The impact of flock demographics on post-vaccination immunity levels against peste des petits ruminants virus in heterogeneous Small ruminant populations

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THE IMPACT OF FLOCK DEMOGRAPHICS ON POST-VACCINATION IMMUNITY LEVELS AGAINST PESTE DES PETITS RUMINANTS VIRUS IN HETEROGENEOUS SMALL RUMINANT POPULATIONS

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SUMMARY

Peste des petits ruminants (PPR) is an acute infectious disease of small ruminants affecting flocks throughout large parts of Africa, Asia and the Middle East. The Global Strategy for Control and Eradication (GSCE), targeting global eradication by 2030, recommends vaccination of small ruminants in endemic regions to attain 70% post-vaccination immunity. We develop a deterministic, age- and sex-structured, demographic model of flock dynamics and conduct a global sensitivity analysis to identify the most important demographic parameters influencing post-vaccination immunity in pastoral small ruminant populations in sub-Saharan Africa. The model is parameterised using empirical demographic data extracted from the literature to explore post-vaccination immunity levels in different flock profiles. We show that under the GSCE recommendation, immunity decays below 70% within 12 months for all profiles. We highlight the importance of tailoring vaccination to local demographic contexts and the need for widely available, standardised demographic data to characterise small ruminant populations.

INTRODUCTION

Peste des petits ruminants (PPR) is an acute infectious disease of small ruminants, caused by peste des petits ruminants virus (PPRV), which is endemic throughout large parts of Africa, Asia and the Middle East. PPRV endemicity disproportionately impacts subsistence farmers in affected regions, with outbreaks causing high morbidity and mortality in susceptible flocks and estimated global economic losses of up to US$2billion per year (Jones et al., 2016). The World Organisation for Animal Health (WOAH) and the Food and Agriculture Organisation of the United Nations (FAO) launched the global strategy for the control and eradication of PPRV (GSCE) in 2015 with the target of global PPRV eradication by 2030 (FAO and OIE, 2015). Central to the GSCE is mass vaccination of endemic small ruminant populations aiming for a post-vaccination immunity level of at least 70% to prevent viral circulation (FAO & OIE, 2015).

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Progress towards PPRV eradication is challenged by the diversity of small ruminant populations affected. In endemic regions, livestock are managed under three main production systems: pastoral, agro-pastoral and mixed crop-livestock. Variations in the geographic and climatic conditions, and religious and cultural contexts in which small ruminants are reared results in adoption of diverse husbandry practices. These differences generate heterogeneity in the demographic characteristics of small ruminant flocks impacting flock turnover rates. The effectiveness of vaccination depends on flock turnover as immune animals exit the flock through deaths (e.g. predation, disease) or offtake (e.g. slaughter, sales, gifts given, loans) and new, susceptible animals enter the flock through births, and intake (e.g. purchases, gifts received) resulting in a decay in flock immunity levels. Demographic processes which are linked to high turnover rates may therefore drive rapid decay in post-vaccination immunity. Through improved understanding of how demographics affect flock turnover and immunity dynamics, it may be possible to characterise types of flock or production systems – associated with certain demographic characteristics – where current vaccination strategies fail to maintain immunity levels, and to inform the design of tailored vaccination campaigns.

The objective of this study was to explore post-vaccination immunity dynamics in different small ruminant populations ("flock profiles") using a deterministic, age- and sex-structured, demographic model of flock dynamics. Through a sensitivity analysis, the most important demographic parameters influencing flock immunity levels were identified, providing targets for data-collection activities. The model was then used to simulate post-vaccination immunity dynamics in different small ruminant flock profiles to assess the effectiveness of the GSCE vaccination programme for small ruminant flocks in PPRV-endemic regions of sub-Saharan Africa.

