, resulting in 100% flock-level seroprevalence. In Isingiro district, flock-level PPRV antibody seroprevalence was 96.4% (27/28). The least number of positive flocks, (13/28), was observed in Serere district with 15 villages having no animal positive for PPRV antibodies resulting in 46.4% flock-level PPR antibody seroprevalence.

3.2. Individual animal-level seroprevalence of PPRV antibodies by district

The individual animal-level true seroprevalence of PPRV antibodies varied from 6.1% to 44.1% across the study area. Prevalence was highest (44.1%) in Nakapiripirit district, a predominantly pastoral production system, and lowest (6.1%) in Serere district where most small ruminants are tethered on ropes in a predominantly mixed crop-livestock production system (Table 1).

The spatial distribution of animal-level PPR antibody seropositivity among flocks was evenly distributed in Isingiro and Nakapiripirit districts. Majority of the villages in Nakapiripirit and Isingiro districts had animal-level seroprevalences ranging between 36.8% and 53.3% and 36.8–59.9% respectively. However, in Serere district, only Ogolai and Agola villages had high seroprevalences of 90.0% and 26.7% respectively. The rest of the 26 villages in Serere district had apparent prevalence ranging between 0% and 6.7% (Fig. 2).

Table 1
Animal-level seroprevalence of PPRV antibodies in goats and sheep (n = 2520) from Isingiro, Nakapiripirit and Serere Districts, Uganda (2022).

District	Production system	N positive [n sampled]	"Apparent" prevalence %	Estimated "true" prevalence [95% CI]
Isingiro	Agropastoral	255 [840]	30.4	31.7 [28.4 – 35.0]
Nakapiripirit	Pastoral	353 [840]	42.0	44.1 [40.6 – 47.7]
Serere	Mixed crop-livestock	52 [840]	6.2	6.1 [4.4 – 7.9]
Total		**660 [2520]**	**26.2**	**27.3 [25.4 – 29.1]**

The number of PPR seropositive animals per village (PPR cases) across the entire study site (Isingiro, Serere and Nakapiripirit districts) was found to be spatially clustered (Moran's autocorrelation statistic I = 0.302337, P = 0.001953) in two most likely clusters. The first most likely cluster was identified along the international border between Uganda and Kenya in Nakapiripirit district (log likelihood ratio = 66.96, p < 0.0001). The second statistically significant cluster was identified at the international border with Tanzania in Isingiro district (log likelihood ratio = 38.16, p = 0.0001) (Fig. 3).

3.3. Individual animal-level seroprevalence of PPRV antibodies by subcounty

The 84 randomly selected villages were distributed across 22 subcounties: Nakapiripirit (5), Isingiro (7) and Serere (10) (Fig. 4). Different sub-counties exhibited varying levels of true PPRV antibody seroprevalence. In Isingiro district, the sub-counties of Rugaaga and Bigango had the highest and lowest seroprevalence of 44.0% [95%CI: 3.2–27.0] and 6.3% [95% CI: 37–51.1] respectively. In Nakapiripirit district, the highest prevalence was recorded in Nakapiripirit town council (57.3% [95%CI: 46.4–68.0]) whereas the lowest true seroprevalence was observed in Moruita sub-county (36.3% [95%CI 30.9–41.8]). In Serere district, the highest true seroprevalence 20.4% [95%CI: 14.1–27.4] was observed in Bugondo sub-county whereas the lowest 3.4% [95%CI: 0.0–10.2] was observed in Kasilo subcounty (Supplementary table 1).

3.4. Individual animal-level seroprevalence of PPRV antibodies by village

Generally, the apparent PPRV antibody seroprevalence ranged from 0% to 96.6% whereas the estimated true seroprevalence ranged from 3.2% [95% CI: 0–9.7] to 95.7% [95% CI: 85.8–99.9]. More than 50% (15/28) of the sampled villages in Serere district had an apparent seroprevalence of 0% whereas only one village flock in Isingiro district (Kaziizi village) had an apparent seroprevalence of 0%. The lowest apparent animal-level seroprevalence at village level in Nakapiripirit was 6.0%. Ihunga village in Isingiro district, Alapat village in Nakapiripirit district and Ogolai village in Serere district had the overall highest PPRV antibody seroprevalences of 96.6%, 83.3% and 90% respectively (Supplementary table 2).

True animal-level seroprevalence in flocks was more spread out in Isingiro district than in Nakapiripirit and Serere districts. Isingiro district had more villages with seroprevalence lower than the median true prevalence value (34.0%) whereas majority of the villages in Nakapiripirit district had true seroprevalence estimates above the median value (47.5%). Over 90% of the villages in Serere district (26/18) had true seroprevalence below 10% (Fig. 5).

