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Using Genomics as a Decision Support Tool in Smallholder Pig Enterprises in Uganda

submitted by

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Affidavit

I hereby declare that I have authored this dissertation independently, and that I have not used any assistance other than that which is permitted. The work contained herein is my own except where explicitly stated otherwise. All ideas taken in wording or in basic content from unpublished sources or from published literature are duly identified and cited, and the precise references included. Any contribution from colleagues is explicitly stated in the authorship statement of the published papers.

I further declare that this dissertation has not been submitted, in whole or in part, in the same or a similar form, to any other educational institution as part of the requirements for an academic degree.

I hereby confirm that I am familiar with the standards of Scientific Integrity and with the guidelines of Good Scientific Practice, and that this work fully complies with these standards and guidelines.

Vienna, December 14, 2021 Brian Martin Babigumira (manu propria)

Dedication

This thesis is dedicated to the memory of my father Mr. Balikaki Festo Blaze Babigumira who always believed in me.

Thou wilt keep him in perfect peace, whose mind is stayed on thee: because he trusteth in thee.

- Isaiah 23:6 KJV

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Preface

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List of abbreviations

%	Percentage
χ^2	Chi-square
ADG	Average Daily Gain
BL	Body length
CL	Confidence Level
cm	Centimeter
d	Day
DF	Degrees of Freedom
g	Gram
HG	Heart girth
Kg	Kilogram
LMEM	Linear Mixed effects Model
LSM	Least Squares Mean
ME	Modern European
SE	Standard Error
TBA	Total number of piglets born alive
TNW	Total number of piglets weaned
UGX	Uganda Shilling (1United States Dollar ≈ 3650 UGX; year 2019/20)
UNCST	Uganda National Council of Science and Technology
USD	United States Dollar
WT	Body weight

List of publications

Publications that comprise the main part of this cumulative dissertation

Brian Martin Babigumira, Emily Ouma, Johann Sölkner, and Karen Marshall. Pig breeding practices of smallholder farmers in Uganda. Acta fytotechnica et zootechnica (accepted November 25, 2021)

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Brian Martin Babigumira, Emily Ouma, Johann Sölkner, Maria Wurzinger, and Karen Marshall. Few signs of transition: results of a survey of smallholder pig practices in rural areas of Hoima and Kamuli districts, Uganda. ILRI, Nairobi, Kenya. (in preparation)

Brian Martin Babigumira, Johann Sölkner, Gábor Mészáros, Maria Wurzinger, Christina Pfeiffer, Craig R. G. Lewis, Ben Lukuyu, Emily Ouma, and Karen Marshall. Effect of proportion of Modern European ancestry on grower and sow performance of pigs in smallholder systems in Uganda. (submitted to Journal of Animal Science)

Abstract

Pig production in Uganda is an important socioeconomic activity for over a million smallholder producers. However, smallholders are faced with several production constraints related to pig health, nutrition, and breeding. Pig breeding practices remain poorly characterized and inferior breed performance a common complaint of the farmers. To address information gaps in pig breeding, a baseline survey was used to collect data on production characteristics of smallholder pig farmers. Results showed that replacement stock was obtained from animals born in the herds or purchased from other smallholder farmers. Village boar service rather than Artificial Insemination was used. Heat detection in the gilt/ sow was by observing for changes in the vulva. Sow reproduction problems were around small litter size and long farrowing intervals. Record keeping and animal identification were hardly practiced, and production focus was either animals for slaughter, breeding or both. Cognizant of the role of gender in livestock production, we conducted a gender evaluation of the farmers' perceptions to reasons for keeping the pigs and trait and breed preferences. Both women and men pig farmers kept the animals for income/ insurance and savings. Traits considered important by both genders were related to growth (faster rate), disease tolerance and reproduction (litter size). Preferred pig breeds were exotic over crossbred over local. Overall, no significant differences suggested gendered breeding objectives are required for smallholder farmers in Uganda. The genetic background of pigs in Uganda is not well documented, and it is often assumed that smallholder pigs are inbred due to inappropriate husbandry practices. Therefore, we undertook a genomic survey of pigs kept in these smallholder herds that revealed a mix of Old British and Modern European breed ancestry and very low inbreeding. Given the production focus, trait, and breed preferences of the smallholder farmers, we conducted an ancestry-sensitive genomic evaluation of grower and sow performance using longitudinal data. Linear mixed effects models tested the effect of proportion of Modern European ancestry (ME) on growth and litter size. ME was not a significant effect on body weight or total number of piglets born alive but was a significant effect on total number of piglets weaned. There was an upward trend from low to high ME levels for number of piglets weaned. Overall, this study demonstrated the potential of using genomics to support livestock breeding and conservation programs in smallholder systems in developing countries. However, while the ever-reducing genotyping costs point to a bright future, phenotyping costs remain high. Development of low-cost phenotyping tools as well as of organizational structure of properly using this information will go a long way in ensuring appropriate management of livestock genetic resources in developing countries.

Kurzfassung
Die Schweineproduktion ist eine wichtige sozioökonomische Aktivität für über eine Million Kleinbauern in Uganda. Kleinbauern sind jedoch mit mehreren Produktionsbeschränkungen im Zusammenhang mit der Gesundheit, Ernährung und Zucht von Schweinen konfrontiert. Schweinezuchtpraktiken sind schlecht charakterisiert und schlechte Leistung ist eine häufige Beschwerde der Landwirte. Um Informationslücken in der Schweinezucht zu schließen, wurden in einer Basiserhebung Daten zu Produktionsmerkmalen von Kleinbauern erhoben. Die Ergebnisse zeigten, dass Tiere zum Ersatz von Abgängen in den Herden geboren oder von anderen Kleinbauern gekauft wurden. Die Anpaarung weiblicher Tiere erfolgte durch Dorf-Eber, künstliche Besamung wurde nicht angewandt. Der Östrusnachweis der Jungsauen erfolgte durch Beobachtung von Veränderungen der Vulva. Probleme bei der Reproduktion der Sauen waren geringe Wurfgröße und hohe Zwischenwurfzeiten. Aufzeichnungen und die Identifizierung von Tieren wurden kaum praktiziert, und der Produktionsschwerpunkt lag entweder auf Schlachttieren, Zucht oder beidem. Wir führten eine Gender-Bewertung der Wahrnehmung der Landwirt*innen zu den Gründen für die Haltung der Schweine und zu den Präferenzen für Merkmale und Rassen durch. Sowohl weibliche als auch männliche Schweinehalter hielten die Tiere für Einkommen / Versicherung und Ersparnisse. Merkmale, die als wichtig angesehen wurden, bezogen sich auf Wachstum, Krankheitstoleranz und Fortpflanzung (Wurfgröße). Exotische Schweinerassen wurden gekreuzten über lokalen Typen vorgezogen. Insgesamt gab es keine signifikanten Unterschiede zwischen Geschlechtern bei den vorgeschlagenen Zuchtzielen. Der genetische Hintergrund von Schweinen in Uganda ist nicht gut dokumentiert, und es wird auch oft angenommen, dass sie aufgrund unangemessener Haltungspraktiken stark ingezüchtet sind. Wir führten eine genomische Untersuchung von Schweinen durch, die in diesen kleinbäuerlichen Herden gehalten wurden und fanden, dass sie eine Mischung aus alter britischer und moderner europäischer Abstammung haben und der Inzuchtgrad sehr gering ist. Angesichts des Produktionsschwerpunkts und der Rassepräferenzen der Kleinbauern führten wir eine genomische Bewertung der Leistung von Züchtern und Sauen unter Verwendung von Daten wiederholter Messungen über einen Zeitraum von rund 18 Monaten durch. Lineare Mixed-Effects-Modelle testeten den Einfluss des Anteils der modernen europäischen Abstammung (ME) auf Wachstum und Wurfgröße. ME war kein signifikanter Effekt auf das Körpergewicht oder die Gesamtzahl der lebend geborenen Ferkel, aber ein signifikanter Effekt auf die Gesamtzahl der abgesetzten Ferkel. Bei der Zahl der abgesetzten Ferkel war ein postiver Trend von niedrigen zu hohen ME-Werten zu

beobachten. Insgesamt zeigte diese Studie das Potenzial der Nutzung der Genomik zur Unterstützung von Zuchtprogrammen in kleinbäuerlichen Systemen in Entwicklungsländern. Während die Genotypisierungskosten ständig sinken, bleiben die Phänotypisierungskosten hoch. Die Entwicklung kostengünstiger Phänotypisierungsinstrumente sowie einer Organisationsstruktur für die ordnungsgemäße Nutzung dieser Informationen wird einen großen Beitrag zur Gewährleistung einer angemessenen Bewirtschaftung der genetischen Ressourcen von Nutztieren in Entwicklungsländern leisten.

Chapter 1 General introduction

1.1. The role of livestock in food security

When people have unrestricted access to safe and nutritious food, they are food secure (FAO, 1996). Around 800 million people globally are food insecure (World Health Organization, 2019). The global human population is projected to grow to 9.8 billion by 2050 and the sub-Saharan African population will grow to 2.0 billion, accounting for more than half of the global growth (United Nations and Social Affairs, 2019). This growth will require more food production, particularly animal-based protein, driven by increased urbanization and incomes (FAOSTAT, 2017). Livestock contribute to food security by providing animal source food; traction, transportation and manure for agriculture; and household savings and income (Sansoucy, 1995). Despite their small size (less than two hectares), smallholder farms produce between 50 and 80% of the food consumed globally (Lowder et al., 2014; Ricciardi et al., 2018). Livestock supports at least one billion smallholder farmers globally and more than 900 million smallholder producers in low- and middle-income countries derive their livelihood from livestock (Dolberg, 2001; Herrero et al., 2009; Herrero-Medrano et al., 2014). Pork and poultry are the major animal protein sources (OECD-FAO, 2011) and by 2013, they contributed around 50% of the total animal source food (Lassaletta et al., 2016). Only recently is pork second to poultry as the most consumed meat globally (OECD, 2021). This change in ranking for pork could be related to the recent African swine fever outbreaks in China, the largest global producer of pigs (Zhou et al., 2018; FAO, 2019; FAOSTAT, 2021).

1.2. Domestication of the pig

Pig domestication was preceded by speciation of *Sus* species in Island South-East Asia (ISEA) (Larson et al., 2005) and divergence of European and Asian lineages (Groenen et al., 2012; Frantz et al., 2013). Following these events, pig domestication independently occurred 9,000 years ago in Eastern Anatolia and China (Megens et al., 2007; Rothschild et al., 2011). The ancestor of the domestic pig is the wild boar, *Sus Scrofa*. The range of *Sus scrofa* covers Europe, North Africa and Asia (Ruvinsky and Rothschild, 1998). Since domestication of Sus scrofa, over 600 breeds of pigs have been bred globally (Scherf and Pilling, 2015). Pig breeding was mainly done in Europe and China producing local and specialized breeds (Clutton-Brock, 1990). Hybridization between Asian and European pigs happened between the 18th and 19th centuries. Asian pigs were used to improve European pig breeds leading to the formation of commercial breeds (Darwin, 1868; Larson et al., 2005). Some of the breeds formed by the hybridization were the British Berkshire and Large White (Jones, 1998). The Meishan, a Chinese pig bred for high prolificity has been used extensively to improve several commercial breeds (Cesar et al., 2010; Groenen et al., 2012). Due to the high level of pork consumption, the domestic pig has global distribution and most European pigs have British origins (Porter, 1993). No evidence, genetic, lingual, historic or archeologic, exists pointing to pig domestication in Sub-Saharan Africa (SSA) and none of the native wild *Suids* in the region mate with domestic pigs (Blench, 2000). Yet, the domestic pig is widely distributed in Africa (Porter, 1993). Pigs in SSA are often categorized into indigenous, exotic and crosses (Blench, 2000). Indigenous breeds have been reported in several African countries including Ghana, Nigeria and Uganda (Adebambo and Dettmers, 1982; Mbuza, 1995; Blench, 2000; Abdul-Rahman et al., 2016). However, unlike their exotic counterparts, indigenous breeds in SSA are poorly characterized and their breed status is not fully known. The consensus is that SSA pigs were introduced to the continent (Amills et al., 2013).

1.3. Genomics and its application in pig production in Sub-Saharan Africa

1.3.1. Overview of genomics

Gregor Mendel's hereditary theories changed clinical (disease diagnosis) and agricultural (crop and animal breeding) practices. However, most of the work relied on what could be observed or measured, that is phenotypes. Little was known about Mendel's hereditary factors (Mendel, 1965), later called genes (Johannsen, 1909), until the discovery of deoxyribonucleic acid (DNA) (Avery et al., 1944; Dahm, 2005), its structure (Watson and Crick, 1953) and processes to determine the order of its nucleotides (Sanger, 1981). Since then, molecular markers have had huge application in medicine and agriculture. Molecular (genetic) markers include microsatellites, Restriction Fragment Length Polymorphism (RFLP), Amplified Fragment Length Polymorphism (AFLP) and Single Nucleotide Polymorphism (SNP) among others. The SNPs are nonrepetitive sequence variants that are distributed throughout the genome (all the genes) of an individual. Low-cost microarray technology has contributed to the development of several SNP Chips for whole-genome sequencing in plants and animals (for example the porcine 60K SNP Chip). While genetics studies the structure, function and inheritance of individual genes, genomics studies all genes, that is, the genome of an individual.

The term genomics was first used by Thomas Roderick in 1986. It has three branches namely, structural, functional, and comparative genomics. Structural genomics studies the structure of the whole genome of an organism. It deals with sequencing and mapping of genes (Kim, 1998; Burley et al., 1999). Functional genomics studies the function of all the genes within the genome of an organism and deals with the transcriptome and proteome (Hieter and Boguski, 1997). Comparative genomics compares the genomes of two individuals from different species to discriminate conserved from divergent DNA (non- and functional) (Hardison, 2003). Genomics has been applied to livestock production for a range of purposes including genetic improvement and breed verification. Outlined here are a few of the common applications of genomics to support decisions in livestock production.

Genomic selection. By the early 1990s, marker-assisted selection (MAS) was tested and tried out to complement traditional animal breeding methods, mass selection and Best Linear Unbiased Prediction (BLUP). With the advent of SNP genotyping technology, genomic selection (GS) became possible (Meuwissen et al., 2001). GS is a form of MAS in that it uses SNPs and phenotypic information. In principle, GS involves recording phenotypes on animals from a genotyped reference population. The effects of each SNP, that is, genomic estimated breeding values (GEBV) are estimated in the reference population. The GEBVs are used to select breeding animals irrespective of the accuracy of their phenotypes. In case of availability of phenotype and genotype information of large numbers of animals, GS overcomes the limits of traditional breeding methods, improves accuracy, and shortens the generation interval. Some of the traits that have been improved using GS include feed conversion efficiency in poultry, litter size in pigs, health, conformation, and milk yield in dairy cattle.

Breed composition and traceability. Livestock production systems use purebred or crossbred animals. For comparison of breed-types (whether pure or admixed) it is important to know the breed composition of animals. In the absence of pedigree recording (as is common in smallholder systems) genomics makes this possible. Breed composition can be predicted based on a panel of genome-wide markers (Hulsegge et al., 2013). Genomics makes it possible to evaluate the performance of crossbred animals to determine adaptability to various environments particularly in cases of missing or pedigree errors (Kuehn et al., 2011). Further, genomics makes it possible to authenticate breed labeled products (Wilkinson et al., 2012).

Genomic precision mating. optimal contribution theory is used to balance selection of parents with other concerns (e.g., inbreeding, profile of traits in the progeny etc.). But use of genomics does allow for additional types of specific mating. However, with genomic information (GEBV and genomic kinship), it is possible to determine the best combination of parental genotypes to mate to optimize offspring performance (Akdemir and Sánchez, 2016). In cases where carrier status of certain genetic defects or major genes that are segregating in the breed is known, genomic co-ancestry can be incorporated to planning mating to maximize productivity of the offspring (Bérodier et al., 2021).

Genomic management of genetic diversity. Genomics makes it possible to plan utilization and conservation programs for rare and endangered breeds (Oldenbroek, 2017). Using genomics, the level of inbreeding in populations (F_{ROH}) can be estimated by Runs of Homozygosity (ROH) (Gibson et al., 2006; Hill and Weir, 2011). The goal of genomic management of inbreeding is to avoid inbreeding depression, loss of genetic variation in traits that may have future use and drifting of recessive disease alleles (Meuwissen et al., 2020).

1.3.2. Application of genomics to pig production in Sub-Saharan Africa

The application of genomics in cattle, sheep, goats and chicken in developing countries has been recently reviewed (Marshall et al., 2019a). Pig production in SSA is based on herds believed to consist of indigenous and exotic animals (Blench, 2000). However, no evidence exists that points to pig domestication and therefore, the origin of indigenous pigs in SSA. A series of studies have been undertaken themed around diversity and population structure of pigs in Africa. The first study on the diversity of African pigs was based on microsatellites (Ramirez et al., 2009). The authors reported high frequencies of European alleles in pigs from West Africa and European and far Eastern alleles in pigs from East Africa. Another microsatellite-based study was conducted in Uganda and in addition to the findings of Ramirez et al., (2009), reported Indian ancestry in Ugandan pigs (Noce et al., 2015). Recently the SNP-based breed composition and admixture analysis of African pigs in Kenya (Mujibi et al., 2018) and South Africa (Hlongwane et al., 2020b) also point to the European origin of African pigs.