MATERIALS AND METHODS

Overview

A deterministic, age- and sex-structured flock dynamics model was developed to explore the impact of demographic processes on small ruminant flock immunity levels following vaccination. A global sensitivity analysis was conducted to assess the sensitivity of post-vaccination immunity levels to uncertainty in different demographic parameters. The model was parameterised using empirical demographic data, extracted from the literature, to represent different small ruminant flock profiles in PPRV endemic regions of sub-Saharan Africa (primarily East and West Africa). The model was used evaluate the effectiveness of the GSCE vaccination-programme.

Demographic Model Structure

The model considered a single small ruminant flock, structured into age classes and differentiated by sex (denoted m for males and f for females). The model was in discrete time (t), with a timestep of 1 week, such that animals within each age group (denoted i) could move into the next age-class (i+1), or leave the flock, within a timestep.

Health State Transitions

The model comprised two mutually exclusive health states: susceptible (S, animals with no history of infection or vaccination) and immune (R, animals with lifelong immunity from vaccination). At time T_v a proportion , p_v, of susceptible animals (S) were vaccinated and moved into the immune state (R). For animals under 4 months ($i \leq 17$ weeks) only, an additional compartment, *born-immune* (B), was included to account for offspring which gain PPRV immunity due to maternal antibodies. Newborn offspring born to immune females (R_f) entered the *born-immune* state ($B_{f,1}, B_{m,1}$) with probability p_B or the susceptible state ($S_{f,1}, S_{m,1}$) with probability $1 - p_B$. In each timestep, *born-immune* animals (B_i) could transition to susceptible (S_i) with rate τ_i. The decay in maternal immunity was informed by empirical data on the waning of maternal antibodies in lambs born to vaccinated mothers (Bodjo et al., 2006).

Demographic Transitions

Within a timestep animals exited the flock through mortality and offtake, and entered the flock through births and intake. Females above the minimum age of reproduction (A_R) reproduced with rate α, defined as the mean number of (live) offspring produced per female within a timestep (one week). α was fixed and equal for all reproductive females for the duration of the simulation and the ratio of female to male offspring was 1:1. Hence, female births per timestep could be computed from equations 1 and 2:

$$B_{f,1}(t) = \frac{\alpha}{2} \cdot p_B \cdot \sum_{i=A_R}^{A_F} R_{f,i}(t-1) \tag{1}$$

$$S_{f,1}(t) = \frac{\alpha}{2} \cdot (1 - p_B) \cdot \sum_{i=A_R}^{A_F} R_{f,i,}(t-1) + \frac{\alpha}{2} \cdot \sum_{i=A_R}^{A_F} S_{f,i}(t-1) \tag{2}$$

The weekly mortality risk (μ_i) varied with age but was equal between sexes, with μ_1 for animals younger than 6 months ($i \leq 26$ weeks), and μ_2 for animals older than 6 months ($i > 26$ weeks) such that $\mu_1 \gg \mu_2$ accounting for the high reported mortality in young stock (Otte & Chilonda, 2002; Hassen & Tesfaye, 2014). A maximum age for males (A_M) and females (A_F) was defined as the final age category ($\mu_{i,f} = 1$ for $i = A_F$, and $\mu_{i,m} = 1$ for $i = A_M$). The weekly net offtake risk (θ) was the net movement of animals out of the flock (θ = weekly intake – weekly offtake). A minimum age of exchange, A_X, was defined such that male or female animals could be exchanged if $i \geq A_X$. θ was age and sex stratified resulting in 4 offtake parameters: θ_y for animals (male or female) younger than the minimum age of exchange ($i < A_X$), here we assumed $\theta_y = 0$; θ_f for females older than the minimum age of exchange ($i \geq A_X$); θ_{m1} for young adult male animals, older than the minimum age of exchange and younger than 24 months ($i \geq A_X$ and $i \leq 104$ weeks) and θ_{m2} for adult male animals older than 24 months ($i > 104$ and $i < A_M$). The young adult male offtake risk (θ_{m1}) accounted for the high reported offtake risks of males from puberty to 2 years such that $\theta_{m1} \geq \theta_{m2}$ and $\theta_{m1} \gg \theta_f$ (Hassen & Tesfaye, 2014; Lesnoff, 1999; Tadesse et al., 2014). For each group, θ was fixed and constant throughout the simulation (although see Hammami et al., 2016 for an evaluation of the impact of temporal offtake dynamics on post-vaccination immunity dynamics). The demographic equations for female animals were computed as follows:

$$B_{f,i}(t) = B_{f,i-1}(t) \cdot \tau_{i-1} \cdot \left(1 - \theta_{f,i-1}\right) \cdot \left(1 - \mu_{f,i-1}\right) \qquad if\ i \leq 17 \tag{3}$$

$$S_{f,i}(t) = \begin{cases} S_{f,i-1}(t-1) \cdot \left(1 - \theta_{f,i-1}\right) \cdot \left(1 - \mu_{f,i-1}\right) + B_{f,i-1}(t-1) \cdot \left(1 - \tau_{i-1}\right) & if\ i \leq 17 \\ S_{f,i-1}(t-1) \cdot \left(1 - \theta_{f,i-1}\right) \cdot \left(1 - \mu_{f,i-1}\right) & if\ i > 17 \end{cases} \tag{4}$$

$$R_{f,i}(t) = R_{f,i-1}(t-1) \cdot (1-\theta_{f,i-1}) \cdot (1-\mu_{f,i-1}) \qquad if\ i \leq 17 \qquad (5)$$

Global Sensitivity Analysis

A global sensitivity analysis was conducted to determine the most important demographic parameters influencing post-vaccination immunity levels. Demographic parameter ranges were extracted from the literature, and supplemented by expert opinion where data were lacking, to represent pastoral and agro-pastoral small ruminant flocks in PPRV endemic regions of sub-Saharan Africa (primarily East & West Africa) (Table 1). A latin hypercube sampling procedure was used to generate 200,000 parameter sets with 10 variable demographic parameters included using the R sensitivity package (Iooss et al., 2023). The simulation period was 25 years and all animals were initially susceptible. Vaccination was implemented at the mid-point of the simulation (12.5 years, $T_v = 652$) allowing time for flock growth rates and age-sex structures to stabilise before vaccination. At T_v, 100% animals were vaccinated within one timestep, assuming a post-vaccination immunity level of 100% (i.e. 100% efficacy). Three immunity metrics were computed to analyse post-vaccination immunity dynamics: (i) immunity at 6 months post-vaccination, (ii) immunity at 12 months post-vaccination and (iii) weeks post-vaccination with immunity ≥70%. Population growth in the final 10 years of the simulation was also computed. Model outputs were validated against the expected growth rates and age-sex structures of pastoral and agro-pastoral small ruminant populations (Table 2). Parameter sets failing to meet these criteria were discarded. Partial rank correlation coefficients (PRCCs) were computed using the epiR package in R (Stevenson et al. 2023). PRCCs are commonly used in sensitivity analyses of infectious disease models (Sanchez and Blower, 1997; Wu et al., 2013; Sumner et al., 2019; Sumner and White, 2022), providing a measure of the monotonicity between model inputs and outputs to indicate the extent to which uncertainty in input parameters accounts for variation in output metrics while considering possible correlations between input parameters.

Table 1. Demographic parameter ranges extracted from the literature for global sensitivity analysis, representing pastoral and agropastoral small ruminant flocks in sub-Saharan Africa