3.5. Animal-level risk factors of PPRV antibody seropositivity

There was no significant difference between PPRV antibody seroprevalence between goats and sheep (p = 0.423). Female small ruminants were more than twice more likely to be PPRV antibody seropositive as compared to male small ruminants (OR = 2.46, 95% CI: 1.70–3.47, p < 0.001). The likelihood of being PPRV antibody seropositive significantly increased with increasing small ruminant age. Compared to animals aged below 1 year, animals older than 3 years were more than thrice more likely to be PPRV antibody seropositive (OR = 3.41, 95% CI: 2.39–4.85, p < 0.001). Similarly, animals aged between 2 and 3 years were more than twice as likely to be seropositive whereas those aged between 1 and 2 years were nearly twice as likely to be PPRV antibody seropositive compared to the younger animals aged less than 1

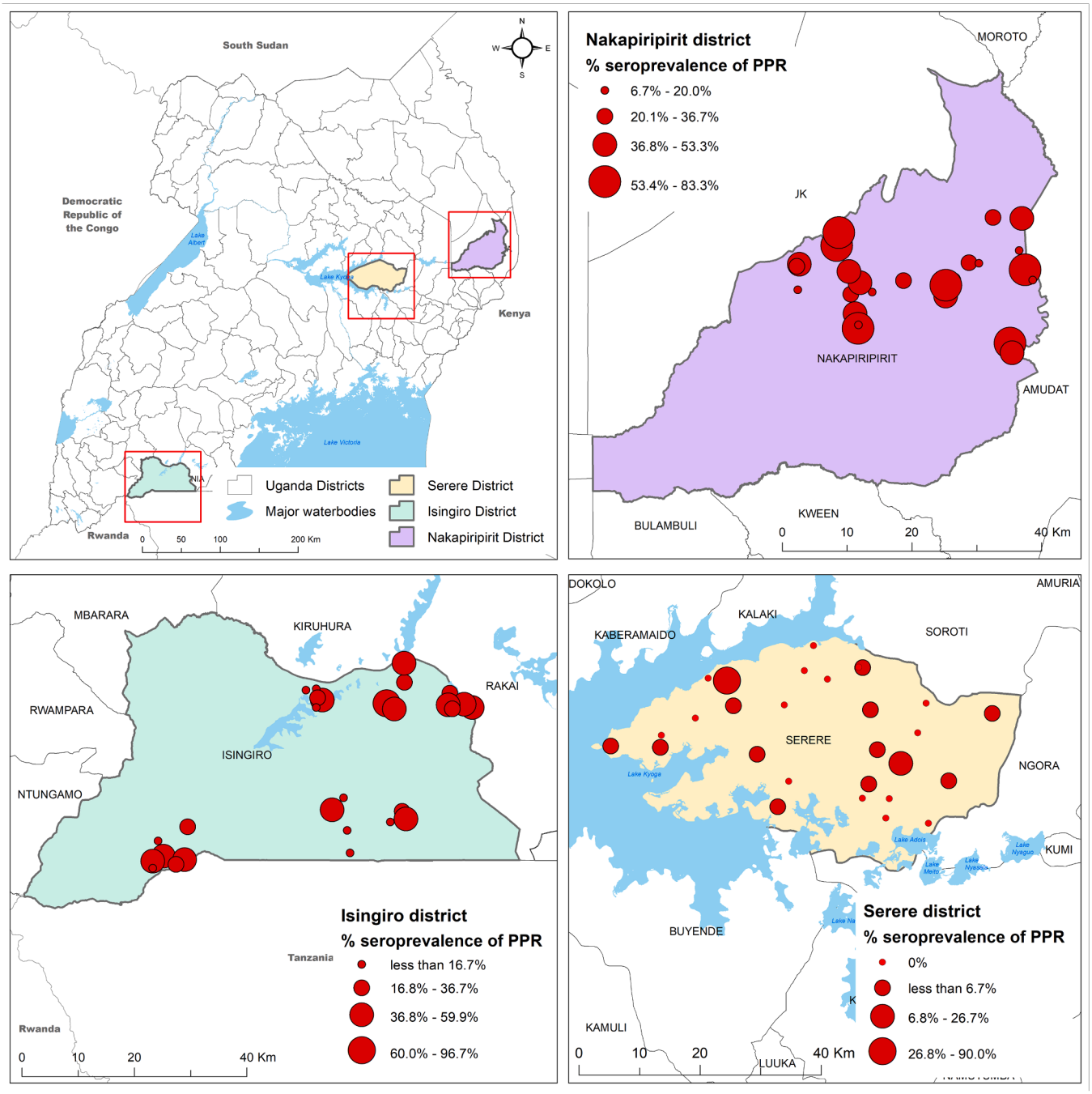

Fig. 2. Spatial distribution of animal-level PPRV antibody seropositivity among flocks in Isingiro, Serere and Nakapiripirit districts in Uganda (2022) as generated using ArcMap 10.7 software with open-source datasets.

year.