Unlike their exotic counterparts, African pigs are poorly characterized (Amills et al., 2013). The description of the African pig is an animal with a small body, black or pied coat, long snout and popped swept back ears (Blench, 2000). Genomics could be applied to decipher the origins of pigs in Africa. Further, this would also elucidate their ancestry (admixture levels) and allow genomic evaluation of important production and functional traits across various production environments (Rothschild and Plastow, 2014; Marshall et al., 2019a). However, the utilization of genomic tools in SSA, as in other developing regions, is still limited. Use of genomic selection, and potentially other genomic tools, needs to be embedded in breeding programs / genetic improvement strategies. Further, building the capacity of a range of actors is important (Rothschild and Plastow, 2014; Ducrocq et al., 2018). African swine fever (ASF) is one of the key deterrents of pig production in SSA (Hal, 2012; Dione et al., 2016). While efforts are being made towards ASF vaccine development (Revilla et al., 2018), genomic tools might fast track the process. Use of genomic approaches in research to determine genomic variants underpinning tolerance to ASF is underway (Shirley et al., 2011; Rothschild and Plastow, 2014).

1.4. Smallholder pig production in Uganda

Agriculture is the backbone of Uganda's economy and contributes 24.5% to the national Gross Domestic Product. Approximately 77% of the total labor force is employed in agriculture and comprises mostly women and youth in rural areas (UBOS/MAAIF, 2009). Livestock contributes 17% to the agricultural GDP of Uganda (MAAIF, 2010) and at least one type of livestock is owned by 60% of households in Uganda (Enahoro et al., 2018). Pig production is an important socioeconomic activity in Uganda. Uganda ranks third among the top producing African countries (FAOSTAT, 2021). The national pig herd of Uganda has experienced exponential growth from 0.016 million animals in 1961 (FAOSTAT, 2021) to 4.2 million in 2019 (UBOS, 2020). Its importance is further underscored by more than one million households (17.8% of all households) that directly benefit from pig production (UBOS/MAAIF, 2009).

Smallholders represent over 70% of the pig producers in the country. They keep pigs for savings and insurance and income (Babigumira et al., 2019). The income is spent on household need ranging from school fees, medical bills, food and clothing (Ouma et al., 2015; Carter et al., 2017). The pigs are typically managed in a low-input system in which they may be let to free-range, tethered or housed and when provided, housing is usually inadequate (Dione et al., 2014). Pigs are fed on crop residues by most farmers (Pezo et al., 2014; Carter et al., 2015; Okello et al., 2021). Small herds of one to three sows are kept with a production focus on weaners, growers or both (Tatwangire, 2014; Ouma et al., 2017). The animals kept comprise non-descript local, crossbred (cross of local and exotic) or exotic pigs (Babigumira et al., 2019). Though marginalized, women and youth provide most of the labor in the pig enterprise (Pezo et al., 2014; Ouma et al., 2015). Pig farming is attractable to women and youth because of the small size of the animals and the low investment needed for a startup (ILRI (International Livestock Research Institute), 2011). Domestic demand for pork is high and the annual per capita consumption of pork is 3.4 kg (Tatwangire, 2014; FAOSTAT, 2018). However, most of the pig production is informal and farmers have limited or no access to markets. Slaughter animals are sold from the farmgate to traders who are often vertically integrated in the smallholder pig value chain. The other roles taken on by traders include bulking, transportation, slaughter of pigs and sale of pork (Ouma et al., 2017). Pigs may be slaughtered from the backyard or in designated slaughter places (slaughter slabs) under veterinary inspection. High urban consumption continues to grow amidst minimal to little consumer awareness and demand for quality and biosafety of pork (Ouma et al., 2014; Ouma et al., 2015). Extension services are usually provided by both private and government veterinarians, but some farmers also treat their animals (Dione et al., 2014). Pig farming is increasingly drawing policy attention as an important pro-poor socioeconomic activity (MAAIF, 2016).

Despite the remarkable growth of Uganda's pig sector, pig farmers continue to face several technical and management constraints related to pig feeding, health and breeding (Tatwangire, 2013). High pig feed costs force the farmers to rely on home mixed rations that are largely based on crop residues such as sweet potato vines and roots. However, most farmers are not knowledgeable about the daily nutritional requirements of their pigs and will often feed unbalanced rations to the pigs (Carter et al., 2015; Carter et al., 2017). Most of the feeds are high in fiber and energy but low in protein. Further, pig health remains an important production constraint and most farmers have inappropriate animal health practices coupled with limited access to veterinary extension services (Muhanguzi et al., 2012). Most farmers are discouraged from using private veterinarians by the high service costs (Okello et al., 2020). While a plethora of diseases and parasites affect the pigs, African swine fever (ASF) is of socioeconomic importance because of high mortalities (70-100% of the pigs) (Dione et al., 2017). Further, quarantines are usually imposed during ASF outbreaks and this impacts on household incomes from pig sales (Chenais et al., 2017). The control of ASF is complicated by lack of biosecurity measures on most smallholder farms and panic sales during outbreaks (Dione et al., 2017). Pig genetics is the other important constraint identified by women and men smallholder farmers in

Uganda (Baker et al., 2015; Ouma et al., 2015). A list of pig breeds allowed to be reared in the country is available in the Animal breeding act, 2001 (Nakimbugwe et al., 2002). This list includes exotic breeds like Large White and Landrace. However, pig breeding in Uganda is unstructured (Muhanguzi et al., 2012; Dione et al., 2014; Greve, 2015). Most smallholder farmers purchase replacement stock from each other through village-level linkages (Ouma et al., 2015; Lichoti et al., 2016). Further, record keeping and animal identification are hardly practiced on smallholder farms (Muhanguzi et al., 2012). Given the high cost of maintaining breeding animals, sows are kept by few farmers and most rely on village boar service. Payment for village boar service is usually by cash or a piglet when the sow farrows (Dione et al., 2014; Ouma et al., 2015). The pig breeding practices of smallholder farmers have not been fully documented nor is it known how breeding animals are selected or which breed(s) is/are kept.

1.5. Background, aim and objectives

Africa holds 4.7% of the world's total pig population (FAOSTAT, 2019b) with most of the animals managed in low-input systems (FAO, 2021). The pigs in Africa are poorly characterized (Amills et al., 2013) especially in light of the events leading to *Sus scrofa* domestication (Rothschild et al., 2011). Nevertheless, it is common to categorize the pigs into local, crossbred or exotics breeds (Blench, 2000). Further, studies that have attempted to characterize local African pigs have often reported inferior performance for growth and reproduction traits, an occurrence that some have attributed to inbreeding depression (Ajala et al., 2007; Akanno et al., 2013; Tatwangire, 2014; Greve, 2015; Abdul-Rahman et al., 2016; Abah et al., 2019). On the other hand, the tradeoff is that the local pigs are adapted to the challenges typical of traditional pig production (Mbuza, 1995; Mutua et al., 2010; Mutua et al., 2011a; Mbuthia et al., 2015a). The findings by these authors precipitate several questions. First, if pigs in Africa comprise local breeds yet domestication did not happen (as is generally accepted), where did the local pigs come from and what is their ancestry? Second, is the poor performance of local pigs because of inferior genotypes, inbreeding, poor husbandry practices or all three? Answers to the questions would provide valuable information for the implementation of breeding and conservation programs for pigs in Africa.

Uganda holds the third position among the top pork producing countries in Africa and the largest pig herd in East Africa (FAOSTAT, 2019a). Further, over a million smallholder households directly benefit from pig production (UBOS/MAAIF, 2009). Since 2012, the international livestock Research Institute (ILRI), has implemented projects aimed at improving the livelihoods of smallholder pig farmers in Uganda. These projects have identified key intervention areas, of which some have been addressed by follow-on projects that have provided technical solutions to challenges in the domains of pig health, nutrition, and marketing (Ouma et al., 2015; Ouma, 2017; Ouma et al., 2018). While women and men smallholder farmers in Uganda have identified genetics as a key constraint to pig production (Baker et al., 2015; Ouma et al., 2015), few studies have been done in terms of molecular characterization and performance evaluation of their pig herds (Greve, 2015; Noce et al., 2015). To address this concern and as sequel to previous ILRI projects that focused on health and nutrition mostly, in 2017, ILRI and the University of Natural Resources and Life Sciences, Vienna (BOKU) led a project titled "Sustainable intensification of the pig value chain in Uganda – for improved rural livelihoods and enhanced food security" (Uganda Pig Genetics Project-UPG). The project focused on identifying the most appropriate genetics for smallholder pig production.

This PhD study was undertaken in the framework of the Uganda Pig Genetics project with the aim of harnessing genomics to support on-farm decisions in smallholder pig enterprises in Uganda. The specific objectives of this study are as below, as well as an indication of how the related research findings can benefit the Uganda pig sector:

a) Characterization of pig breeding practices of smallholder farmers in Uganda. The breeding practices of smallholder pig farmers in Uganda are poorly documented. Understanding them would inform key intervention areas.

b) Gender evaluation of perceptions on pig keeping objectives, trait, and breed preferences of these smallholder farmers. Incorporating gender information in the design of a genetic improvement strategy breeding program for smallholder farmers would cater for gender differences, if any.

c) Genomic characterization of pigs reared on these smallholder farms. Given the limited knowledge on the genetic constitution of pigs in Uganda, this study aimed at understanding the breed composition of animals kept by smallholder farmers, as well as the origin of the local pig breed.

d) Genomic evaluation of grower and sow performance among these pig herds. Breed composition information can be incorporated in performance evaluation making it possible to determine if breed proportions are affecting key production traits.

1.6. The study area- Hoima and Kamuli districts, Uganda

This study was undertaken in the districts of Hoima and Kamuli in Uganda (Figure 1). Hoima district is located at 1° 25′ 0″ N and 31° 5′ 0″ E in Western Uganda and shares district boarders with Kibaale (South), Masindi (North East), Buliisa (North), Kyankwanzi (East), Ntoroko (South West) and Lake Albert/ DR Congo (West). About 90% of the human population are rural dwellers. The literacy rate stands at 74% with an adult female literacy rate of 68.4% (UBOS, 2018). Subsistence agriculture is the main livelihood, provides employment for over 85% of the labor. Average household land holding is two hectares in a crop-livestock system. The total population of Hoima is 572,896.

Kamuli District is located at 00°55′N and 33°06′E in Eastern Uganda and shares district boarders with Buyende (North), Luuka (East), Jinja (South), and Kayunga (West). Children (under 18) account for 59% of the population. Literacy rate stands at 61.8% with females at 54.6% and males at 69.7%. Average household size of 5.1 (UBOS, 2018). Subsistence agriculture is the main livelihood source for 80.5% of the labor while only 6.5% derive livelihoods from employment income. Average household land holding is one hectare in a crop-livestock system characterized by low crop yield (30%).

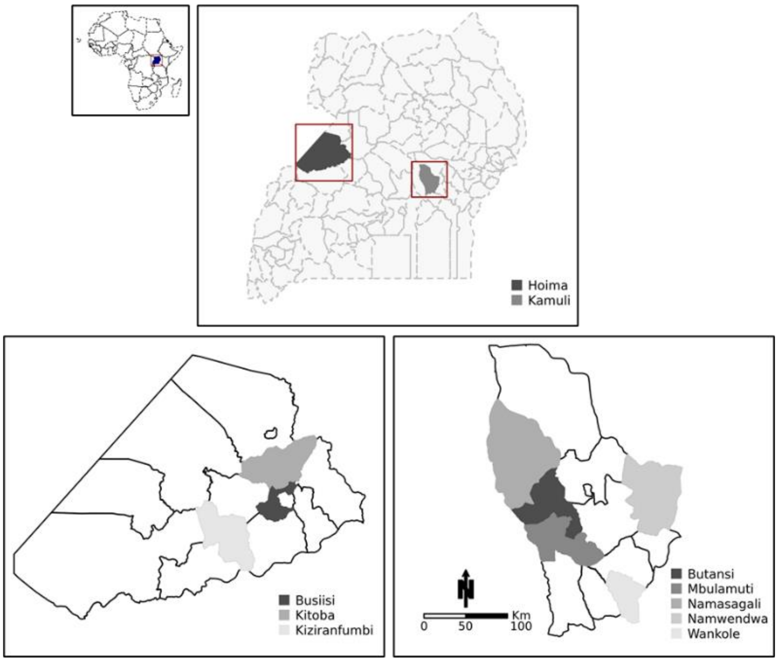

Figure 1. Map of Africa (top left) showing location of Uganda. Map of Uganda (top center) showing location of the districts of Hoima (bottom left map) and Kamuli (bottom right map). The shaded regions in the map of each district are the sub-counties where the study was undertaken.

1.7. Outline of the thesis

This cumulative doctoral thesis consists of seven chapters.

Chapter 1 is a general introduction and background of the doctoral study. The literature reviewed concerns the importance of livestock to food security, the origin of the domestic pig, the application of genomics to livestock production and an overview of smallholder pig production in Uganda.

Chapter 2 contains the results of a survey of pig production that was conducted in the study area and therefore provides context to the chapters that follow.

Chapter 3 is about pig breeding practices of smallholder farmers in Uganda.

Chapter 4 is a gender evaluation of farmer's perceptions of reasons for keeping pigs and trait and breed preferences.

Chapter 5 is about a genomic characterization of smallholder pigs in Uganda using high density marker panel.

Chapter 6 is about a genomic evaluation of sow and grower performance in the smallholder system.

Chapter 7 is about the general discussion of the results of this study and the implications of using genomics as a decision support tool on smallholder pig farms.

Chapter 2 Few signs of transition: results of a survey of smallholder pig practices in rural areas of Hoima and Kamuli districts, Uganda

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(in preparation for submission to ILRI)

2.1. Abstract

Pig farming is an important livelihood source in Uganda. The objective of this study was to identify the demographic characteristics, husbandry, and marketing practices within the smallholder pig value chains in Hoima and Kamuli districts of Uganda. A purposively selected sample of 200 smallholder farmers participated in a multistage cross-sectional survey. Data on household characteristics alongside that on pig feeding, health, breeding, housing, and management practices were collected using a structured questionnaire. Descriptive statistics were generated in R environment. Most household heads were aged between 20 and 60 years (77.3%) and had attained primary or secondary education (79.8%). Monthly household incomes were between ~30 and 120 US$ (converted from Uganda Shillings) for 77% of households, the income was lower for 7.7% and higher for 14.3% of households. Half of the households owned 2.5 or less acres of land, 15.5% owned more than 5 acres. One to five local pigs were owned by 58.5% households. Worms affected local and crossbred sows and piglets on many farms (45 to 67% households). African swine fever was reported by around 25 to 50% of the households. Animal health care services were provided by private veterinarians for about 75% households and farmers treated their pigs in around 30% households. Generally, the households had highly diverse feed baskets (home mixed rations) based on maize or rice bran and a range of crop residues. The brans were purchased while the crop residues were obtained on-farm. The sources of breeding animals included those born on the farm (64.0 to 85.0% households), purchased from other smallholder farmers (32.0 to 65.0%) and village boar service for a fee (45.4% households). None of the households used artificial insemination. Genetic improvement strategies included selection of breeding animals from those born on the farm or purchased (including boar service). Constraints to genetic improvement were around availability and affordability of good breeding animals. Sow reproductive problems included delayed return to estrus in sows, repeat breeding, small and few litters over the sow's lifetime. Most farmers performed heat detection based on changes in the vulva such as reddening (92.9%) while less than 3.0% used the standing heat method. Record keeping and animal identification were practiced by nine to 12.0% of households. Pig sties were constructed by only 30.2% households using wood, earth, or cement. Most farmers (40.0 to 90.0% households) were knowledgeable of sales outlets for fattening, breeding and boar service within only their district. The main pig products sold by around 50.0 to 78.0% households were fattener weaners, breeding animals and finishers for slaughter. Most sales of pig products (60.0 to 100.0%

households) were done from the house directly to individual customers and traders. Smallholder farmers were the main customers of boar service, fattening and breeding animals as were traders for finishers for slaughter. Future studies around key intervention areas will benefit the smallholder farmers as they transition from subsistence to commercial pig production.

2.2. Introduction

Uganda is a low-income country and 21.4% of the population still lives below the poverty line (UBOS, 2018). Agriculture is the backbone of the economy and contributes 24.6% to the national Gross Domestic Product (GDP) (UBOS, 2018; World Bank, 2019). Attempts to alleviate poverty have focused on agriculture-based interventions (Nahdy, 2004). Livestock makes an important contribution to the national economy by contributing 17% to the agricultural GDP (UBOS, 2018). Pig production is an important livelihood source for smallholder farmers in Uganda (Mangheni, 2014; Ouma et al., 2015; Babigumira et al., 2019). Further, the government of Uganda prioritized pork as one of the livestock meat commodities in the Agriculture Sector Strategic Plan 2015/16-2019/20. The plan was to enhance production and productivity along the pork value chain with a production target of over 130,000 metric tons by 2019 (MAAIF, 2016). The pig sector of Uganda is characterized by a per capita consumption of 3.4 Kg per annum (FAOSTAT, 2018). The national herd has increased to 4.2 million pigs and over one million households directly benefit from pig production (UBOS/MAAIF, 2009; UBOS, 2019). Uganda ranks third among pork producing countries in Africa (FAOSTAT, 2021). Under the third National Development Plan (NDPIII 2020/21 – 2024/25), GoU plans to reduce dependence on subsistence agriculture as a primary livelihood source from 68.9 to 55.0% (NPA, 2020). Transitioning from subsistence to commercial agriculture is possible through various avenues including adoption of appropriate husbandry practices and technologies. This baseline study was conducted as part of a broader project “sustainable intensification of the pig value chain in Uganda – for improved rural livelihoods and enhanced food security” with an emphasis on appropriate genetics. This work presents results of a baseline study conducted as part of a broader project “sustainable intensification of the pig value chain in Uganda – for improved rural livelihoods and enhanced food security” with an emphasis on appropriate pig genetics. Therefore, this study investigated smallholder farmers’ husbandry practices including pig breeding and marketing for a holistic understanding of the status of pig production in the study area.