Parameter	Symbol	Minimum	Maximum	References
Net offtake risk, young[a]	θ_y	0	0	Hassen & Tesfaye, 2014
Net offtake risk, young male[a]	θ_{m1}	0.4	0.99	Lesnoff, 1999; Hassen & Tesfaye, 2014; Tadesse et al., 2014
Net offtake risk, adult male[a]	θ_{m2}	0	0.3	Otte & Chilonda, 2002; Tadesse et al., 2014; Yirga et al., 2020
Net offtake risk, adult female[a]	θ_f	0	0.3	Otte & Chilonda, 2002; Tadesse et al.,; Yirga et al., 2020
Mortality risk young[a]	μ_y	0.15	0.55	Otte & Chilonda, 2002; Hassen & Tesfaye, 2014
Mortality risk adult[a]	μ_a	0.05	0.33	Otte & Chilonda, 2002; Hassen & Tesfaye, 2014; Tadesse et al., 2014; Yirga et al., 2020
Birth rate[a]	α	1	2.5	Otte & Chilonda, 2002; Hassen & Tesfaye, 2014; Tadesse et al., 2014; Yirga et al., 2020
Minimum age of exchange (months)	A_X	9	14	Hassen & Tesfaye, 2014; Tadesse et al., 2014
Age of first parturition (months)	A_R	10	18	Otte & Chilonda, 2002; Tadesse et al., 2014; Yirga et al., 2020
Maximum age of males (years)	A_M	3	5	Kosgey et al., 2008
Maximum age of females (years)	A_F	7	12	Kosgey et al., 2008

[a]Annual risk/rate.

Table 2. Flock growth and age-sex structure conditions extracted from the literature representing pastoral and agro-pastoral small ruminant flocks in sub-Saharan Africa

Parameter	Minimum	Maximum	References
10-year growth	0.85	1.15	Tadesse et al., 2014; Yirga et al., 2020
Female <6months	0.05	0.19	Gebre Mariam, 1991; Tadesse et al., 2014; Tesfahun et al., 2017; Yirga et al., 2020
Female 6-12months	0.06	0.15	Gebre Mariam, 1991; Tadesse et al., 2014; Tesfahun et al., 2017; Yirga et al., 2020
Female >12months	0.21	0.62	Gebre Mariam, 1991; Tadesse et al., 2014; Tesfahun et al., 2017; Yirga et al., 2020
Male <6months	0.05	0.16	Gebre Mariam, 1991; Tadesse et al., 2014; Tesfahun et al., 2017; Yirga et al., 2020
Male 6-12months	0.04	0.15	Gebre Mariam, 1991; Tadesse et al., 2014; Tesfahun et al., 2017; Yirga et al., 2020
Male >12months	0.01	0.15	Gebre Mariam, 1991; Tadesse et al., 2014; Tesfahun et al., 2017; Yirga et al., 2020

Applied Analysis

The effectiveness of the PPRV GSCE vaccination programme was assessed by analysing post-vaccination immunity dynamics in different small ruminant populations. Flock profiles were extracted from the literature to represent populations found in PPRV-endemic regions, including sheep and goat flocks under pastoral and mixed crop-livestock systems in different agro-ecological zones across East and West Africa (Otte and Chilonda, 2002). For each flock profile, 10,000 parameters sets were generated through latin hypercube sampling of the parameter ranges reported, if no range was provided $\pm$10% variation was added to the reported value. Net offtake of young males (θ_{m1}) was rarely specified, we assumed that the lower boundary was equal to the minimum net offtake risk of the flock and the upper boundary was equal to the maximum value which produced valid population growth and age-sex structures in the global sensitivity analysis (Methods; *Global Sensitivity Analysis*). The simulation period was 20 years (1040 weeks), and all animals were initially susceptible. The GSCE vaccination programme was simulated including 4 consecutive annual campaigns, beginning at the mid-point of a simulation (T_v = 520 weeks). In rounds 1 and 2, animals aged over 4 months were vaccinated and in rounds 3 and 4 animals aged 4 to 12 months were vaccinated, as specified in the GSCE (FAO and OIE, 2015). Each vaccination round was implemented within one timestep, and all eligible animals gained immunity (i.e. pV = 100% for eligible animals with 100% vaccine efficacy assumed). Flock growth over the ten-year simulation period, and the stable age-sex structure for each parameter set were initially validated against the conditions used for the global sensitivity analysis (Table 2). Parameter sets failing to meet these criteria were discarded and, for the remaining parameter sets, immunity at 6 months post-vaccination, immunity at 12 months post-vaccination, and the number of weeks with immunity ≥70%, were computed. The proportion of immune animals at the first timestep following vaccination, was also computed. Model development and all analyses were carried out using R statistical computing environment (R Core Team, 2023).