Goats and sheep from Nakapiripirit and Isingiro districts were 35 and 19 times respectively more likely be PPRV antibody seropositive than small ruminants from Serere district (Table 2).

The animal-level risk factors model random effects parameters were $\sigma^2 = 3.29$, $\tau 00_{Village} = 2.02$, ICC = 0.38, $N_{Village} = 84$, Obs = 2520, Marginal R2 / Conditional R2 = 0.337 / 0.591. The Moran's I test over the residuals of the final mixed effects regression model revealed that the data were dispersed (Moran's I = 0.031, z-score = −5.885, p-value < 0.001). The spatial clustering observed when we ran raw data (Fig. 3) disappeared after we incorporated the independent variables in the regression model. Our independent variables explain the spatial dependence that we originally found in the raw data.

3.6. Village-level risk factors of PPRV antibody seropositivity

Villages where flocks interacted with neighboring flocks daily were more likely to have PPRV antibody seropositive animals (IRR = 1.59, 95% CI: 1.19–2.13) whereas villages where flocks only interacted with other flocks less than once a month were significantly associated with reduced chances of having PPRV seropositive animals (IRR = 0.50, CI: 0.26–0.90) as compared to villages whose flocks were confined.

Villages whose water source for their animals was waterhole (IRR = 1.89, CI: 1.39–2.56) and swamp (IRR = 1.32, CI: 1.07–1.61) were strongly correlated with increased likelihood of having PPRV antibody seropositive animals compared to villages that did not use these water source types. However, using borehole as source of water for the small