2.3. Materials and methods

2.3.1. Ethics statement

The study was approved by the by the Vector Control Division Research and Ethics Committee of Ministry of Health, Uganda (VCD-REC (MoH)) and Uganda National Council of Science and Technology (UNCST). It was also approved by International Livestock Research Institute's (ILRI's) Institutional Research Ethics Committee (IREC), registered by National Commission for Science Technology and Innovation (NACOSTI), Kenya, as well as ILRI's Institute Animal Care and Use Committee (IACUC).

2.3.2. Study area

The study was conducted in the districts of Hoima in the west and Kamuli in the east of Uganda, East Africa. (Figure 1). The districts were selected because of importance of pig production as a livelihood source for smallholder households and the diversity in breed types and management systems practiced. Subsistence agriculture is the main economic activity in the study area, and it engages over 80% of the population (UBOS, 2018).

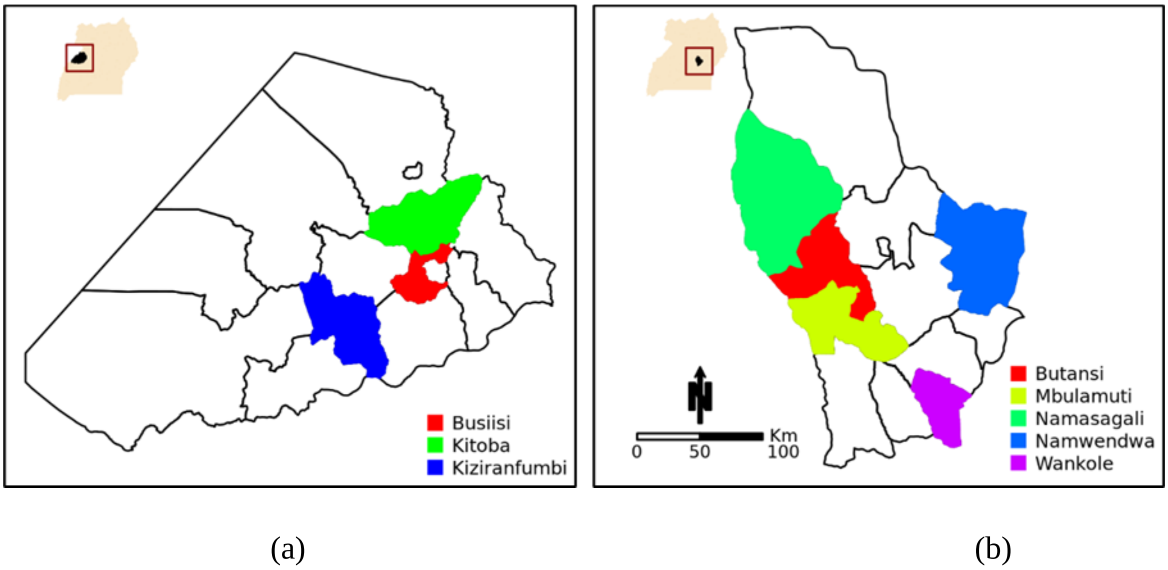

Figure 2. Maps of Hoima (a) and Kamuli (b) districts showing study sites and inset is a map of Uganda showing location of each district.

2.3.3. Data collection, management, and analysis

Data was collected between April and August 2018 in a household-level baseline survey using structured questionnaires. The survey involved 200 smallholder households, 100 each from Hoima and Kamuli and was done in three stages. IN the first stage data on household characteristics were collected. Here survey respondents included both the household head as well as adult-females in male-headed households. In the second stage, data on pig production practices was collected with the main person who took care of the pig (hereafter referred to as the pig keeper) as the respondent. The data on production practices covered pig breeding, feeding, health and housing management. The data were entered into the Census and Survey Processing System (CSPro) (U.S. Census Bureau, 2012) and later reposited on the ILRI data portal (Rutto et al., 2019). For purposes of this paper, we analyzed data on household characteristics that included size, age, and level of education of household head, ethnicity and religion, land and livestock ownership and income. We also analyzed data on pig production practices that included production system, breed and number of pigs kept, health, breeding, feeding, housing, and marketing. Descriptive statistics of the variables were generated in R environment (R Core Team, 2021) and are presented as percentages in either tables or text

2.4. Results and discussion

2.4.1. Household characteristics

Table 1 contains the descriptive statistics for household size, household head's age and level of education, religion, ethnicity, income, and land ownership. The number of respondents varied with the question. Around 75% of the household heads were aged between 20 and 60 years of age and had attained wither primary or secondary education. Thirty-three, 41.5, 6.5, 74.0 and 99.5% of the 200 households owned 274, 293, 45, 2037 and 825 cattle, goats, sheep, chicken, and pigs respectively. Most households (96.5%) practiced Christianity and the common ethnic groups were Banyoro and Basoga. Total monthly household incomes were between 30 and 120 US$ (converted from Uganda Shillings (UGX)) for 77% of households (UGX; 1USD≈3650UGX, 2018). The total size of land owned by half of the households measured less than 2.5 acres (50% households).

Table 1. Household demographic characteristics

Characteristic	Households (%)
Household members (persons)	N=200
1 to 5	48.0
Greater than 5 to 10	42.0
Greater than 10	10.0
Age of household age (years)	N=198
20 to 40	31.3
Greater than 40 to 60	46.0

Greater than 60	22.7
Household head's education level	N=198
Never attended school	9.1
Pre-school education	0.5
Primary education	46.5
Secondary education	33.3
Vocational training	0.5
High school	1.0
Tertiary training	5.6
University degree (undergraduate)	3.5
Household's religion	N=200
Christian	96.5
Faith of unity	1.5
No religion	2.0
Household's ethnicity	N=200
Banyoro	48.0
Basoga	46.0
Others e.g., Baganda, Banyankole	6.0
Household's income (UGX/month)	N=161
Less than 100,000	8.7
100,000 to 200,000	21.7
Greater than 200,000 to 400,000	36.6
Greater than 400,000 to 600,000	18.6
Greater than 600,000	14.3
Size of total land owned by household (acres)	N=200
Less than 2.5	50.0
2.5 to 5	34.5
Greater than 5	15.5

The average household size of Uganda is 5 and the literacy rate is 76% (UBOS, 2021). Most of the farmers (79.8%) had attained either primary or secondary education. However, this may be similar elsewhere in Uganda (Dione et al., 2021) or different (Alarakol et al., 2021) depending on location of the farmers. A previous study found a positive correlation between level of education of the farmers with the herd size of their pigs (Twine and Njehu, 2020) and a significant effect of education on expenditure on health care of pigs (Okello et al., 2020).

2.4.2. Description of the pig enterprise

Majority of the households (96.9%; n=199) practiced a combination of farrow-to-wean and farrow-to-finish systems. Therefore, the description of the pig enterprise is based on the herds owned by these households. The constitution of the pig herds varied with the household, but they generally comprised boars, sows, and piglets (Table 2). The households owned between one and 25 pigs with a median of 3 pigs per household.

Table 2. Pig enterprise characteristics

Number of pig units managed	N=199
1	97.0
2	2.5
3	0.5
Category and breed of pig kept	N=192
Sow	
None	1.0
Local	61.9
Crossbred	29.7
Exotic	3.1
More than one of the three breeds	4.3
Piglet	
None	2.0
Local	55.8
Crossbred	28.6
Exotic	3.6
More than one of the three breeds	10.0
Boar part of the pig unit	
None	17.7
Local	50.5
Crossbred	24.5
Exotic	3.1
More than one the three breeds	4.2
Boar not part of the pig unit	
None	15.6
Local	54.7
Crossbred	25.5
Exotic	0.5
More than one the three breeds	3.7

The range of herd sizes kept by most smallholder farmers in our study is close to what has been reported in Tanzania (Kimbi et al., 2015) and the breed status is reported by farmers. The households may keep one to three pigs as either sows, piglets, or boars (Ouma et al., 2015; Dione et al., 2017). The trend in percentage of households keeping the different categories of local, crossbred and exotic pigs in our study had been reported elsewhere in Uganda (Ikwap et al., 2014). However, this may differ in other areas of Uganda with more crossbred and exotic than local pigs are kept (Muhanguzi et al., 2012). Local pigs are preferred because they are adapted to the low input system practiced by the farmers. Smallholder farmers make minimal financial investment in the pig enterprise (Ouma et al., 2014).

2.4.3. Pig production practices

2.4.3.1. Health

2.4.3.1.1. Diseases and parasites of sows and piglets

The diseases and parasites that affected local sows that at least 20% of the households (n=136) reported were worms (66.2%), fever (47.1%), mange (43.4%), African swine fever (43.4%), skin problems e.g., rashes (28.7%) and diarrhea (21.3%). Crossbred sows were affected by worms (60.3%; n=78 households), mange (46.2%), fever (38.5%), African swine fever (33.3%), diarrhea (25.6%) and skin problems (25.6%). A small number of households (n=17) kept exotic sows that were mostly affected by mange (35.5%).

The diseases and parasites that affected local piglets that at least 20% of the households (n=134) reported were worms (50.7%), fever (41.8%), diarrhea (35.1%), mange (29.1%), African swine fever (27.6%) and skin problems e.g., rashes (23.1%). Crossbred piglets were affected by worms (45.5%; n=77 households), fever (36.4%), diarrhea (25.9%) and African swine fever (24.7%). A small number of households (n=18) kept exotic piglets that were mostly affected by fever (38.8%).

The range of diseases reported here concurs with what has been reported in Kenya (Wabacha et al., 2004b; Kagira et al., 2010) and Uganda (Dione et al., 2014). Worms affected both sows and piglets irrespective of breed. Deworming, for example using Ivermectin or Levamisole, is one of the common husbandry practices of most smallholder farmers (Kagira et al., 2010; Dione et al., 2014). This may be done by the farmers themselves or by a para-veterinarian (Dione et al., 2014). The farmers use acaricide to kill external parasites (Kagira et al., 2010; Dione et al., 2014). African swine fever is another important disease with mortality rate higher than 70% (Dione et al., 2014).

2.4.3.2. Animal health care and product service providers

Most of the farmers relied on private veterinarians (75.4%; n=199 households), themselves (30.7%) and government veterinarians (16%) for animal health care services. For animal health products, the farmers mostly (77.9%) used the agrovet shop (a shop that sales agricultural and veterinary farm inputs) located outside their village and the agrovet shop within their village (25.1%), veterinary or community animal health care worker (23.1%) and the market (17.1%). Most smallholder farmers rely on private veterinarians for animal health care (Okello et al., 2020) because public extension services are usually not easily available (Muhanguzi et al., 2012). In Uganda, wholesale drug shops are the main source in the district, and these distribute to veterinary pharmacies which in turn distribute to the village agrovet shops (Dione et al., 2014). Although these agrovet shops provide reasonably good services, they are also located far from the farms and are too expensive for the farmers (Tatwangire, 2014)

2.4.3.3. Feeding

2.4.3.3.1. Dry and wet season feeding

During the dry season, the households fed the pigs on maize bran (90.6%, n=199), *Amaranthus spp* (69.3%), sweet potato roots (68.3%), kitchen leftovers (raw swill; 66.8%), rice bran (50.8%), raw cassava leaves (49.3%), sweet potato vines (48.7%), banana peels (31.5%), yam leaves (29.1%) and weeds (18.1%) among others not mentioned for brevity. During the wet season, the households fed the pigs on maize bran (88.9%, n=199), sweet potato vines (82.4%), raw cassava leaves (72.9%), sweet potato roots (70.9%), kitchen leftovers (boiled swill; 70.9%), kitchen leftovers (raw swill; 67.3%), *Amaranthus spp* (59.3%), wandering Jew (53.2%), rice bran (49.2%), yam leaves (42.7%), spurge (42.2%) and banana peels (31.2%) among others not mentioned for brevity.

2.4.3.3.2. Sources of feed

Most farmers obtained maize bran (85.5%; n=179) and rice bran (80.2%; n=101) from the feed supplier/ shop. They obtained sweet potato vines (96.3%; n=162), sweet potato roots (97.9%; n=140), raw cassava leaves (97.9%; n=143), yam leaves (98.8%; n=85), *Amaranthus spp* (99.1%; n=117), wandering Jew (98.1%; n=104), kitchen leftovers (boiled swill; 98.6%; n=141), kitchen leftovers (raw swill; 97.7%; n=133), spurge (100%; n=82) and banana peels (100%; n=61) from their own farm.

The household-level pig feed diversity reported in our study is comparable to that reported elsewhere in Uganda (Dione et al., 2015; Okello et al., 2021) and falls within the spectrum of locally available feed stuffs (Carter et al., 2015). Maize bran is considered a nutritious pig feed by most farmers especially improving growth rates (Lumu et al., 2013).

However, because of the high cost of commercial feed (maize or rice bran), the base feed is usually a crop residue largely sweet potato vines (Peters, 2008; Dione et al., 2015). Further, to minimize feed costs, the farmers mix different feeds and feed them to the pigs as home mixed rations (Katongole et al., 2012; Lumu et al., 2013; Dione et al., 2015). Nevertheless, some farmers are unaware of methods of processing crop residues such as sweet potato vines into silage as feed pig (Peters, 2008; Dione et al., 2015). Those that have used sweet potato vine silage have reported increased herd sizes of the pigs that have translated into increased incomes (Lukuyu et al., 2017). Given the high cost of commercial feed, small herd sizes and that most farmers rely on home mixed rations using locally available feeds, technical effort should continue towards development of low-cost formulations for these low input systems.

2.4.3.4. Breeding

2.4.3.4.1. Source of breeding animals

The respondents were asked about where they had sourced the breeding pigs in their herds. Most households had sourced breeding animals from within their herds and from another smallholder farmer. Boar services had been sourced from owners of a village boar for a fee (Table 3).

Table 3. Sources of breeding animals used by the households

Source of breeding animal	Source used in last two years (yes; %)	
	Sow	Boar
Own sow or boar - born on farm	84.3	64.5
Purchase of:		
breeding female or boar from a large scale / commercial pig farm	8.6	9.1
breeding female or boar from a livestock market in the village.	2.0	1.0
breeding female or boar from a livestock market outside the village.	2.0	2.0
breeding female or boar from another smallholder / friend / neighbor	64.6	32.8
Gifted from friends / family	3.6	2.5
Provided though an NGO or other program	2.5	3.0
Use of a boar sire service (e.g., village boar) for a fee	0.0	45.4
Free use of neighbor’s or friend’s boar for free	0.0	3.0
Artificial Insemination (AI)	0.0	0.0

Availability and access to breeding stock whose performance matches farmers’ expectations is the hallmark of a viable enterprise. Pigs born on-farm is one of the immediate sources of breeding animals available to smallholder farmers as found in this study. The sow is important because her weaned piglets are a source of income to the household. The boar is important because of the boar:sow mating ratio (Mbuthia et al., 2015a) and his genotype. Boar genotype may influence the performance of his offspring and that of the sow both during gestation and postpartum (litter size or rate of return to service) (Scofield and Penny, 1969). However, even when boars were born on most farms, they have high maintenance costs and are therefore, kept by very few smallholder farmers (Dione et al., 2014). These boars may be castrated (Dione et al., 2014), culled early and an off-farm boar used to control breeding (Kadirvel et al., 2013). These scenarios suggest that smallholder pig farmers mostly rely on off-farm boars to service their sow as did the 45.4% of households in this study. The pivotal role of village boar service in smallholder pig production is further underscored by studies in Vietnam and Kenya (Wabacha et al., 2004a; Lemke et al., 2006). One challenge with on-farm selection of animals is the narrow choice base because of the small herd sizes (one to three pigs) of smallholder (Wabacha et al., 2004a; UBOS/MAAIF, 2009; Ouma et al., 2015). Another important source for breeding animals used by the farmers was local or crossbred pigs purchased from other smallholder farmers or neighbors. Neighbors are an important source of breeding stock for the smallholder farmers in Uganda and Namibia (Petrus et al., 2011; Lichoti et al., 2016). Artificial insemination was not used by the farmers possibly because it is not common and most of them rely on a communal boar for mating (Dione et al., 2014; Barnes et al., 2020).

2.4.3.4.2. Genetic improvement of pig herd and related constraints

Around a quarter of the farmers (25.6%; n=199) had attempted to improve their herds genetically. This they had done by selecting the best sows from their herds (64.7%), purchasing genetically better sows from outside their own herds (33.3%), selecting best boar from own herd (21.6%), using a different village boar owner with better boars (15.7%) and changing breed of boar (17.6%) and sow (15.7%). The best animals may be selected based on trait preferences of the smallholder farmers in the study area (Babigumira et al., 2019). However, smallholder farmers are unable to correctly assign their pigs to known breeds such as Large White or Landrace (Ouma et al., 2015). This means that the genetic improvement strategy of changing the breed of boar or sow, especially when breed composition is unknown as is the case in Uganda, may not be as efficient as expected. In such cases, genomic analysis may be used to ascertain breed of origin.