RESULTS

Global Sensitivity Analysis: the most influential demographic parameters on flock immunity

When validated against flock growth and age-sex structure conditions (Table 2), 4140 of the 200,000 parameter sets generated through latin-hypercube-sampling produced valid outputs. Invalid parameter sets were discarded from the sensitivity analysis. The PRCCs for the flock immunity metrics and each of the 10 demographic parameters are given in Table 3. All PRCCs were statistically significant ($p<0.05$) except the PRCCs for the maximum age of males, the maximum age of females, and the net offtake risk of adult females. The order of the PRCC indicates the degree to which uncertainty in a given demographic parameter influences variability in post-vaccination immunity. The PRCCs indicated that the demographic parameters which were most influential on post-vaccination immunity levels (i.e. PRCC $> \pm 0.5$), in pastoral and agro-pastoral small-ruminant flocks were young male offtake risk, birth rate, minimum age of offtake, minimum age of reproduction, and youth mortality risk (based on PRCCs for weeks with >70% immunity, in descending order of magnitude). Demographic parameters which were positively correlated with flock immunity levels, an increase in the parameter value resulted in higher flock immunity levels, included: the minimum age of offtake, the minimum age of reproduction, and the mortality rate of young animals. Demographic parameters which were negatively correlated with flock immunity levels, i.e. an increase in the parameter value resulted in lower flock immunity levels, included: birth rate, the mortality risk of adults and net offtake risks (θ_{m1}, θ_{m2}, θ_f).

Applied analysis: the effectiveness of GSCE vaccination in different small ruminant populations

This analysis of flock immunity following GSCE vaccination in different small ruminant flock profiles focuses on immunity levels following the first annual vaccination campaign (at T_v = 520). Following vaccination of all eligible animals the median flock immunity level was 0.849 over all flock profiles (range 0.78-0.90). The proportion of animals which failed to gain immunity is accounted for by the proportion of animals younger than 4 months which are not eligible at the time of vaccination. Post-vaccination immunity levels were highly variable within and between different flock profiles, however, at 12 months post-vaccination, immunity was not maintained above 70% in any flock profile. The median duration of immunity above the 70% threshold was 32 weeks post-vaccination, approximately 7 months (range 20-50 weeks) (Table 4, Fig.1).

Table 3. Partial Rank Correlation Coefficient (PRCC) values for flock immunity metrics and 10 demographic parameters, ranked in descending order of magnitude for weeks with immunity >70%

Parameter	Symbol	Weeks with immunity >70%		Immunity at 6 months		Immunity at 12 months	
		PRCC	p	PRCC	p	PRCC	p
Net offtake risk, young male[a]	θ_{m1}	-0.865	<0.001	-0.903	<0.001	-0.860	<0.001
Birth rate[a]	α	-0.802	<0.001	-0.859	<0.001	-0.813	<0.001
Minimum age of exchange[a]	A_X	0.759	<0.001	0.825	<0.001	0.612	<0.001
Age of first parturition[a]	A_R	0.722	<0.001	0.791	<0.001	0.746	<0.001
Mortality risk, young[a]	μ_y	0.640	<0.001	0.469	<0.001	0.695	<0.001
Net offtake risk, adult male	θ_{m2}	-0.285	<0.001	-0.331	<0.001	-0.287	<0.001
Mortality risk, adult	μ_a	-0.250	<0.001	-0.336	<0.001	-0.222	<0.001
Net offtake risk, female	θ_f	-0.085	<0.001	-0.022	0.167	-0.125	<0.001
Maximum age of males	A_M	0.016	0.323	0.013	0.424	-0.008	0.590
Maximum age of females	A_F	0.008	0.622	-0.052	0.001	0.022	0.164

[a] Parameters with PRCC>$\pm$0.5 for weeks with immunity >70%.