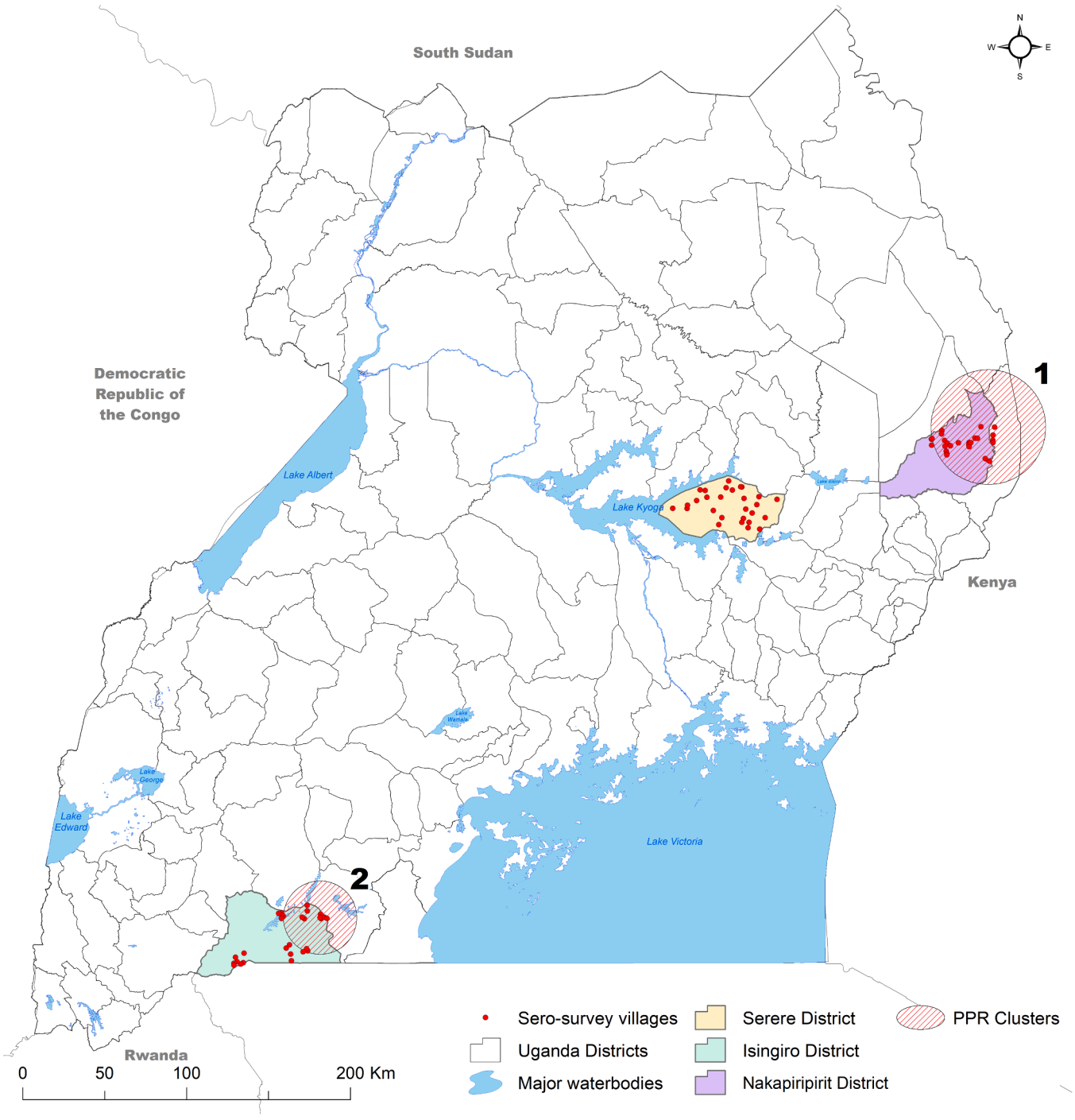

Fig. 3. Statistically significant clusters of PPR seropositivity in Isingiro, Serere and Nakapiripirit districts in Uganda (2022). The two clusters were identified using the Bernoulli method in SaTScan software and visualized in ArcMap 10.7 software.

ruminants was significantly correlated with reduced chances of having PPRV antibody seroprevalence animals (IRR = 0.55, CI: 0.43–0.69).

Villages in which households kept cattle and pigs in addition to small ruminants were 1.9 and 1.3 times respectively more likely to have PPRV antibody seropositive animals compared to villages that only kept small ruminants. Villages that maintained small ruminant flocks for at least one year were more likely to have PPRV seropositive animals than villages that purchased sheep and goats in the previous year.

Villages from Isingiro and Nakapiripirit districts were more than 10 times more likely to have PPRV antibody seropositive animals than those from Serere district. Villages where farmers reported that PPR vaccination had occurred in the past 12 months were 1.9 times more likely to be seropositive compared to villages where no PPR vaccination had not been conducted (Table 3).

4. Discussion

In this study we set out to determine the prevalence of PPRV antibodies across the three main small ruminant production systems in Uganda as well as the village- and animal-level risk factors of PPRV exposure.

The overall PPRV antibody seroprevalence estimates we report in this study are generally lower than what had been previously reported in similar settings in Uganda. The 42.0% apparent PPRV antibody