The constraints to genetic improvement of pig herds reported by the farmers (n=116) were: lack of information on animals that could be purchased or used as breeding animals (42.2%), the available good breeding sows were too expensive (39.7%), lack of good breeding boars to use (37.9%), lack of good breeding sows to purchase (25.9%), lack of knowledge on how to genetically improve the pigs (12.9%), the good breeding boars available were too expensive (12.0%), insufficient breed choice (11.2%) and Artificial Insemination was too expensive (6.0%). The constraints identified by the farmers related to availability and affordability of breeding animals as has been reported in Kenya (Mbuthia et al., 2015b) and previously in Uganda (Baker et al., 2015). Ideally, the knowledge gaps identified could be filled through training on aspects related to breed identification and methods of genetic improvement of livestock by extension services. However, the smallholder farmers have limited access to extension services (Chema and Gathuma, 2004; Muhanguzi et al., 2012).

2.4.3.4.3. Sow reproductive problems and heat detection

Sow reproductive problems were reported by 39.6% (n=199 households) and included delayed return to estrus post-weaning (60.8%), late age at first litter (44.3%), small litter size (30.8%), repeat breeding (26.6%) and few litters over the sow's lifetime (26.6%). Other problems reported by 10% and less households were abortion, mummification and agalactia. Delayed return to heat post-weaning may be due to effects of poor nutrition on cyclicity or expression of heat signs in the sow. Further, village boars are not always available when needed by farmers. This could lead to reproductive problems and sow disposal (Wabacha et al., 2004a). Village boars are managed under low input systems and their breeding soundness is questionable due to poor nutrition and health. Poor health will lower the reproductive performance of boars (Lanada et al., 2005) and this will manifest as sow reproductive problems. The movement and natural mating of sows have implications for farm biosecurity. Interestingly, sow reproductive diseases, abortions and still births were reported by none to a few farms. African swine fever (ASF) is an important constraint to pig production in Uganda (Muhanguzi et al., 2012; Dione et al., 2014). The high mortality rates and control measures related to ASF outbreaks have implications for availability of village boar service, sow culling decisions and scale of production. Sow's uterine capacity is related to litter size (Ford et al., 2002) and heritability of litter size is between 0 and 0.76 (Rothschild and Bidanel, 1998). Given that heterosis improves litter size (Aherne, 2002), breeding sows to crossbred or purebred boars especially by AI would overcome this problem.

The respondents (n=199) were asked to mention methods of heat detection in the sow used over the last five years. Most farmers looked for changes in the vulva such as reddening (92.9%), restlessness of the sow (58.3%), special sounds made by the sow (45.2%), sow shows increased interest in the boar (21.6%), sow mounts other sows (18.1%), sow stands with arched back (6.5%) and standing heat (2.5%). Only 1.0% of the farmers did not practice heat detection because the sow had access to the boar at any time. Poor heat detection leads to reproductive failure manifested as delayed return to estrus, late age at farrowing and repeat breeding in the sow. These problems in turn lead to low numbers of litters farrowed per sow per year. Although considerably fewer farmers performed heat detection by the standing heat method than they did by vulva signs, the former is equally effective (Am-in et al., 2010). Further, none of the farmers used a boar to perform heat detection and this underscores the role of the farmers in breeding the sow. The farmers challenged by the sow reproduction problems could be trained in aspects of heat detection with emphasis on the least used methods such as standing heat.

2.4.3.4.4. Record keeping and animal identification

The records were kept by only 11.8% (n=195) farmers. The records kept included those recalled (56.5%), written (26.1%) and both recalled and written (17.4%). Animal identification was practiced by only 9.2% (n=185) farmers. The identification methods used by the farmers included coat color (47.1%) and the dam of the animal (52.9%).

Most smallholder farmers did not keep on-farm records as reported by other authors (Muhanguzi et al., 2012; Barnes et al., 2020). Record keeping and animal identification are important management practices making it possible to evaluate individual performance (Bett et al., 2009) and for traceability (Šenk et al., 2013). Farmers who don’t keep records could do so if they were trained on how and why to do so (Mbuthia et al., 2015b). Animal identification methods such as ear tags or notches (Hernández-Jover et al., 2008) were not used by farmers in our study although these have been used in Kenya (Mbuthia et al., 2015b). Pig identification by their coat color is not sufficient for traceability or breeding (Gosálvez et al., 2007).

2.4.3.5. Housing

Pig housing was constructed by only 30.2% (n=199) of the households. The floors of the pig sties were constructed from earth/ soil (46.7%; n=60), cement (38.3%) or wood (20.0% households). Majority of the households had sties with partly built walls that did not reach the roof (95%) while 5% had full walls. The walls were constructed from wood (71.7%), bricks (21.7%), earth/soil (5.0%) and iron sheets (1.7%). The roof of the pig sties was constructed from iron sheets (66.8%), grass (23.3%), polythene (5.0%) and tree shade (3.3%). Only 3.3% households had sties without a roof. Ventilation of the sties was via partly built walls (91.7% households) and windows (5.0%). Only 1.7 households had sties without ventilation. The pigs were able to exercise within the sties (65.0% households) or within an exercise space joined to the sties (1.7%). Sties owned by 33.3% households had no exercise area for the pigs. Only 10% of the households had sties with a wallow for the pigs.

The percentage of households with sties in our study is close to what has been reported elsewhere in Uganda (Ouma et al., 2014) and Kenya (Kagira et al., 2010; Mutua et al., 2011a) although the percentages may also be as higher in urban areas of Uganda (Dione et al., 2014; Roesel et al., 2017). Most rural smallholder pig farmers (over 60%) tether their animals (Muhanguzi et al., 2012; Ouma et al., 2014; Dione et al., 2017) as they consider it a cheaper option to construction of sties (Lekule and Kyvsgaard, 2003; Dione et al., 2014). Tethering involves tying one end of the rope to part of the animal's body such as the limb and the other to a pole or a tree (Ikwap et al., 2014; Roesel et al., 2017). The building materials used by the smallholder farmers in this study are similar to those used in other parts of Uganda (Muhanguzi et al., 2012; Dione et al., 2014), Kenya (Wabacha et al., 2004a) as compared to bamboo used in Indonesia (Leslie et al., 2015). Notably, the sties were designed with partly built walls as the main means of ventilation. This type of natural ventilation from partly built wooden walls is practiced by farmers in Indonesia (Nugroho et al., 2015). Ventilation of sties is important given the physiology of pigs and heat stress under tropical conditions. Although wallowing is part of a pig's adaptive behavior to heat stress (Bracke, 2011), only a few households provided a wallow for their pigs. A study in Uganda reported that the smallholder pig farmers highly ranked wallowing as a heat management option (4.48 out of 5 on a Likert scale). However, the authors also reported that its use was limited by lack of designs compatible with available sties and farmers' perceptions about the dirt and diseases associated with it (Zaake, 2019).

2.4.3.6. Marketing

2.4.3.6.1. Availability of pigs for purchase and boar service

The respondents were asked if they had knowledge of sources of pigs and boar service for purchase within and without their district of residence. Most respondents (43.4 to 98.0% households) had knowledge of such sources within their districts for local and crossbred piglets, young females for uses as breeders and boar service (Table 4).

Table 4. Sources of pigs and boar service for purchase

Pig type	Households having knowledge of a source (%)		
	Within district		Outside district
	Within village	Outside village	
Piglets for fattening			
Local	98.0	85.9	5.1
Crossbred (local x exotic)	58.3	58.1	5.1
Exotic	11.6	18.7	3.6
Young females for use as breeders			
Local	75.9	69.3	6.1
Crossbred (local x exotic)	43.4	43.9	6.1
Camborough	1.0	2.5	1.0
Large White	4.5	8.1	2.0
Other exotic	1.0	1.0	0.0
Exotic breed type unknown	5.6	9.1	2.0
Boar service			
Local	89.8	79.2	4.6
Crossbred (local x exotic)	54.6	53.6	4.1
Camborough	4.6	5.6	1.5
Large White	2.0	4.1	2.1
Other exotic	2.6	2.6	0.0
Exotic breed type unknown	4.1	4.1	1.0
By artificial insemination	0.0	0.5	0.0

Pigs are sourced and sold through locally based networks within or between villages (Lichoti et al., 2016). Indeed, the farmers were knowledgeable of sources within or outside the village for fatteners, young breeding females or boar service. However, the farmers tend to rely on locally available boar service before looking to sources outside the village especially when the local source is unavailable (Kadirvel et al., 2013) Boar service availability is one of the main challenges faced by smallholder farmers (Wabacha et al., 2004a; Kadirvel et al., 2013).

Although pig Artificial Insemination (AI) is still uncommon in Uganda (Dione et al., 2016) attempts to popularize AI as a low-cost technology through research have attained some progress (Makerere University, 2017; Bamundaga et al., 2018). Performance of AI or boar service has no effect on number of piglets born alive, number of inseminations per conception or litter size (Kang et al., 2013; Niyiragira et al., 2018). However, sow factors such as parity may have an influence on litter size (Niyiragira et al., 2018). Additionally, the experience of the AI technician may influence totals of number of piglets born and the number born alive

(Visalvethaya et al., 2011). The heterotic advantages of crossbred pigs obtained include higher body weight and a higher number of piglets per delivery than non-descript pigs (Kadirvel et al., 2013). Further, sows bred by AI have lower return rates and higher farrowing rates than those mated naturally (Am-in et al., 2010). AI in the study areas can be promoted through use of a specialized agency particularly for benefits such as disease control, enhanced access to quality genetics and aversion of boar maintenance cost (Dione et al., 2014; Ouma, 2017; Niyiragira et al., 2018).

2.4.3.6.2. Pig products sold by households

The different types of pig products sold by households included weaners for fattening (78.6%; n=196 households), finishers for slaughter (52.0%), young females for use as breeders (50.5%), sows for slaughter (31.1%), young males for use as breeders (30.6%), boars for slaughter (6.1%), weaners for slaughter (5.6%), boar sire service (3.1%), sows for breeding (1.5%) and pig meat (0.5%). Most of the fattening, slaughter, and breeding pigs; boar service and pig meat sold were of local and crossbred pigs with the former being the majority (Table 5).

Table 5. Breed of pig products sold by the households

Pig product	Breed of pig (% households)			Total households
	Local	Crossbred	Exotic	
Weaners for fattening	63.0	34.4	2.6	154
Weaners for slaughter	72.7	27.3	0.0	11
Finishers for slaughter	55.9	41.2	2.9	102
Young females for use as breeders	65.7	34.3	0.0	99
Young males for use as breeders	56.7	41.7	1.7	60
Sows for slaughter	61.7	38.3	0.0	60
Boars for slaughter	75.0	25.0	0.0	12
Boar sire service	66.7	33.3	0.0	6
Pig meat	100.0	0.0	0.0	1
Sows for breeding	100.0	0.0	0.0	3

More local and crossbred pig products were sold than were exotic ones implying the lack or limited availability of exotic pigs in the smallholder herds. However, under typical low input systems, local pigs and their crosses are preferred for their ease of management owed to resistance to diseases and ability to feed on locally available feed stuffs such as *Amaranthus spp*, sweet potato vines and cassava and maize bran (Mutua et al., 2011a; Okello et al., 2021).

2.4.3.6.3. Marketing methods used by the households and their customers

Most households (70 to 100% households depending on the pig product) sold fattening and slaughter weaners and young breeding animals; boar service and pig meat from their houses to individual customers. Finishers and boars for slaughter were mostly sold to pig traders (78 to 80% households). Very few households sold pig products to slaughterhouses or from the market (Table 6).

Table 6. Marketing methods used by the households

Pig product	Marketing method used (% households)				Total households
	Sold from house to		Sold directly to a pig slaughterhouse	Sold from market	
	Individual customers	Pig traders			
Weaners for fattening	90.8	8.5	0.7	0.0	153
Weaners for slaughter	70.0	20.0	10.0	0.0	10
Finishers for slaughter	17.0	80.0	2.0	1.0	100
Young females for use as breeders	97.0	3.0	0.0	0.0	99
Young males for use as breeders	100.0	0.0	0.0	0.0	60
Sows for slaughter	18.3	78.3	3.3	0.0	60
Boars for slaughter	8.3	91.7	0.0	0.0	12
Boar sire service	100.0	0.0	0.0	0.0	6
Pig meat	100.0	0.0	0.0	0.0	1
Sows for breeding	33.3	66.7	0.0	0.0	3

Notably, a big number of households in our study sold the pig products to customers directly from the house. Generally, most traders in Uganda purchase slaughter pigs directly from the farmgate (Atherstone et al., 2019). This individualized sale of pig products implies the lack of an organized marketing channel such as a cooperative as in the case of Vietnam (Schöll et al., 2016). Further, similar to the situation in Vietnam, a previous study in Ugandan also found higher farmer participation in farmer groups if they were supported by Non-Government Organizations (NGOs) such as Volunteer Efforts for Development Concerns (VEDCO) and World Vision in Kamuli district (Ouma et al., 2014). Marketing of pig products by individual farmers predisposes them to exploitation from middlemen (Ouma et al., 2017). On the other hand, establishment of a pig cooperatives would improve sales and incomes of the smallholder farmers (Lapar et al., 2006; Tatwangire, 2013; Ouma et al., 2018).

Smallholder farmers were the main customers of weaners for fattening (80.9%; n=152 households), weaners for slaughter (44.6%; n=9), young females for use as breeders (95.9%; n=99), young males for use as breeders (100%; n=60) and boar sire service (83.3%; n=6). Majority of smallholder farmers buy replacement stock from other farmers (Kagira et al., 2010) and represent the largest group of customers.

The main customers of finishers for slaughter were the local village (56.6%) and Kampala city (36.4%; n=99 households) traders. The two were also the main customers (51.7% and 36.7%; n=60) of sows for slaughter. The local village trader was the main customer of boars for slaughter (75.0%; n=12). Contrary to our findings, previous studies have reported local butchers as an important customer for smallholder slaughter pigs (Kagira et al., 2010; Ouma et al., 2014). However, it is possible that the village traders also double as butchers in these areas (Ouma et al., 2017). The traders may operate under a trading group or not (Atherstone et al., 2019). The lack of designated slaughter facilities motivates traders to setup unregulated backyard slaughter premises (Ouma et al., 2017).

The respondents were asked to mention which information was provided by the customers who purchased the pig products. The smallholder farmers provided information on diseases of pigs (33.1% households: n=121), product price (26.5%), preferred characteristics of the product (21.5%) and advisory services on pig feeds (19.0%). Extension services in the tropics are usually inadequate (Chema and Gathuma, 2004; Wabacha et al., 2004b; Muhanguzi et al., 2012) leaving the smallholder farmers to rely on each other for advice (Kagira et al., 2010).

The Kampala city traders provided information on product characteristics (37.5%; n=40 households); product price (35.0%) and diseases associated with the product (27.5%). The local village trader provided information on product characteristics (34.4%; n=64 households), product price (31.2%), diseases associated with product (21.9%), and advisory services on pig feeds (12.5%). Most pig traders can identify sick pigs based on clinical signs (Atherstone et al., 2019). The range of information provided by the different customers points to the constraints faced by smallholder producers namely inadequate information and extension services (Ouma et al., 2017).

2.5. Conclusion

Pig production in the study area is generally typical for smallholders in Uganda, that is, a low input system. However, low-cost input alternatives seem readily available for pig feed and technological support towards formulation of low-cost pig feed would improve productivity. On the other hand, most farmers rely on professional veterinary service underscoring the need for technological and policy intervention to enhance coverage and affordability. While pig breeding is constrained by availability and affordability of ‘good’ animals and services, the current practices precipitate questions about the preparedness of the farmers to uptake high performing stock. Studies to determine the most appropriate breed/ genetics for the smallholder farmers would answer some of these questions. Most smallholder farmers traded pigs among themselves and only accessed pork consumers through traders (middlemen). Strategies to enhance smallholder farmer participation along the value chain, for example, through producer groups/ cooperatives, would increase their market share.

The results of our study seem to resonate with what previous surveys have reported underscoring the slow transition in pig production practices in Uganda. The drivers of growth of the pig sector in Uganda have not been fully documented. It would be interesting to know if technological or other intervention is driving growth along the pig value chain. What seems to be happening is an increase in numbers of pigs (national herd size) and producers (smallholder households) at least from available statistics (UBOS/MAAIF, 2009; UBOS, 2020). Future studies around key intervention areas will benefit the smallholder farmers as they transition from subsistence to commercial pig production.

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Chapter 3 Pig Breeding practices of smallholder farmers in Uganda

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3.1. Abstract

Uganda is among the top five pork producing countries in Africa, with pig production and local pork consumption being on an increase. Smallholder pig farming systems in Uganda are not very well documented. A household level survey of 199 households conducted between July and August 2018 in Kamuli and Hoima districts evaluated the smallholder pig breeding practices. Differences between districts were assessed with a chi-squared test. Farmers mainly relied on animals born on farm, from mating of a sow with an on-farm boar as well as boar service, and animals bought in for use as breeding animals. They were knowledgeable of off-farm sources for fattening and breeding animals. Local and crossbreds of local with 'exotic' types like Large White, Landrace and Camborough pigs were the predominant types of animals accessed by the farmers. The farmers seemed conversant with heat detection methods in the breeding sow. Sow reproductive problems reported by about 40% of the farmers were small litter size and few litters farrowed over the sow's lifetime. While important for farm management and breeding purposes, animal identification and record keeping were generally lacking. Main marketing pathways were sales to other farmers and traders at farm gate. Farmers would benefit from participatory strategies that enhance access to quality genetic material. The local pig is an important resource of the smallholder pig herd and additional studies on important traits (heat tolerance, disease resistance and feed utilization) would add valuable information.