Table 4. Summary statistics for post-vaccination immunity levels after 1 round of vaccination in small ruminant populations in sub-Saharan Africa. Vaccination was implemented with 100% coverage of animals older than 4 months

Immunity metric	Mean	Median	Minimum	Maximum
Flock proportion immune at first timestep post-vaccination.	0.847	0.849	0.780	0.901
Flock proportion immune 6-months post-vaccination.	0.734	0.738	0.642	0.824
Flock proportion immune 12-months post-vaccination.	0.580	0.585	0.432	0.705
Weeks with immunity >70%	31.8	32	20	50

DISCUSSION

The global sensitivity analysis indicated that young male offtake, births, the minimum age of exchange, age of first parturition, and youth mortality were the most important influences on post-vaccination immunity levels in pastoral and agro-pastoral small ruminant flocks. A small number of studies have explored the impact of different demographic features on post-vaccination flock immunity dynamics in specific small ruminant populations (Hammami et al., 2016, 2018; El Arbi et al., 2019), however, this sensitivity analysis offers more general conclusions about the relative importance of different demographic parameters for diverse PPRV-affected small ruminant populations. Understanding the role of different demographic parameters in driving post-vaccination immunity dynamics can provide insights to inform data-collection activities, enabling the prioritisation of important parameters and optimised resource allocation (Wu et al., 2013). This is particularly relevant in PPRV endemic regions where data collection activities can be limited due to lack of resource (economic, logistic) and practically challenging due to the characteristics of extensively managed, mobile small ruminant populations.

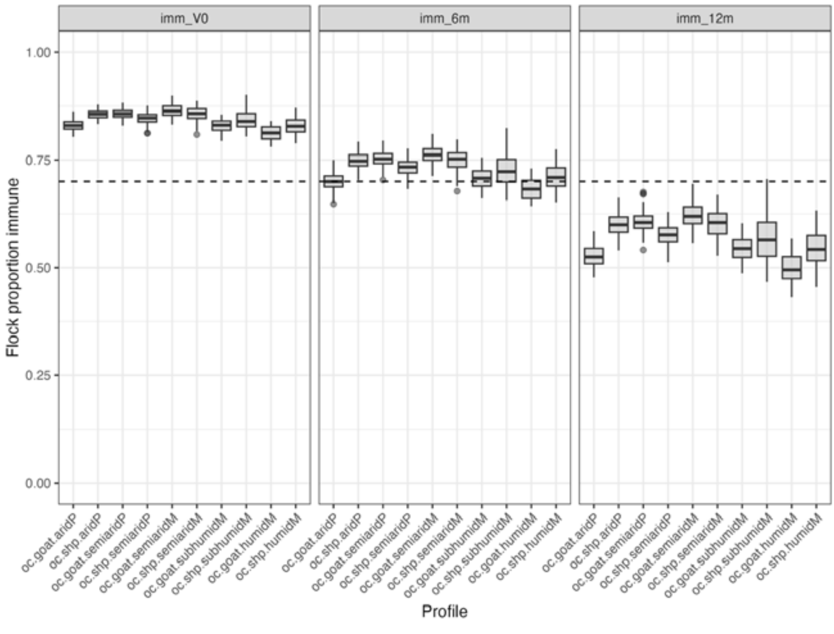

Figure 1. Box-and-whisker plots of post-vaccination flock immunity metrics for different small ruminant flock profiles in sub-Saharan Africa. Dashed line indicates flock immunity level = 70%. Immunity abbreviations: flock proportion immune at first timestep (imm_V0), at 6 months (imm_6m) and at 12 months post-vaccination (imm_12m). Flock profile abbreviations: goat flocks (oc.goat), sheep flocks (oc.shp), pastoral (P), mixed crop-livestock (M)