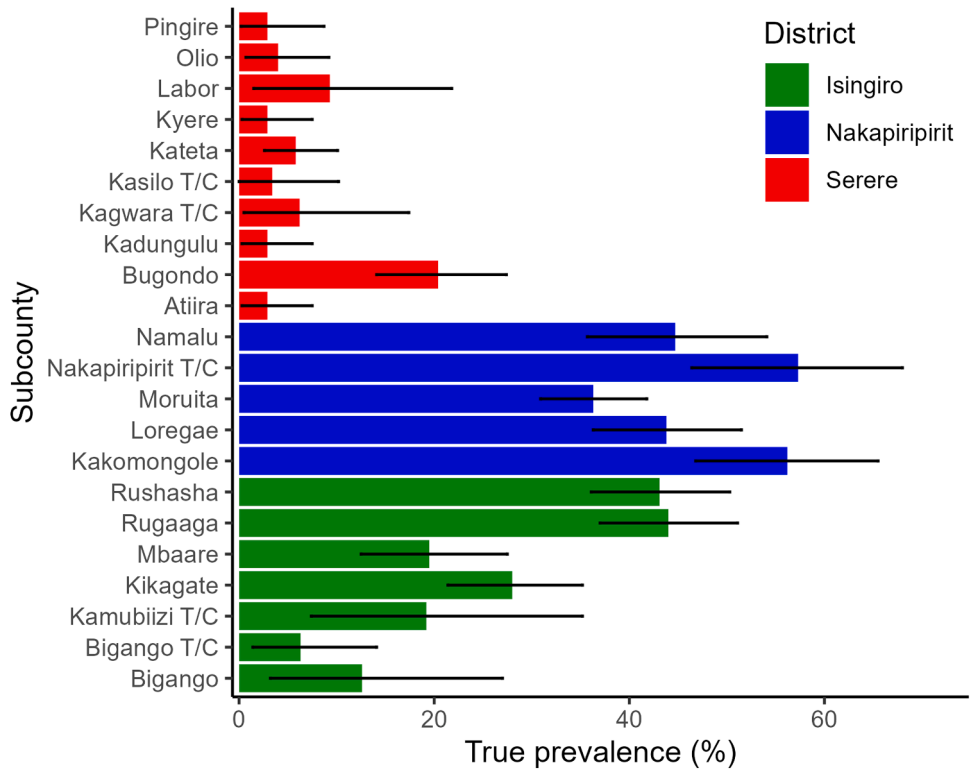

Fig. 4. True animal-level seroprevalence of PPRV antibodies in goats and sheep [n = 2520] from Isingiro, Nakapiripirit and Serere districts, Uganda (2022), as summarized at the subcounty-level. The "error bars" represent the lower and upper limits of the 95% confidence intervals from the Bayesian method.

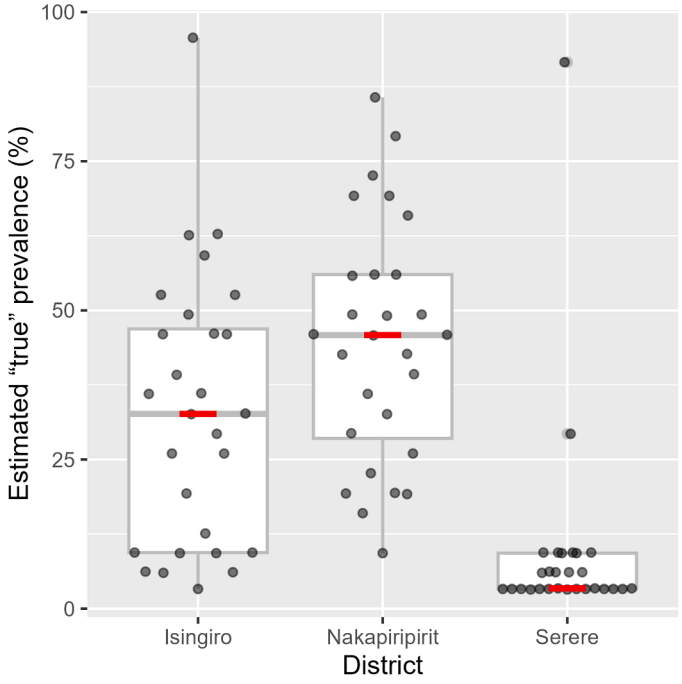

Fig. 5. Distribution of animal-level true seroprevalence of PPRV antibodies in goats and sheep [n = 2520] from Isingiro, Nakapiripirit and Serere districts, Uganda (2022), summarized by village/flock and district.

Table 2
Final multivariable mixed effects logistic regression model for animal-level risk factors of PPRV antibody seropositivity with village as a random effect [N = 2520] in Serere, Nakapiripirit and Isingiro districts, Uganda (2022).

Risk factors	n sampled [%]	n positive [%]	Odds Ratios	95% CI	p
1. **Species**					
i. Goats	1973 [78.3]	538 [27.3]	Ref		
ii. Sheep	547 [21.7]	122 [22.3]	0.87	0.63 – 1.21	0.423
2. **Sex**					
i. Male	390 [15.5]	73 [18.7]	Ref		
ii. Female	2130 [84.5]	587 [27.5]	2.46	1.74 – 3.47	< 0.001 * **
3. **Age (years)**					
i. < 1	593 [23.5]	98 [16.5]	Ref		
ii. 1–2	786 [31.2]	212 [27.0]	1.61	1.16 – 2.24	0.004 *
iii. 2–3	302 [14.3]	91 [30.1]	2.09	1.38 – 3.16	< 0.001 * **
iv. > 3	839 [30.9]	259 [30.8]	3.41	2.39 – 4.85	< 0.001 * **
4. **District**					
i. Serere	840 [33.3]	52 [6.2]	Ref		
ii. Isingiro	840 [33.3]	255 [30.4]	18.85	7.44 – 47.75	< 0.001 * **
iii. Nakapiripirit	840 [33.3]	353 [42.0]	35.15	13.94 – 88.64	< 0.001 * **