3.2. Introduction

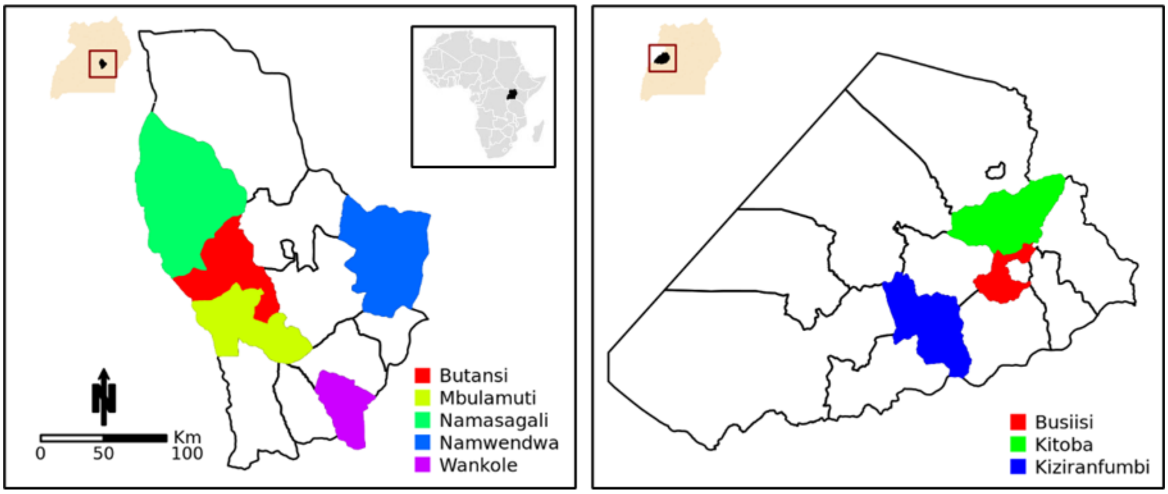
The pig sector of Uganda employs 1.1 million smallholder households with a national herd of 4.1 million pigs (UBOS/MAAIF, 2009; UBOS, 2018). Per capita pork consumption in Uganda is 3.4 kg per annum (FAOSTAT, 2018), a comparably high proportion of the annual per capita total meat consumption of 10 kg. Pork production has become a national priority commodity with a forecast production of 139,000 metric tons by 2020 (MAAIF, 2016). To meet such a target and the growing demand for pork, pig farmers must overcome constraints such as poor breeding stock and management (Muhanguzi et al., 2012; Baker et al., 2015). However, there is limited information on breed types and breeding practices in different production systems (Tatwangire, 2014). Additionally, appropriate breeding strategies are absent (Kidoido and Korir, 2013). The main smallholder management systems in Uganda are free range, tether and housing and the main breeds are local, crossbred and exotic (Muhanguzi et al., 2012; Dione et al., 2014; Ikwap et al., 2014). The local pig is small, black and adapted to challenges in the local environment such as disease and poor quality feed stuffs (Mbuza, 1995). Pig breeding in

Uganda is unstructured. Sows are bred to communal boars at a fee (cash or piglet) or to boars born on the farm. Further, free ranging sows may access roaming boars particularly in the rural areas. Castration of male animals to control breeding is done under the free-range system (Dione et al., 2014; Ouma et al., 2015). In some cases, sows may fail to access boars from constraints related to lack of knowledge/information (Ouma et al., 2015). The aim of this study was to collect information on pig breeding practices of smallholder farmers in Kamuli and Hoima districts. The implications for the design of a breeding program are discussed.

3.3. Material and methods

3.3.1. Study site and households

The selection of Kamuli and Hoima districts (Figure 1) was based on the importance of pig production to the district implied by the pig population reported in national livestock census (UBOS/MAAIF, 2009) and the high number of pig farmers. Pig production is a priority enterprise in the district plans of Hoima. One hundred ninety-nine households purposively selected based on breed type and management combinations in Kamuli (n=100) and Hoima (n=99) participated in the study.



(a) (b)

Figure 3. Maps of Kamuli (a) and Hoima (b) districts showing study sites which include five sub-counties in the former and three in the latter. Inset on the left is a map of Uganda showing location of each district. The inset on the right in (a) is the map of Africa showing location of Uganda.

3.3.2. Baseline survey

The survey conducted between July and August 2018 targeted the main pig keeper in each household, defined as the main person who fed the pigs. The survey collected information on pig husbandry practices (included pig nutrition, health, housing, and breeding), pig marketing, pig farming equipment and phone ownership and usage of phone related services. Only the breeding and marketing sections are relevant to the current study. The 199 respondents that participated in the survey included both women (64.3%) and men (35.7%). Majority of the households (98.9%) kept and managed one pig unit (all animals herded together). The main (96.5%) pig enterprise practiced was a mix of farrow to wean and farrow to finish.

3.3.3. Data collection, management, and analysis

For purposes of this study, the primary data collected through a structured questionnaire during a single visit to each household included breeding information (source of breeding animals, knowledge of sources of different pig types within the village, outside the village and outside the village but within the district, animal recording and identification, sow reproductive problems and heat detection in sows). The marketing information included primary, secondary, and tertiary products, breed of product, buyer of the product and method of sale of the product. We considered marketing information relevant to this study as it sheds light on how farmers may define breeding goals and objectives. The survey data was entered into Census and Survey Processing program (U.S. Census Bureau, 2018). Descriptive analysis generated percentages of respondents in R computing program (R Core Team, 2019). A standard Chi square test at a 0.05 level of significance compared the descriptive information between districts. Note that the differences found between districts need to be assessed with care as households were purposively selected based on breed type and management combinations.

3.4. Results and discussion

The purpose of this study was to evaluate the breeding practices of smallholder pig farmers in Kamuli and Hoima districts of Uganda. District and enumerator could be confounding factors for some of the results.

3.4.1. Sources for breeding animals

The main sources used for breeding sows and boars were those born on the farm, from sows serviced by the own boar or a village boar for a fee (see Table 1). Purchases of young pigs from other smallholder farmers were also very frequent. Livestock markets (within or outside the village), large-scale farms, gifts, non-government organizations were the least likely sources for breeding animals. Use of free boars from neighbors or artificial insemination or gifts from friends or family were much less likely sources for breeding sows and boars. There was a significantly ($P<0.05$) higher percentage of farmers in Hoima than Kamuli that used sows and boars born on the farm. While the difference in purchases of breeding females was not significant between districts, a significantly higher percentage of farmers in Hoima purchased breeding boars from other smallholder farmers. A significantly ($P<0.05$) higher number of farmers in Kamuli than Hoima used boar service.

Table 7. Sources of breeding sows and boars used by the household in the last two years. The number of respondents with valid answers was between 95 and 98 depending on the question

Source of breeding animal	Sow			Boar		
	Kamuli (%)	Hoima (%)	P-value	Kamuli (%)	Hoima (%)	P-value
Own sow or boar - born on farm	76.8	91.9	0.0034	36.7	91.9	<0.0001
Purchase of breeding female or boar from:						
large scale / commercial pig farm	8.1	9.1	0.7998	5.1	13.1	0.0505
livestock market in the village.	3.1	1.0	0.3075	1.0	1.0	0.9942
livestock market outside the village.	3.1	1.0	0.3075	3.1	1.0	0.3075
another smallholder / friend / neighbor	69.7	59.6	0.1371	16.2	49.5	<0.0001
Gifted from friends / family	7.1	0.0	0.0068	5.1	0.0	0.0228
Provided though an NGO or other program	4.1	1.0	0.1705	5.1	1.0	0.0947
Use of a boar sire service (e.g., village boar) for a fee				54.1	36.7	0.0147
Free use of neighbors of friends' boar for free				3.1	3.0	0.9899
Use of artificial insemination				0.0	0.0	

Farmers in Uganda have in the past complained about poor performing pig genotypes (Tatwangire, 2014; Baker et al., 2015; Ouma et al., 2015). This study found that majority of farmers in both districts used sows and boars born on the farm as breeding animals. The advantage of using animals born on the farm is the performance information available to guide selection. However, in the absence of a mating system, as is the case in Uganda, the chances of mating close relatives are high and this could lead to inbreeding depression of litter size and growth rate (Worsley, 2013; Tatwangire, 2014). Smallholder pig farmers keep small herds of one to three animals (Ouma et al., 2015) reflecting the limited mating options available to them, often being communal boars for servicing their sow (Dione et al., 2014). It is often assumed that livestock production in low input systems includes mating of close relatives, potentially due to the long use of male breeding animals, also mating their daughters. Mating of close relatives leads to inbreeding which causes a reduction in performance referred to as Inbreeding depression and mostly affects traits related to fitness (DeRose and Roff, 1999; Charlesworth and Willis, 2009). However, a recent study (Babigumira et al., 2021) found low levels of genomic inbreeding (estimated from runs of homozygosity (F_{ROH}=0.043)) in smallholder pigs in Uganda, being owned by farmers also involved in the current study. The authors claimed that boar keepers usually source boars from outside the local area and the piglets received as payment for boar service are sold. Additionally, farmers with sows may source village boar service from sources outside their village depending on boar availability (Ouma et al., 2014; Lichoti et al., 2016). Another factor that would contribute to low F_{ROH} is that smallholders enter and exit pig keeping all the time (due to their need for money, loss of animals e.g., due to African swine fever (ASF)). This means that they are often sourcing new animals from different places (for example, neighbors, markets, or traders) including distant ones (e.g., following an ASF outbreak in the community). These scenarios suggest a low likelihood of mating related individuals, thus keeping inbreeding levels low. Low levels of inbreeding based on ROH were found for African goats kept in village conditions, also contrary to popular expectation (Nandolo et al., 2017; Nandolo et al., 2019). The percentage of farmers in Kamuli that had used boars born on their farm was nearly a third of those in Hoima. Dione et al., 2014 found that smallholder farmers in Uganda did not keep boars on their farms when maintenance costs were limiting. Sows and boars purchased from other smallholder farmers were another source used by farmers in both districts. Similar finding were reported in Teso and Lango regions of Uganda where female breeding pigs may be acquired on credit and payment made when sows farrow

(Ssewannyana and Mukasa, 2004). A significantly higher percentage of farmers from Hoima (49.5%) had purchased breeding boars from other smallholder farmers. This study found that a higher percentage of farmers in Kamuli had used boar service for a fee as a source of breeding animals. Ouma et al. (2014) found that when farmers had easy access to a communal boar, over 90% serviced their sows when in heat with payments made in cash or a piglet. In-kind payment was very important means for women to obtain pigs in Kenya and Tanzania (Njuki et al., 2013). Payment in kind allows easy access to the breeding boar since sows may fail to access the boar when farmers are required to pay cash (Mangheni, 2014). Boars determine the productivity of the sow (litter size and weaning rate). Therefore, selection and proper use of the village boar for improved productivity should be included in appropriate genetic strategies (Kidoido and Korir, 2013). Less than 10% of the households from both districts had purchased breeding sows or boars from large commercial farms or livestock markets (within or outside the village). A small but significant percentage (7.1%) of farmers in Kamuli had received breeding pigs as a gift. None of the smallholder farmers had used artificial insemination (AI) as a source of breeding males. Pig breeding by AI is carried out by a few breeding centers in Uganda and is generally unavailable along existing technology uptake pathways (Worsley, 2013).

The respondents had knowledge of sources for local breed, crossbred and exotic piglets for fattening within the village (Table 8). Significantly higher percentages of respondents in Hoima had knowledge of such a source outside the village but within the district. Further, significantly higher percentage of farmers in Hoima had knowledge of a source for local breed young females for breeding both within the village and outside the village but within the district. A significantly higher percentage of respondents in Hoima had knowledge of a source of local, crossbred and Camborough boar service outside the village but within the district. Less than 10% of the respondents in both districts had knowledge of sources of different pig types outside the district.

Table 8. Respondents who had knowledge of the sources of different pig types within the village, outside the village but within district and outside the district. (Number of respondents with valid answers was 95-100 per site, depending on question)

Pig Type	Within district						Outside district		
	Within village			Outside village					
	Kamuli (%)	Hoima (%)	P-value	Kamuli (%)	Hoima (%)	P-Value	Kamuli (%)	Hoima (%)	P-value
Piglets for fattening									
Local	97.0	99.0	0.317	79.0	92.9	0.005	3.0	7.1	0.194
Cross-bred (local x exotic)	57.0	59.6	0.710	47.5	68.7	0.002	3.1	7.1	0.200
Exotic	8.0	15.2	0.115	9.1	28.3	0.001	2.0	5.1	0.254
Young females for use as breeders									
Local	66.0	85.9	0.001	52.0	86.9	0.000	3.0	9.1	0.074
Cross-bred (local x exotic)	43.4	43.4	1.000	38.4	49.5	0.115	4.1	8.1	0.241
Exotic	1.0	1.0	1.000	1.0	4.0	0.174	1.0	1.0	0.994
Exotic-Large White	3.0	6.1	0.306	4.0	12.1	0.037	1.0	3.0	0.317
Other exotic	2.0	0.0	0.155	2.0	0.0	0.155	0.0	0.0	NA
Exotic breed type unknown	3.1	8.1	0.125	4.1	14.1	0.014	2.1	2.0	0.984
Boar Service									
Local	85.7	93.9	0.056	64.3	93.9	0.000	1.0	8.1	0.018
Crossbred	49.5	59.6	0.155	40.2	66.7	0.000	2.1	6.1	0.162
Exotic-Camborough	2.1	7.1	0.094	2.1	9.1	0.033	1.0	2.0	0.579
Exotic-Large White boar	2.1	2.0	0.984	2.1	6.1	0.157	2.1	2.0	0.975
Other exotic	4.2	1.0	0.167	4.2	1.0	0.163	0.0	0.0	NA
Exotic breed type unknown	5.2	3.0	0.443	4.2	4.0	0.952	2.1	0.0	0.147
Artificial insemination	0.0	0.0	NA	1.1	0.0	0.306	0.0	0.0	NA

The smallholder farmers had knowledge of sources of local or crossbred piglets for fattening, young breeding females and boar services within the village or outside the village. Comparing the percentages of respondents who had knowledge of sources of local or crossbred boar service and those who had used boar service over the past two years, the latter are much lower. This could arise from several factors such as absence of an on-farm sow (no need for a boar) or presence of the boar on the farm. Over 75% of the farmers in the districts had used an on-farm boar. One of the limitations to using boar services are the associated costs (fees and transportation) (Mangheni, 2014). The other is related to biosecurity, African swine fever in particular, as boars are moved between farms in Uganda and Tanzania (Kimbi et al., 2015; Dione et al., 2017).

In a recent study, Babigumira et al., (2021) investigated levels of ancestries of smallholder pigs in Hoima and Kamuli based on high throughput genomic SNP marker data. The results indicate that hardly any of the pigs genotyped had more than 50% exotic (i.e., Modern European) ancestry. This is in accordance with the results of this study, with few farmers knowing about sources of pure exotic germplasm.

3.4.2. Sow reproductive issues and breeding management

A higher percentage of respondents in Kamuli (73.4%) than Hoima (51.5%) reported no sow reproductive issues in the last five years (Table 3). A significantly higher percentage of respondents in Hoima reported delayed return to heat a few days post-weaning, late age at farrowing, few litters over the sow’s life and repeat breeding. Abortions, mummies and stillborn were hardly reported in both districts.

Table 9. Sow reproductive issues over the last five years

Problem	Respondents who answered the question		
	Kamuli (%; n=94)	Hoima (%; n=99)	p-value
No reproductive problem	73.4	51.5	0.002
Delayed return to heat a few days post weaning	13.8	35.4	0.001
Several abortions	1.1	3.0	0.338
Many mummies / stillborn piglets	0.0	3.0	0.089
Very small litter size	13.8	11.1	0.567
Repeat breeding	5.3	16.2	0.016
Late age at first farrowing	0.0	36.4	<0.001
Not have enough litters over her life	0.0	21.2	<0.001

The problems reported by the farmers in Hoima included failure to come back on heat within few days of weaning, late age at first farrowing, repeat breeding and few litters over her productive life. Farmers from both districts complained about very small litter size. Sow productivity may be influenced by sow nutrition and piglet care (Lanada et al., 2005) but also genetics. Sow nutrition is important for conception and maintenance of pregnancy as well as care of suckling piglets. The effects of poor nutrition could prolong the days open by delaying return to estrus post weaning. The study found that the farmers mainly purchased local and crossbred young breeding females. Local pigs tend to be slow growing and late maturing. This could explain the late age at first farrowing. This study found that local and crossbred boars were the main breeding males used by the farmers. Boar genotype may influence sow reproductive performance (litter size, number born alive and number weaned) as indicated by a study in Zimbabwe (Ncube et al., 2003).