The results of the applied analysis demonstrated that the current GSCE vaccination programme fails to maintain flock immunity levels above the targeted 70% threshold up to 12 months post-vaccination in populations with constant reproduction. This finding supports previous research which showed a decay of flock immunity to below 70% within a year of vaccination (Hammami et al. 2018). In this study, flock immunity was maintained above 70% for a median of 31 weeks (or 7-months), suggesting that implementing vaccination campaigns twice per year may be more appropriate. The highest immunity level attained immediately following vaccination was 80%, with the non-immune proportion comprised of animals younger than 4 months which were ineligible for vaccination. In small ruminant populations which breed consistently throughout the year (often more sedentary, mixed crop-livestock production systems), as modelled here, achieving immunity levels >80% may be challenging due to the continuous presence of young animals. In this context, the GSCE recommends vaccination campaigns at 6-month intervals to maintain flock immunity levels. The timing of vaccination, in any population, should be scheduled to maximise the proportion of immune-competent animals (animals in good body condition) and according to the local agricultural calendar (e.g. accounting for periods of transhumance and availability of funds to pay for vaccination; FAO & OIE, 2015). Where breeding is seasonal, resulting in defined birth peaks, campaigns may be more easily scheduled to maximise the proportion of animals older than 4 months and eligible for vaccination. Previous research has indicated that, in arid regions of West Africa (Senegal), the highest flock immunity levels can be achieved through vaccination between 2 to 4 months preceding a parturition peak when a large proportion of animals are eligible for vaccination (older than 4 months) and additional factors such as periods of transhumance and small ruminant body condition are considered (Hammami et al., 2018; El Arbi et al., 2019). The lack of seasonality in our model is a limitation, however, further work is ongoing to explore the effect of seasonal breeding on flock immunity dynamics in the pastoral flock profiles included here.

The applied analysis demonstrated considerable variation in post-vaccination immunity levels both within and between flock profiles, reflecting reported variation among flock demographics and highlighting the importance of accounting for population demographics in vaccination strategies. In PPRV-endemic regions, detailed, longitudinal, demographic data are rarely available with studies commonly using cross-sectional surveys which require respondents to recall flock dynamics over long periods. Across studies, data can be inconsistent due to annual variations in flock demographics dependent on environmental conditions, differences in the selection and definition of parameters reported and the age-sex stratification of flocks. Through global sensitivity analysis, young male offtake was identified as the most influential parameter driving post-vaccination immunity dynamics however, despite qualitative reports of high young male offtake (Gebre Mariam, 1991; Hassen and Tesfaye, 2014; Tadesse et al., 2014), the parameter is rarely specified within datasets. The lack of high-quality, detailed demographic data to characterise different small ruminant populations can limit the accuracy and practical application of studies incorporating flock demographics. Lesnoff et al. (2014) proposed a framework, and associated tool, to facilitate collection of standardized demographic data in tropical livestock herds. Widespread adoption of this approach would increase the availability of comprehensive, standardized demographic data for diverse small ruminant populations. This would facilitate more accurate assessment of the factors influencing flock dynamics, and improve the quality of studies reliant on demographic data including studies of infectious disease transmission, post-vaccination immunity dynamics and livestock productivity.

The global sensitivity analysis indicated the most important demographic parameters impacting post-vaccination immunity levels in pastoral and agro-pastoral small ruminant populations, offering insights to inform data-collection activities in data-limited settings. The applied analysis demonstrated that the GSCE vaccination programme with annual vaccination, fails to maintain immunity above the targeted 70% threshold in small ruminant flock profiles if breeding is non-seasonal. This supports the findings of previous studies that, where births occur consistently throughout the year, two vaccination rounds per year may be more effective. This study offers insights into the influence of flock demographics on post-vaccination immunity dynamics, however increased availability of detailed demographic datasets is required to enable more accurate characterisation of small ruminant flocks.

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