Level of statistical significance: 0 '* ** ' 0.001 '* *' 0.01 '* '

seroprevalence reported in Nakapiripirit district in the current study was lower than the overall average seroprevalence of 57.6% previously reported in the Karamoja region (Mulindwa et al., 2011). It was also lower than the 72.0%, 85.0% and 63.2% seroprevalence reported from the Karamoja districts of Nakapiripirit, Kotido and Moroto, respectively (Mulindwa et al., 2011). The study by Mulindwa et al. (2011) was conducted following the first major reported PPR outbreak in the Karamoja region in 2007, a situation that might have led to overestimation of PPRV seroprevalence. Additionally, Mulindwa et al. (2011) set out to

Table 3
Final multivariable Poisson regression model for village-level risk factors of PPRV antibody seropositivity [N = 84] in Serere, Nakapiripirit and Isingiro districts, Uganda (2022).

Risk factors	No. villages [%N]	Estimate	Std. Error	IRR	95% CI	p-value
Other flock contact frequency						
Never	20 [23.8]	Ref				
Daily	61 [72.6]	0.46	0.15	1.59	1.19 – 2.13	0.002**
< once a month	3[3.6]	-0.69	0.31	0.5	0.26 – 0.90	0.028*
Water source¶						
Communal	68 [81.0]	-0.90	0.15	0.41	0.30 – 0.54	< 0.001***
Swamp	25 [29.8]	0.27	0.10	1.32	1.07 – 1.61	0.009**
Borehole	44 [52.4]	-0.61	0.12	0.55	0.43 – 0.69	< 0.001***
Other livestock owned¶						
Cattle kept	72 [85.7]	0.65	0.15	1.91	1.43 – 2.56	< 0.001***
Pigs kept	31 [36.9]	0.26	0.12	1.30	1.03 – 1.64	0.027*
Restocking¶						
Goats purchased	25 [29.8]	-0.30	0.11	0.74	0.60 – 0.93	0.008**
Sheep purchased	16 [19.0]	-0.38	0.14	0.69	0.52 – 0.90	0.008**
Goats born within	44 [52.4]	0.65	0.15	1.92	1.44 – 2.57	< 0.001***
Other flock contact	58 [69.0]	0.42	0.27	1.52	0.87 – 2.53	0.124
Vaccination status¶						
PPRvaccinated	19 [22.6]	0.66	0.11	1.93	1.56 – 2.38	< 0.001***
District						
Serere	28 [33.3]	Ref				
Isingiro	28 [33.3]	2.37	0.25	10.65	6.65 – 17.40	< 0.001***
Nakapiripirit	28 [33.3]	2.41	0.21	11.14	7.49 – 16.90	< 0.001***

Level of statistical significance: 0 '* ** ' 0.001 '* *' 0.01 '* ' 0.05, R^2 Nagelkerke = 0.992, IRR= incidence rate ratio, Std. Error = standard error, ¶ These were binary categorical variables (yes or no); only "yes" is tabulated for ease of visualization, otherwise "no" is the reference category.

collect 354 samples but for some reason they were only able to sample a total of 280 animals in the four study districts, which might have further underpowered their study leading to potential overestimation of prevalence.

Our PPRV seroprevalence estimate from the pastoral production system was lower than 55.26% (Luka et al., 2011) previously reported from a sero-monitoring study and 51.4% (Akwongo et al., 2022) reported from a study that only focused on communal protected kraals as primary sampling units. Following vaccination, the antibody prevalence is expected to be higher than expected in apparently healthy flocks whereas protected kraals maximise the chance of nose-to-nose contact between small ruminants and thus increasing their likelihood of exposure to PPRV. The lower animal-level prevalence reported in this study could therefore partly be explained by a larger and more representative sample as well as a shift in time and dynamics in small ruminant flocks because of fast small ruminant enterprise turnover. The recent reduction in the number of PPR outbreaks in the Karamoja region could have resulted in less PPRV exposure and hence a reduction in PPRV seroprevalence (Nkamwesiga et al., 2022).

The PPRV seroprevalence of 30.4% for Isingiro district reported in this study was higher than 22.2% reported from a convenient sample of sheep from communities around the wildlife-livestock interface in Kasese district, southwestern Uganda (Fernandez Aguilar et al., 2020). In southwestern Uganda, Isingiro district, an agropastoral production system (fenced grazing with occasional transhumance), experience extreme drought seasons each year. Drought seasons in turn result in informal animal movements into other neighboring districts in Uganda (Nkamwesiga et al., 2022) and across the international border, in northern Tanzania with reported PPRV antibody seroprevalence ranging from 21% to 78% (Idoga et al., 2020) which potentially increases the risk of small ruminant exposure to PPRV. There has also been evidence of animal movement across international borders for purposes of trade and other social functions such as traditional weddings which also increase the risk of disease introduction into previously free areas (Wieland et al., 2020).