Table 10. Methods of heat detection in the sow used over the last five years

Heat detection method	Kamuli (%; n=94)	Hoima (%; n=99)	p-value
Not required, as sow can mate boar anytime	0.0	2.0	0.1660
Look for swollen / red vulva	93.6	98.0	0.1286
Sow makes special sound	21.3	70.7	<0.0001
Sow stands with arched back	0.0	13.1	0.0003
Sow becomes restless	47.9	71.7	0.0007
Standing heat method	2.1	3.0	0.6932
Sow tries to mate other sows	33.0	5.1	<0.0001
Sow shows increased interest in boar	34.0	11.1	0.0001

Table 4 provides information about methods of heat detection. Heat detection is an important aspect of sow breeding management. It is important in sows since the estrus period lasts only 2-3 days and the sow must access the boar if she is to conceive (Aiello et al., 2016). The signs used by the majority farmers (over 90%) in both districts to detect heat in sows were swollen / red vulva as reported in the Philippines (Lanada et al., 2005). In Hoima, additional signs used were restlessness, special sounds and the sow standing with an arched back. In Kamuli, additional signs were increased interest in the boar and mounting other sows. Failure to detect heat could lead to repeat breeding (Dagorn and Aumaitre, 1979). However, this study found that 5% of the farmers in Kamuli and 16.2% in Hoima reported repeat breeding as a sow reproductive problem.

3.4.3. Record keeping and animal identification

Most of the respondents in both Kamuli and Hoima kept no records. The most common form of record keeping was mental records, which was more commonly practiced in Kamuli than Hoima (Table 5). Most respondents in Kamuli (89.5%) and Hoima (91.9%) did not identify their pigs. A small percentage in Kamuli (10.5%) used coat color and 8.1% in Hoima identified pigs through the dam.

Table 11. Types of records kept

Record kept	Kamuli (%; n=96)	Hoima (%; n=99)	p-value
No records	82.3	93.9	0.0310
Mental records only	10.4	3.0	0.0313
Written as well as mental records	3.1	1.0	0.2802
Written records only	4.2	2.0	0.3488

Livestock recording and identification is an important aspect of animal breeding since it makes it possible to track the progress of individual animals. This study found that majority (over 80%) of the farmers did not keep records or use any method to identify their pigs. Record keeping is an important source of pedigree information. This is particularly important in the design and implementation of breeding strategies for the selection and use of village boars to enhance farmer access to quality breeding materials from multiplier units (Kidoido and Korir, 2013).

3.4.4. Products produced and marketed from the pig enterprise

The primary product produced and marketed from the pig enterprise by majority households in Kamuli was weaners for fattening (82.1%). The weaners for fattening were local (61.5%), crossbred (33.3%) or exotic (5.1%), according to breed types provided by the farmers. The buyers of weaners for fattening pigs were a trader from Kampala (9.2%), a local village trader (18.4%) and smallholder farmers (68.4%). Weaners for fattening were sold at farm gate to individual customers (83.3%) and pig traders (14.1%). The secondary product in Kamuli was finishers for slaughter (72.1%). The finishers for slaughter were local (48.4%), crossbred (46.8%) or exotic (4.8%). The buyers of finishers for slaughter were Kampala trader (44.4%) and local village trader (55.6%). Finishers for slaughter were sold farm gate to individual customers (9.8%; n=61) and pig traders (85.2%) but directly to the pig slaughterhouse (3.3%). The tertiary product in Kamuli was sows for slaughter (54.8%; n=31). The sows for slaughter were local (35.3%) and crossbred (64.7%). The buyers of sows for slaughter in Kamuli were Kampala trader (50%) and local village trader (50%).

The primary product in Hoima was young females to use for breeding (65.7%). The young females for breeding were local (58.5%) or crossbred (41.5%). The buyers of young females for use as breeders were smallholder farmers (98.5%). The young females for breeding were sold from farm gate to individual customers (98.5%). The secondary products in Hoima were weaners for fattening (22.2%), young females for use as breeders (23.2%) and young males for use as breeders (39.4%). The weaners for fattening were local (63.6%) or crossbred (36.4%); the young female for use as breeders were local (78.3%) or crossbred (21.7%). The young males for use as breeders were local (53.8%), crossbred (43.6%) or exotic (2.6%). Smallholder farmers in Hoima were the buyers of weaners for fattening (95.5%), young females for use as breeders (95.7%) and young males for use as breeders (100%). The weaners for fattening were sold farm gate to individual customers (95.5) and traders (4.5%); young females for use as breeders farm gate to customers (91.3%) and traders (8.7%) and young males for breeding farm gate to individual customers (100%; n=39). The tertiary product in Hoima was weaners for fattening (34.3%), young males for use as breeders (19.2%) and sows for slaughter (25.3%). The weaners for fattening were local (58.8%), crossbred (38.2%) or exotic (2.9%). Smallholder farmers were the buyers of weaners for fattening (97.1%) and young males for use as breeders (100%). The local village traders were the buyers of sows for slaughter (68.0%).

Table 12. Primary, secondary, and tertiary products produced from the household pig enterprises. The number of respondents with valid answers ranged between 31 and 99 depending on the question

Product	Primary			Secondary			Tertiary		
	Kamuli (%)	Hoima (%)	P-value	Kamuli (%)	Hoima (%)	P-value	Kamuli (%)	Hoima (%)	P-value
Weaners for fattening	82.1	14.1	<0.001	4.7	22.2	0.0006	6.5	34.3	0.0025
Weaners for slaughter	3.2	1.0	0.2926	4.7	2.0	0.3137	3.2	0.0	0.0728
Finishers for slaughter	9.5	9.1	0.9268	72.1	7.1	<0.001	19.4	9.1	0.1185
Young females for use as breeders	1.1	65.7	<0.001	3.5	23.2	0.0001	3.2	6.1	0.5417
Young males for use as breeders	0.0	2.0	0.1638	0.0	39.4	<0.001	0.0	19.2	0.0083
Sows for slaughter	3.2	1.0	0.2926	12.8	4.0	0.0297	54.8	25.3	0.0021
Boars for slaughter	0.0	5.1	0.0265	0.0	2.0	0.1851	0.0	5.1	0.2019
Boar sire service	1.1	0.0	0.3061	1.2	0.0	0.2820	12.9	0.0	0.0003
Pig meat	0.0	0.0		0.0	0.0		0.0	1.0	0.5743
Sows for breeding	0.0	2.0	0.1638	1.2	0.0	0.2820	0.0	0.0	

The goal of any breeding undertaking is an animal that matches the needs of the farmers (customer/ end user). Tatwangire, 2014 has previously described three types of pig farmers in Uganda: breeders, growers and a third category of farmers who practice a mix of breeders and growers (keep sows to produce piglets and keep pigs for slaughter). The primary products produced by majority of the smallholder farmers were weaners for fattening in Kamuli and young females for breeding in Hoima. Other secondary or tertiary products produced across the districts were either weaners for fattening, young females and males for breeding and sows for slaughter. Therefore, while this study found that majority of farmers practice a mix of wean to finish and farrow to finish, they may be inclined to one of the two.

3.5. Conclusions

Smallholder (village) breeding schemes could improve pig productivity by disseminating improved genetics while controlling levels of inbreeding. The study identifies strong and weak points of the current breeding practices. The circumstances under which these smallholder farmers use breeding animals born on farm may predispose the herd to inbreeding. The farmers would benefit from participatory breeding strategies that supply them with quality genetic material from multiplier units. There is a general lack of animal identification and record keeping which is a potential drawback to selective breeding. There is an opportunity to train farmers to record performance data that could feed into a breeding program. This would also support the way farmers select replacement animals from within their herds. The main products are animals for breeding or slaughter and therefore, breeding goals and objectives should account for the heterogeneity in farmer needs.

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Chapter 4 Perceptions of women and men smallholder pig keepers in Uganda on pig keeping objectives, and breed and trait preferences

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4.1. Summary

The objective of this study was to compare the perceptions on livestock keeping objectives, breed and trait preferences of smallholder women and men pig farmers in Uganda. To this end, the study interviewed adult males and females from 200 pig keeping households, within two study sites. The main pig keeping objectives of both women and men were savings and insurance, income from the sale of pigs for fattening or slaughter, or income from the sale of pigs for use as breeding animals. The most preferred breed-types for both women and men were the same with exotic breeds the most preferred, followed by the cross of the exotic and local breeds. Many key traits, such as those for reproduction, growth, and disease resistance, were of similar importance to men and women. Overall, the results suggest that gender differentiated breeding objectives, and breed and trait focus, are not required as part of a pig breeding program in Uganda.

4.2. Introduction

Uganda, located in East Africa, is one of the world's poorest countries. Within Uganda, pig farming is an important livelihood to about 1.1 million poor smallholder farmers. Uganda's current pig population is about 3.2 million and rapidly increasing. Currently there are no structured pig breeding programs within Uganda, however efforts to establish one at a national level are underway. In low-and-middle income countries, there is strong recognition that the gender of stakeholders is important to consider in the design of rural development interventions. This ensures, for example, that both adoption and benefits are maximized and equitable. Gender has also been shown to matter in the design and implementation of livestock breeding programs in terms of ownership and control of animals (Marshall et al., 2019b). As background information feeding into the design of such a program, this paper compares Ugandan women and men smallholder pig farmers, in terms of their reasons for keeping pigs, and preferences for breeds and traits. The implication of these results on design of the potential Ugandan pig breeding program is also discussed.

4.3. Materials and methods

4.3.1. Study site and pig breeds present

The project study sites were within Kamuli and Hoima districts of Uganda, selected due to having a relatively high number of pig keeping households. Two hundred pig-keeping households, with 100 households in each site, participated in the study. The main pig types kept comprise local, exotic, and crosses between the two. The local breed is a small black pig, well adapted to the local environmental conditions. The exotic breeds comprise of Large White, Landrace, and the Camborough line from PIC. The exotic breeds are recent introductions to increase productivity. Various crossbreed types exist because of the unstructured crossbreeding between the local and exotic breeds.

4.3.2. Baseline survey

A baseline survey was administered separately to the female and male adult within each study household between April and May 2018. There were 200 female respondents (of which 19.5% were household heads and 80.5% were spouses) and 161 male respondents (all household heads). The survey comprised a questionnaire that collected data on household characteristics (such as structure, membership, education, livelihoods, asset base, food security etc.), as well as pig production practices.

4.3.3. Rating scales and statistical analysis

All ratings were based on Likert scales. For ratings of the importance of reasons for pig keeping and traits, the scale was 0 to 5, where 0 was no importance, 1 was the lowest importance, and 5 was the highest importance. For breed preference, the scale was 1 to 5, where 1 was strongly dislike and 5 was strongly like. To test differences between the average ratings by men and women, an independent t-test was applied under assumptions of normality and equal variances. The level of significance used was 0.05.

4.4. Results and discussion

4.4.1. Types of household pig enterprises, and their importance to livelihoods

Most households (92%) practiced a combination of farrow to wean and farrow to finish pig production systems. Most commonly, 1 to 3 sows were kept, with 2 to 16 piglets. Pig farming was the primary livelihood for 32% of women and 15% of men and secondary for 45% of women and 63% of men.

4.4.2. Reasons for keeping pigs

Women and men farmers rated reasons for keeping pigs, using a pre-defined list of reasons from literature (Ouma et al., 2015) with the option of including additional reasons (Table 13). The most important reasons for both genders were for savings and insurance purposes (keeping of pigs to sell in times of need) and income from sale of animals (both for fattening or slaughter, and as breeding animals). Women rated the keeping of pigs for savings and insurance purposes significantly more important than men, though the difference was small (Table 1). A similar result has been previously reported (Marshall et al., 2014). Both genders assigned lower importance to keeping pigs for income from boar sire service (likely because not all households keep boars) and manure for cropping. Keeping of pigs for home consumption of pig meat and income from manure sale was of almost no importance. This information was asked to help inform development of breeding objectives for the Ugandan pig breeding program. Results suggest that a common breeding objective, i.e., for both women and men, is appropriate. This objective would center around ensuring pig keeping translates into household income from both planned and emergency pig sales. Further development of this objective will be performed in collaboration with stakeholders.

Table 13. Average ratings for reasons for keeping pigs, by women and men farmers. The P-value indicates the significance of the difference between women's and men's ratings

Reason for keeping pigs	Women	Men	P-value
Savings / insurance (keeping of pigs to sell in	4.2	3.9	0.04
Income from the sale of pigs for fattening or	3.7	3.8	0.71
Income from the sale of pigs for use as	3.7	3.8	0.4
Income from boar sire service	1.2	1.1	0.66
Manure for cropping	0.9	0.7	0.4
Home consumption of pig meat	0.3	0.3	0.65
Income from the sale of manure	0.1	0.1	0.09

4.4.3. Breed preferences

Women and men respondents were asked to rate their preferences for the breed-types they were familiar with. The proportion of women familiar with local, crossbred, and exotic pigs were 69%, 41% and 12%, respectively, whilst for men it was similar at 70%, 41% and 17%, respectively. Results (Table 2) showed breed preferences not to be significantly different between the genders, with the most preferred breed (for both sows and fattening pigs) to be the exotic, followed by the crossbreed. Combined results across both genders showed the average rating for the exotic breed was significantly (a difference of 0.5 and P=0.019) higher to that for the crossbreed. Also, the ratings for the local were significantly lower than for cross (-0.73, P<0.001) and exotic (-1.24, P<0.001).

The same respondents named the advantages and disadvantage of the different breeds. The main advantages of local pigs included being adapted to the local environmental conditions (disease resistance, general adaptation, eating local feedstuff) and not requiring special housing, whilst the main disadvantages included low performance (growth, weight, litter size) and low market prices. The main advantages for exotic breeds were high performance, high market price and demand, whilst the main disadvantages were poor adaptation to local environmental conditions, high feed intake, feed cost, and the requirement for housing. For the crossbred, the named advantages and disadvantages were as for the exotic breed. Whilst both genders generally named similar breed advantages or disadvantages, the proportion of women versus men naming a particular advantage or disadvantage differed. Most notably more women than men named ‘high litter size’ and ‘high market price and demand’ as an advantage for the crossbred. On the other hand, more men than women named ‘faster growth’ and ‘high market demand’ as advantages for the exotic breed.

In terms of breeding program design, the breed advantages and disadvantages give some weight to focusing the program on exotic rather than cross-bred or local breeds. However, this result will later be combined with other results from the same study (such as the profit from keeping different breed-types) before a final decision on this choice is made. Continual feedback from the pig-keepers on preferred breed is also recommended, as breed preferences may change as people become increasingly familiar with the breed options.

Table 14. Average ratings for breed preference, by women and men farmers. The P-value indicates the significance of the difference between women’s and men’s ratings

	Sows			Fattening pigs		
Breed	Women	Men	p-value	Women	Men	p-value
Local	3.6	3.6	0.68	3.6	3.5	0.50
Crossbred	4.4	4.3	0.42	4.3	4.3	0.65
Exotic	4.8	4.9	0.62	4.8	4.9	0.47

4.4.4. Trait importance

Women and men respondents rated the importance of traits of sows and fattening pigs, using a pre-set trait list based on Ouma et al. (2015), with the option of including additional traits. The traits comprised of reproduction, growth, size, adaptation, body features (which farmers use to help indicate the breed-type), and others. Trait ratings were not statistically different between the genders, with two exceptions (Table 3). Sow traits that were considered moderately or more important (average ratings of ≥ 3) by both genders were reproduction, and growth / size, as well as disease resistance, ear-shape and feed intake. Traits that were low to moderately important for both genders (average ratings of ≥1 and <3) were heat-resistance, other body feature traits, and temperament. Traits of importance for fattening pigs were similar to those for sows (barring the reproductive traits that are not relevant to fattening pigs). It is of note that temperament was significantly more important to women than men for fattening pigs (and almost for sows), though the difference in ratings was small. This may stem from women being the main labor providers in cooling pigs, which is commonly done via dousing the pigs with water, with the water sometimes fetched from far away. Further, women rated feed intake significantly higher than men did. However, both genders desired the same direction of change in the trait (see Table 3). In considering breeding program design, these results indicate no concerns in having a common trait focus for both women and men pig keepers.

Table 15. Average ratings for trait importance, by women and men farmers. The P-value indicates the significance of the difference between women's and men's ratings

Trait group	Trait	Direction1	Sows			Fattening pigs		
			Women	Men	p-value	Women	Men	P-value
Reproductive	Return to heat	Faster	4	4	0.8			
	Litter size	12,10	4.7	4.5	0.2			
	Teat number	14,12	3.6	3.7	0.51			
Growth, size	Growth rate	Faster	4.4	4.3	0.51	4.6	4.6	0.9
	Body length	Longer	4.3	4.5	0.06	4.4	4.5	0.48
	Wither height	Taller	3.2	3	0.48	3	2.7	0.26
Adaptation	Disease resistance	Higher	4.2	4	0.15	4.2	4	0.26
	Heat resistance	Higher	2.3	2.2	0.89	2.2	2.2	0.71
Body features	Ear-shape	Floppy	3.5	3.3	0.35	3	2.8	0.34
	Back-shape	-[2]	2.5	2.5	0.61	2.4	2.2	0.27
	Mouth-shape	Short	3.1	2.8	0.12	2.8	2.6	0.43
	Colour	White	2.8	2.7	0.51	2.4	2.2	0.26
Other	Temperament	Docile	1.9	1.6	0.06	2	1.6	0.03
	Feed intake	High	3.8	3.5	0.02	4	3.9	0.17

[1]Direction of desired trait change or optimal value. The most common answer, giving singularly if the same for women and men, else for women and men, respectively.

[2]Both a curved and straight back shape was almost equally cited by both women and men

4.5. Conclusion

This work adds to a small, but growing, body of work on whether / how gender matters in the implementation of livestock breeding programs within low-and-middle income countries. In this case gender differentiated breeding objectives, and breed and trait focus, do not appear necessary. However, other studies have found significant differences between women and men for livestock keeping objectives and trait preferences (Marshall et al., 2014; Ramasawmy et al., 2018), which could impact on breeding program design. Despite the similarities between women and men on the issues reported here, a gender-lens should still be applied when considering other aspects of the potential pig breeding program for Uganda (see Marshall et al., 2019 for more details).

Acknowledgements

We gratefully acknowledge the women and men farmers who participated in this study, as well as the local district and project staff. This study is part of the Uganda Pig Genetics project, funded by the Austrian Development Agency and the CGIAR research program on livestock.

Chapter 5 A mix of Old British and Modern European breeds: Genomic prediction of breed composition of smallholder pigs in Uganda

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5.1. Abstract

Pig herds in Africa comprise genotypes ranging from local ecotypes to commercial breeds. Many animals are composites of these two types and the best levels of crossbreeding for particular production systems are largely unknown. These pigs are managed without structured breeding programs and inbreeding is potentially limiting. The objective of this study was to quantify ancestry contributions and inbreeding levels in a population of smallholder pigs in Uganda. The study was set in the districts of Hoima and Kamuli in Uganda and involved 422 pigs. Pig hair samples were taken from adult and growing pigs in the framework of a longitudinal study investigating productivity and profitability of smallholder pig production. The samples were genotyped using the porcine GeneSeek Genomic Profiler (GGP) 50K SNP Chip. The SNP data was analyzed to infer breed ancestry and autozygosity of the Uganda pigs. The results showed that exotic breeds (modern European and old British) contributed an average of 22.8% with a range of 2–50% while "local" blood contributed 69.2% (36.9–95.2%) to the ancestry of the pigs. Runs of homozygosity (ROH) greater than 2 megabase (Mb) quantified the average genomic inbreeding coefficient of the pigs as 0.043. The scarcity of long ROH indicated low recent inbreeding. We conclude that the genomic background of the pig population in the study is a mix of old British and modern pig ancestries. Best levels of admixture for smallholder pigs are yet to be determined, by linking genotypes and phenotypic records.

5.2. Introduction

The pig (*Sus scrofa domesticus*), an even toed ungulate and a member of the genus Sus, was domesticated from its ancestor, the wild boar (*Sus scrofa scrofa*) in multiple domestication centers including the Near East, Europe, China and South-east Asia, about 9000 years ago (Rothschild et al., 2011; Groenen et al., 2012). Wild boar (*Sus scrofa algira*) also inhabits North Africa (Rothschild et al., 2011). Since its domestication, the pig has been genetically improved into several specialized breeds through traditional and marker assisted selective breeding (Dekkers, 2004; SanCristobal et al., 2006; Mote and Rothschild, 2020). Such work is notable for European breeds such as the Pietrain that has been intensively selected for muscle development (Amaral et al., 2011). The Landrace breed originated from British foundation stock imported to Denmark and selected for leanness and fast growth. Commercial breeds such as the Large White, Berkshire and Hampshire were developed from crossbreeding old British and Asian pigs (White, 2011; Amills et al., 2013). Iberian pigs (Toro et al., 2008) were exported during the colonization of the Americas and contributed to development of the Duroc (Jones, 1998). Its adaptive attributes and importance as a source of meat have contributed to the global distribution of the pig (Orr and Shen, 2006). Notably, sub-Saharan Africa is not within the native range of wild boar and no archeological or genetic evidence points to a domestications event there (Ramirez et al., 2009). The origin of pigs in East Africa is traced to both the pre- and colonial eras (Blench, 2000; Ramirez et al., 2009; Blench, 2010). Indian Ocean trade and eventual European settlement have also been associated with the introduction of Asian and European pig breeds to East Africa (Boivin et al., 2013).

Pig production is an important livelihood source for smallholder farms managed under low input systems in African countries, for example Nigeria, Uganda and Malawi. Uganda is an East African inland country linked to the Indian Ocean through Kenya (east) or Tanzania (south-east). Pigs in Uganda are represented by domestic pigs (*Sus scrofa domesticus*) and the wild suids including the Giant forest hog (*Hylochoerus meinertzhageni*), Warthog (*Phacochoerus aethiopicus*) and Bush pig (*Potamochoerus porcus*) (Ghiglieri et al., 1982; Reyna-Hurtado et al., 2014). In the mid-19th century, Britain colonized Kenya and Uganda while Germany colonized Tanganyika (present Tanzania). Pig production for lard or bacon was an important consideration by the colonists and several breeding experiments were done with British pig breeds such as Large White, Yorkshire, Berkshire, Tamworth, and Large Black (Montgomery, 1921; Prosser, 1936). Pigs of the Large White breed imported from Kenya, as well as pigs distributed by the Ugandan veterinary department were kept by Ugandan farmers (UGANDA, 1940). Details of the main breeds kept by the farmers are mostly lacking, but the pig populations in 1945 and 1959 were reported to be 23,158 and 15,668 (Masefield, 1962). Currently, pig production in Uganda is done by more than a million households that manage over 90% of the national herd of 4.2 million pigs (UBOS, 2019). Uganda's per capita consumption is 3.4 kg/year (FAOSTAT, 2018) and the pro-poor significance of pig farming has recently attracted policy recognition (Sentumbwe, 2017).

While one study using microsatellite, data has linked the genetic background of pigs in Uganda to European and Asian ancestries (Noce et al., 2015), the breed composition of most pigs in Uganda is largely unknown and any available breed information is mostly as reported by farmers. A previous study reported local pigs on smallholder farms in Uganda (Mbuza, 1995). According to Blench (2000), African pigs are usually black, with a straight tail and popped swept back ears. Other studies have mentioned exotic breeds like Hampshire, Large White, Duroc, Landrace and Camborough®, which is a cross Large White, Landrace and

Duroc, developed by the Pig Improvement Company (PIC®), having been introduced to Uganda (Ssewannyana and Mukasa, 2004; Walugembe et al., 2014a; Greve, 2015; Roesel et al., 2016). Admixture between the different breed types is common.

Since 2012, the International Livestock Research Institute (ILRI) has provided a range of technical solutions to pig production constraints in districts of Uganda where pork production is important (Ouma et al., 2015). In 2017, the ILRI led Uganda Pig Genetics Project was launched to provide technical solutions to pig breeding constraints to support previous and ongoing initiatives. A key research question of the Uganda Pig Genetics project was to determine the most-appropriate pig breed or crossbreed type for different types of smallholder pig producers, considering a variety of issues including farmer preference and profitability, amongst others. As part of this work, household pig enterprises and the pigs within them were longitudinally monitored with genomic analysis undertaken to determine the breed-type of individual pigs kept. This study draws on this genomic data to quantify the genetic background, diversity and inbreeding levels of pigs on smallholder farms in Uganda using high throughput Single Nucleotide Polymorphism (SNP) data. SNP data from international sources, publicly available or privately owned but provided for this project, was used to place the pigs of Uganda onto a global genomic map.

5.3. Materials and methods

5.3.1. Ethics approval

This research was approved by the Institutional Research Ethics Committee (IREC), Institutional Animal Care and use Committee (IACUC) of the International Livestock Research Institute (ILRI) and Vector Control Division–Research and Ethics Review Committee (VCD-REC) of the Ministry of Health of Uganda (MOH). Prior informed consent was obtained from owners of the pigs sampled in Uganda. Research and access and benefit permits (Research Registration number: SS4550) were granted by Uganda National Council of Science and Technology (UNCST, 1990).

5.3.2. Site and household selection

This study was conducted in the districts of Hoima, Kamuli, Pallisa, Kumi and Soroti in Uganda (Figure 1 (a)-(d)). Hoima and Kamuli were the primary Uganda Pig Genetics project sites selected because of the importance of pig production to these districts, amongst other criteria. A purposively selected sample of 200 smallholder pig keeping households, 100 each from Hoima and Kamuli, participated in the study. The districts of Pallisa, Kumi and Soroti were additional sampling sites for local Uganda pigs.

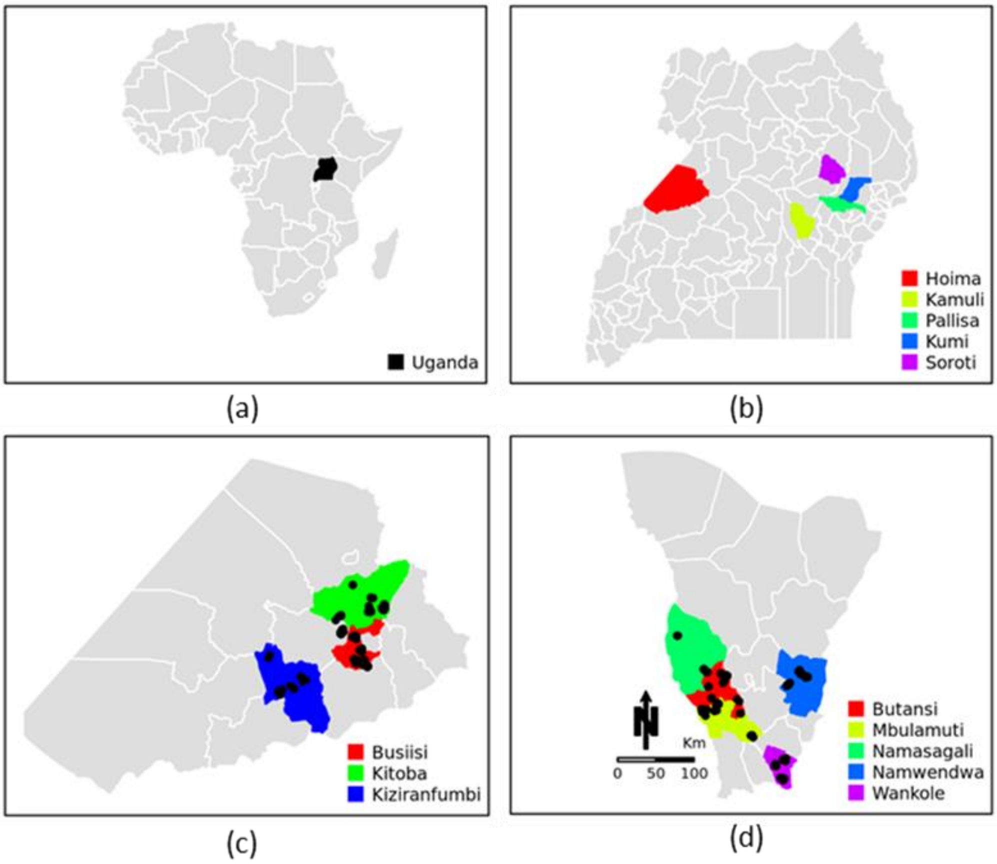


Figure 4. (a) map of Africa showing the location of Uganda. Figure 1 (b) map of Uganda showing the location of Hoima, Kamuli, Pallisa, Kumi and Soroti districts. Figure 1 (c) map of Hoima showing the locations of Busiisi, Kitoba and Kizaranfumbi sub-counties, Figure 1 (d) map of Kamuli showing the locations of Butansi, Mbulamuti, Namasagali, Namwendwa and Wankole sub-counties. The black dots in Figures 1 (c) and (d) show the sampling locations.

5.3.3. Animals and genotyping data

A sample of 422 pigs from the five districts in Uganda: Hoima (n=163) Kamuli (n=218), Kumi (n=11), Pallisa (n=12) and Soroti (n=18) were involved in the study (see Figure 1). A total of 41 animals, showing the characteristics of African pigs according to Blench (2000), were sampled from 41 households having been reported to keep local Uganda pigs by extension staff in the latter three districts. Prevalence of pigs with black coat color, long snout, short legs and popped ears, facing up and backward were criteria of selection of households keeping local pigs. Hair samples taken from the 422 pigs were genotyped using the Neogen GeneSeek Genomic Profiler (GGP) Porcine 50K array (Neogen Europe, 2020). Using literature on East African pigs and phenotypic characteristics of pigs owned by the smallholder farmers in the study area (Figure 2), we chose as putative ancestral populations, Asian, Duroc, British, Iberian and Continental European pig breeds. We explored the ancestry of Uganda pigs in global context by incorporating publicly or privately available genotypes from the putative ancestral populations (Cleveland et al., 2012; Yang et al., 2017; Pena et al., 2019; Pfeiffer et al., 2019; Hlongwane et al., 2020a).The data were merged and manipulated in PLINK1.9 (Chang et al., 2015). Prior to merging the data, the SNP positions in each dataset were updated to the sus scrofa reference 11.1 genome build (Illumina, 2013). Quality control (QC) parameters were applied to exclude closely related individuals from each dataset based on PI_HAT using –genome and –max 0.1 flags. The PIC® dataset consisted of 3359 animals. These were genotyped commercial animals- the Camborough® a first filial generation (F1) cross between the PIC Landrace and PIC® Large White pure lines genotyped with the Illumina PorcineSNP60 chip. The sample consisted of both male and female animals born since 2000 with varying degrees of kinship. Overall, the sampling technique avoided sampling multiple individuals from full-sib families (Cleveland et al., 2012). We use the code CMB throughout this paper to refer to the Camborough® genotypes. The total genotyping rate for CMB data was around 15% lower than for other datasets, therefore we applied the –mind 0.15 flag to only this data. Data merging errors for SNPs with similar positions or on flipped strands were corrected using the –exclude or –flip flags. Samples were randomly excluded when a population exceeded 50. Also breeds without apparent interest to this study, according to literature, were excluded. The merged data (Table 16) was explored using Multidimensional scaling (MDS) and ADMIXTURE analysis (Alexander et al., 2009).

Table 16. Breeds/ populations used in exploration of the ancestry of Uganda pigs

Dataset	Breed/ population	Country
Uganda Pig Genetics	Hoima, Kamuli, Pallisa, Soroti, Kumi	Uganda
Cleveland et al., 2012	Camborough® (Pig Improvement Company)	Great Britain
Pfeiffer et al., 2019; Hlongwane et al., 2020; Yang et al., 2017	Landrace, Large White	Austria South Africa Denmark
Yang et al., 2017	Jinhua, Laihuwei, Lantang, Meishan, Angler Sattelschwein, Bunte Bentheimer	China Germany

	Pietrain	Germany, Netherlands
	British Lop, Saddleback, Gloucestershire, Large Black, Leicester, Middle White, Tamworth, Welsh	Great Britain
	Berkshire, Hampshire	Great Britain, United States of America
	Casertana, Nera Siciliana,	Italy
	Poland Pulawska Spot,	Poland
	Breitov, Livni, Murom	Russia
Yang et al., 2017; Hlongwane et al., 2020	Duroc	America, South Africa
Pena et al., 2019	Entrepelado, Retinto, Entrepelado x Retinto cross Retinto x Entrepelado cross	Spain

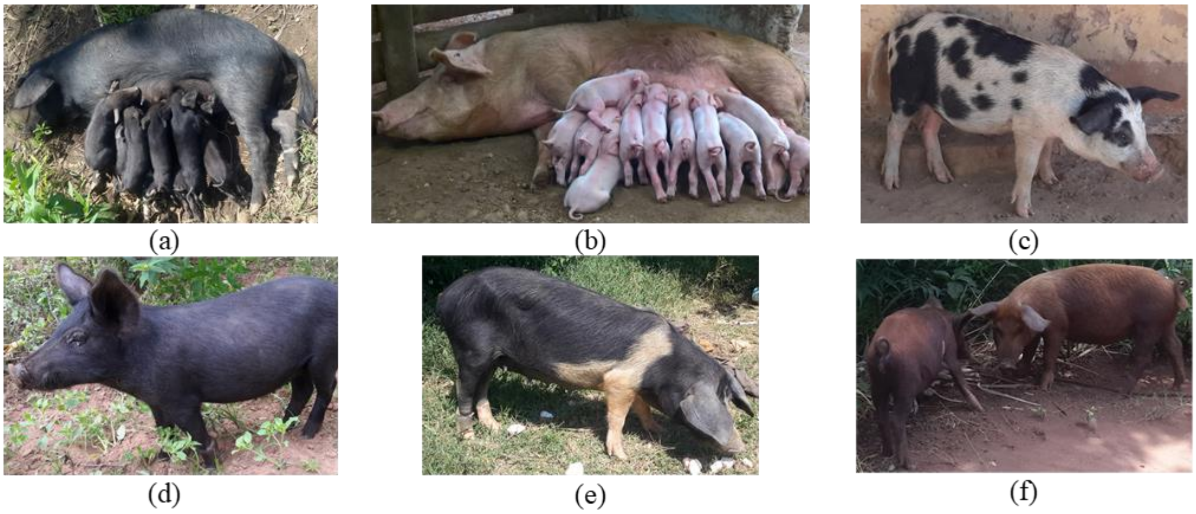


Figure 5. Photographs of pigs of different breed or crossbreed types in Uganda. (a) a local sow with her litter (b) an exotic breed e.g., Camborough® sow with her litter (c) a spotted pig that could be old British (Gloucestershire) or a cross of exotic breeds (Landrace and/ or Large White) (d) a local pig (e) a belted pig that could be a British Saddleback cross and (f) two red coated pigs that could be Duroc or Tamworth. Photo credit: Babigumira Brian Martin/ ILRI/ BOKU.