Serere district [proxy for mixed crop-livestock system] in the Teso subregion in Eastern Uganda is one of the districts where PPRV outbreaks had never been reported by the time of this study. Consistent with a previous small study (Ruhweza et al., 2010), we found a very low (6.2%) PPRV antibody seroprevalence in Serere district. In Teso subregion, small ruminants are often tethered to restrict them from grazing on crops which strongly limits animal co-mingling and therefore the risk of PPRV transmission; thus, explaining the low PPR seroprevalence levels. Owing to the very low seroprevalence estimates in Serere district, there is an urgent need to vaccinate flocks in the mixed crop-livestock production systems to protect them from future PPR outbreaks which often negatively impact livelihoods.

Generally, the seroprevalence of PPR was significantly higher in small ruminants older than one year of age than in those under one year of age. This observation is consistent with previous studies in Uganda and elsewhere (Akwongo et al., 2022; Torsson et al., 2017). Older small ruminants are more likely to have been exposed to PPRV during the course of their lives than those below one year, especially in PPR endemic countries such as Uganda. Additionally, older animals are more likely to have been exposed to vaccination against PPR especially in endemic areas with vaccination campaigns. Being a female small ruminant was identified as a significant animal-level risk factor for PPRV antibody seropositivity. This is in line with previous studies that have suggested female small ruminants have a higher risk of being PPRV antibody seropositive than male small ruminants (Kihu, Gachohi et al., 2015; Megersa et al., 2011; Torsson et al., 2017). It was suggested that female ruminants, owing to their key role in flock multiplication, are often kept for longer times at the farm which increase their likelihood of exposure to PPRV; thus, a higher risk of being seropositive than male small ruminants. However, this relationship could also be spurious because the average number of males is usually much lower than that of females. In our case, males represented only 15.5% (230/2520) of the entire sample.

We found that daily flock contact with neighboring flocks was strongly associated with increased PPRV antibody seropositivity within flocks. On the other hand, flocks that interact less frequently (less than once a month) were associated with decreased likelihood of having PPRV seropositive animals. This can be explained by the fact that PPR

mode of transmission is through direct contact between susceptible and infected animals and therefore the higher the contact frequency, the higher the chances of PPR transmission between flocks (Ekwem et al., 2021).

Flocks from villages where animals are watered at swamps were more likely to have PPRV seropositive animals compared to those that do not have swaps in their areas. Swamps are usually communal watering points usually attracting all animals in a village to drink water which in turn increases chances of interacting with PPRV infectious flocks. This is consistent with previous studies that have reported communal water sources as significant risk factors for infectious disease transmission especially those that require direct contact (Ekwem et al., 2021; VanderWaal et al., 2017). Conversely, villages whose water source was borehole were significantly associated with reduced chances of having PPRV seropositive animals. This is partly because boreholes are more restricted and are more likely restrict animal congregation hence boreholes being a protective factor.

In Uganda, households that keep cattle are the ones that also keep majority of the small ruminants. Moreover, keeping cattle was associated with an increased number of PPRV antibody seropositive animals. Considering that cattle are "dead-end" hosts for PPRV (Herzog et al., 2020), it is highly unlikely that they contribute to PPRV antibody seropositivity in small ruminants. Interestingly, villages where small ruminants were kept in addition to pigs were more likely to have PPRV seroprevalence as compared to villages where no pigs were kept. Pigs have previously been linked to shedding of PPR virus (Schulz et al., 2018), although experimentally, their role in the field epidemiology of PPR needs to be investigated further.

We also found that villages that maintained small ruminant flocks for at least one year (without any foreign introduction via purchase or gift) were more likely to have PPRV seropositive animals than villages that purchased sheep and goats in the previous year. Maintaining the animals in one area for a long period increases the chances of exposure to PPR virus especially in endemic districts whereas purchase of animals to improve breed or increase flock size could introduce naïve animals into the flock, depending on the source of animals and the status of their vaccination. Village where farmers reported that PPR vaccination had occurred in the past 12 months were 1.9 times more likely to be seropositive compared to villages where no PPR vaccination had been conducted. This was likely so because there are veterinarians that carry out private vaccination especially for commercial small ruminant farms, it was the reason we included this question in the questionnaire to try and explain some of the results.

Villages from pastoral and agropastoral production system districts were more than 10 times more likely to have PPRV antibody seropositive animals than those from mixed crop-livestock production system district. Transhumant pastoralists like those in Nakapiripirit district, Karamoja region, tend to move their flocks over long distances in the dry season to water and graze them at communal watering points and pasture fields respectively (Mbyuzi et al., 2014). Animal movements in search of pastures and water are maximal and semi-maximal in pastoral and agropastoral production systems. These two small ruminant production systems have been significantly associated with PPR seropositivity, as reported elsewhere (Fournié et al., 2018; Mdetele et al., 2021). Communal grazing and communal watering of small ruminants increases the likelihood of effective nose-to-nose contact between animals and therefore promotes PPRV transmission (Herzog et al., 2019). Additionally, animal movement, especially for trade purposes, has previously been linked to an increased potential for the spread of infectious diseases (Hasahya et al., 2023). Moreover livestock restocking programs in Uganda by different governmental and non-governmental organizations rarely adhere to strict laboratory screening and/ vaccination guidelines which potentially leads to introduction of infectious diseases such as PPR into naïve flocks, as has been the case with other livestock diseases (Selby et al., 2013).

There were two statistically significant spatial clusters of PPRV infection across the study area (Fig. 3). The spatial clusters of disease are epidemiologically defined as a set of interconnected regions which attains the maximum likelihood ratio as identified by spatial scan statistic as the most likely cluster (MLC) (Tango, 2021). The first cluster was identified around villages in Nakapiripirit district at the international border with Kenyan west Pokot pastoral communities in Turkana county, Kenya, which has previously been associated with high PPRV antibody seroprevalence of 40% and 36% in goats and sheep respectively (Kihu, Gachohi et al., 2015; Kihu, Gitao et al., 2015). The second statistically significant likely cluster was identified around Isingiro district, at the international border with Tanzania. These statistically significant spatial disease clusters are consistent with a previous study that documented confirmed PPR outbreaks over a 14-year period in Uganda (Nkamwesiga et al., 2022). International borders are associated with small ruminant comingling during both official and illicit livestock movement for international trade and in search of pasture and water. These international borders are both occupied by pastoral communities that freely move livestock across frontiers during the dry season.

5. Study limitations

The unavailability of a serological test that differentiates naturally infected animals from those vaccinated against PPR suggests that we could have inadvertently included previously vaccinated animals in the study, possibly leading to overestimation of seroprevalence in some areas. This likelihood is further aggravated by the absence of a livestock identification and traceability system in Uganda which makes it difficult to trace vaccinated animals. Nonetheless, we worked with the area veterinarians to select animals from households that had not participated in PPR vaccination exercise for at least 12 months. Also, the fact that PPR vaccination coverage in Uganda accounts for less than 10% of the total small ruminant population gives us confidence that the estimates from this study are reliable and can be used to guide interventions. There was generally poor record keeping at flock level in livestock keeping communities which could have introduced recall bias especially at village level. However, we made an effort to triangulate our findings with key stakeholders especially district veterinary officials to reduce the effects. This coupled inherent variation in production types per village across districts, these results may not be perfectly generalisable to all districts in Uganda. However, this study provides a starting point to initiation of production system-based interventions.

6. Conclusion

Transhumant pastoral production system was associated with the highest PPR antibody prevalence while smallholder mixed crop-livestock production systems where goats are often tethered reported the lowest PPRV seroprevalence. Agro-pastoral production system presented with mid-range risk of PPR seropositivity. Animal sex (female / male), age (in favour of older animals; >1 year) were the animal-level risk factors of PPR seropositivity while rearing of cattle and pigs, communal water sources and frequency of contact between flocks were production system-based risk factors of PPR seropositivity. Targeting PPR control interventions (vaccination and livestock movement control) to and from pastoral and agro-pastoral small ruminant production systems that are prone to PPR incursions is recommended to prevent PPRV spread to low-risk smallholder small ruminant production systems.

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CRediT authorship contribution statement

JN: study design, data collection and analysis, writing, and reviewing; FK, DPN: data analysis and reviewing; PL: writing, and reviewing; KR: grant acquisition, study conceptualization, study design and reviewing, BW: study conceptualization and reviewing; HK and DM: study design, writing, and reviewing; AP: data analysis, reviewing; all authors have read and approved this manuscript for publication.

Declaration of Competing Interest

None.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.prevetmed.2023.106051.

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