5.3.4. Multidimensional scaling (MDS) and ADMIXTURE analysis

Following the exploratory admixture analysis outlined above, we narrowed down the list of reference populations to a panel that, to the best of our judgement, reflected the admixture seen in the Uganda population. This final reference panel included American (DRC), Chinese (MS), Spanish (IB), Modern European (CMB, LR and LW), Old British (SB and LB) breeds and Local Ugandan pigs (LOC). We run MDS analysis on the merged dataset using the --distance-matrix flag of PLINK1.9 and Classical Metric Multidimensional Scaling and plotted the MDS results in R (R Core Team, 2020). We also run unsupervised ADMIXTURE analysis on the merged dataset for number of ancestral population (K) from two to 10 (Alexander et al., 2009).

5.3.5. Population structure and admixture analysis using CHROMOPAINTERv2, fineSTRUCTUREv4 and GLOBETROTTER

To support the ADMIXTURE and MDS analysis, we analyzed the data using the CHROMOPAINTERv2/ fineSTRUCTUREv4 pipeline supported by the Perl scripts provided with the programs (Lawson et al., 2012). The data was phased using SAHPEIT2 (Delaneau et al., 2011). First, a custom R script (R Core Team, 2020) was run to prepare the genetic maps for each chromosome, as required by SHAPEIT2 based on the Sus scrofa recombination map (Tortereau et al., 2012). We run quality control (--geno 0.2) and split the data by all autosomal chromosomes using PLINK1.9 (Chang et al., 2015). To achieve a successful run with the provided QC measures (considering size of individual populations and number of variants), we included the –force flag in the SHAPEIT2 command line. We run the impute2chromopainter.pl script to transform the SHAPEIT2 files into the phase format usable by Chromopianterv2. Next, we run the convertrecfile.pl script to generate recombination files using as inputs, the phase files from the previous run and genetic maps based on the Sus scrofa recombination map (Tortereau et al., 2012). We used the default settings for both scripts and specified the HapMap format when using the latter. We then run the phase and recombination files in CHROMOPAINTERv2 (Lawson et al., 2012) twice; the first run was to estimate nuisance parameters and the second one was to generate the co-ancestry matrix using the linked model. The Estimation-Maximization (E-M) iteration was run in automatic mode (‘fs’) with the entire dataset for all autosomal chromosomes. Basically, each animal was conditioned on the others in 10 E-M iterations using a sample of ten animals. The main output were two inferred nuisance parameters (Ne, somewhat similar to effective population size and mu, the mutation/ switch rate) (Hellenthal, 2012). These parameters (Ne=34.7106 and mu=0.00500584) were fixed in the CHROMOPAINTERv2 algorithm in the second run. The main outputs were estimation of the c-factor (effective number of chunks; c=0.17931) and copying vectors. These outputs were fed into the Bayesian clustering algorithm of fineSTRUCTUREv4 for all autosomes.

To further investigate the admixture in the Ugandan pig population used in this study, we exploited the analytical capabilities of GLOBETROTTER (Hellenthal et al., 2014). The Bayesian clustering algorithm of fineSTRUCTUREv4 identified 40 clusters, which, when grouped, were generally not different from our labeled data or the output from ADMIXTURE1.3. Therefore, we run GLOBETROTTER to identify, date and describe admixture in the Uganda pigs using as surrogates: MS, DRC, IB, Modern European (CMB, LR and LW) and Old British (SB and LB) and LOC with KAM or HOI as target (recipient) populations (Hellenthal et al., 2014; Hellenthal, 2020). We ran GLOBETROTTER with default settings for all parameters except "prop.ind", "bootstrap.date.ind" and "null.ind". For the first run, we set "bootstrap.date.ind" to 0 and the other two to 1. In the second run, we set "prop.ind" to 0 and the other two to 1. For the third run, we set "null.ind" to 0 and the other two to 1 (Hellenthal, 2020). Here we report the results from the last run.

5.3.6. Autozygosity analysis of Uganda pigs

Autozygosity is the inheritance of alleles that are identical by descent (IBD). Contiguous homozygous genotype segments of the genome are called Runs of Homozygosity (ROH) (Gibson et al., 2006). The ROH can be used to infer the genomic inbreeding coefficient (FROH) and distinguish ancient from recent inbreeding (Keller et al., 2011). We run this analysis using the dataset of Uganda (HOI and KAM) pigs (381 samples and 50,697 SNPs). The analysis was run in the cgaTOH(Zhang and Hewitt, 2003). The ROH analysis was run using minimum run lengths of 2, 4, 8 and 16 Mb and at least 20 SNP. Heterozygous calls in ROH were not allowed up to 16 Mb while only one heterozygous call was allowed for ROH >16 Mb. The proportions of the ROH for each of the cut-offs (FROHi, i = 2, 4, 8 and 16) were computed using as total length of autosome covered by SNPs of 2,259,445,079 bases. The genomic inbreeding coefficient (FROH) was computed (McQuillan et al., 2008) as follows:

$$\boldsymbol{F_{ROH}} = \sum \frac{\boldsymbol{L_{ROH}}}{\boldsymbol{L_{AUTO}}}$$

5.4. Results

5.4.1. Exploratory analysis of Uganda pigs in a global context

The merged dataset used in the exploratory analysis had 28,894 SNPs and 1,198 animals from 44 populations and 31 breeds (Table 16). The first eigenvector of the MDS analysis separated the Chinese and Iberian from the rest of the populations. The second eigenvector separated the Duroc from the rest of the populations. Both eigenvectors explained about 17% of the variation observed (Figure 6). The Ugandan samples were all situated inside a large cluster, including British and Continental European breeds.

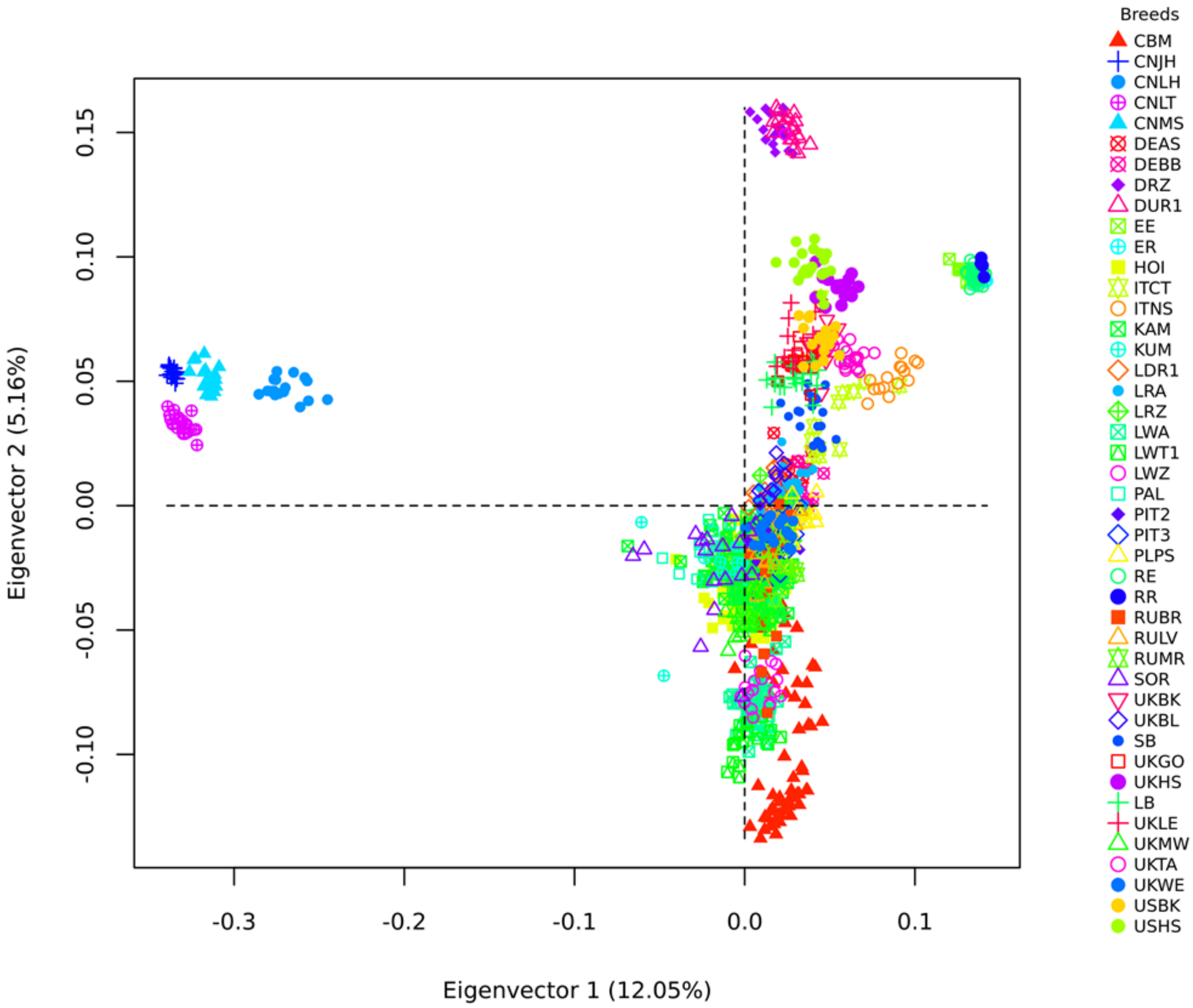


Figure 6. Multidimensional Scaling analysis of Uganda pigs in a global context. CMB: Camborough®; Great Britain; CNJH: Jinhua; CNLH: Laihuwei, CNLT Lantang; CNMS: Meishan-China; DEAS Angler Sattelschwein-Germany; DEBB Bunte Bentheimer-Germany; DRZ: Duroc- South Africa; DUR1: Duroc- United States of America; EE: Entrepelado; ER-Spain: Entrepelado x Retinto cross- Spain; HOI: Hoima-Uganda; ITCT: Casertana- Italy; ITNS: Nera Siciliana-Italy; KAM: Kamuli-Uganda; KUM: Kumi-Uganda; LDR1: Landrace-Denmark; LRA: Landrace-Austria; LRZ: Landrace-South Africa; LWA: Large White-Austria; LWT1: Large White-Denmark; LWZ: Large White-South Africa; PAL: Pallisa-Uganda; PIT2: Pietrain- German; PIT3: Pietrain-Netherlands; RE: Retinto x Entrepelado cross-Spain; RR: Retinto-Spain; RUBR: Breitov-Russia; RULV: Livni-Russia; RUMR: Murom-Russia; SOR: Soroti-Uganda; UKBK: Berkshire-Great Britain; SB: Saddleback- Great Britain; UKGO: Gloucestershire- Great Britain; UKHS: Hampshire- Great Britain; LB: Large Black-- Great Britain; UKLE: Leicester- Great Britain; UKMW: Middle White- Great Britain; UKTA:

Tamworth- Great Britain; UKWE: Welsh- Great Britain; USBK: Berkshire-United Sates of America; USHS: Hampshire-United Sates of America.

Following the exploratory analysis, we retained 30 of the 50 Camborough® (CMB) samples based on proportions of both Large White and Landrace breeds. Further, we removed three local Ugandan pigs that had high exotic proportions. Finally, the panel of ancestral breeds narrowed down to those potentially interesting based on their ancestry contribution in the Uganda pigs. The final dataset (Table 17) had 28,894 SNPs, 587 samples from 9 populations and 7 breeds. The populations were Meishan, Duroc, Iberian, Modern European (Landrace, Camborough® and Large White), old British (Saddleback and Large Black), Uganda (Hoima, Kamuli and Local).

Table 17. Ancestral and Uganda population used in ancestry analysis

Dataset	Population	Breed	Code	Country	Samples
Cleveland et al., 2012	Modern European	Camborough®	CMB	Great Britain	30
Hlongwane et al., 2020	Duroc	Duroc	DRC	South Africa	20
Pena et al., 2019	Iberian	Iberian	IB	Spain	24
	Hoima	Hoima	HOI		161
Uganda Pig Genetics	Kamuli	Kamuli	KAM	Uganda	218
	Local	Local	LOC		38
	Meishan	Meishan	MS	China	20
	Modern European	Landrace	LR	Denmark	20
Yang et al., 2017		Large White	LW		16
	Old British	Saddleback	SB	Great Britain	20
		Large Black	LB		20

5.4.2. Multidimensional scaling (MDS) and Admixture analysis

The first eigenvector of the multidimensional scaling (MDS) analysis of the dataset in Table 17 separates the Chinese and Iberian breeds from the Uganda, American, Modern European and Old British breeds. The second eigenvector clusters some of the modern European breeds (largely comprised of Large White) closely with the Uganda pigs. It also separates the Uganda pigs from the rest of the Modern European, Old British, Duroc, Iberian and Chinese breeds (Figure 4).

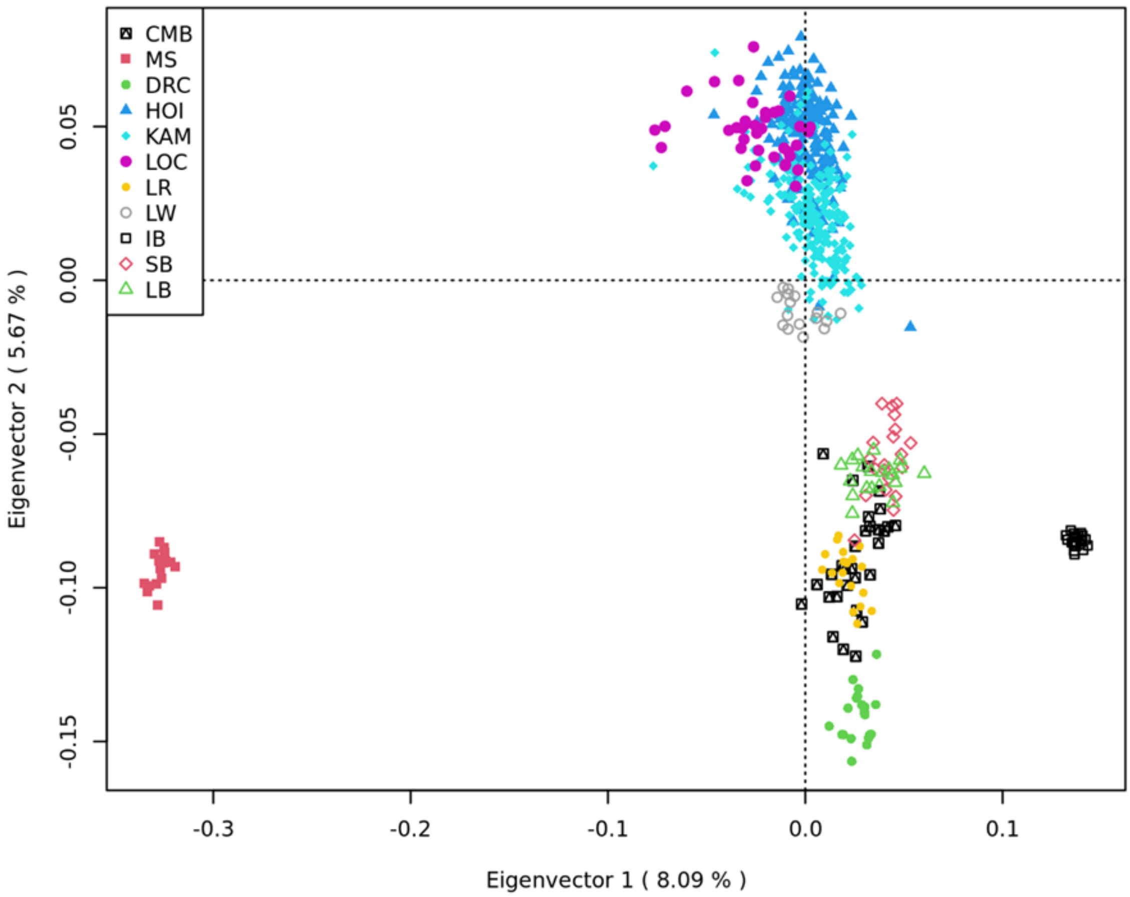
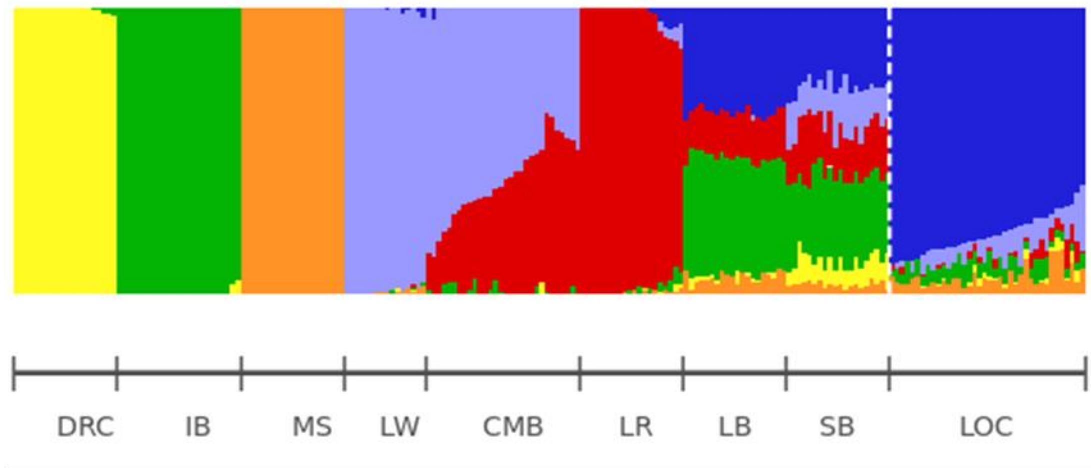
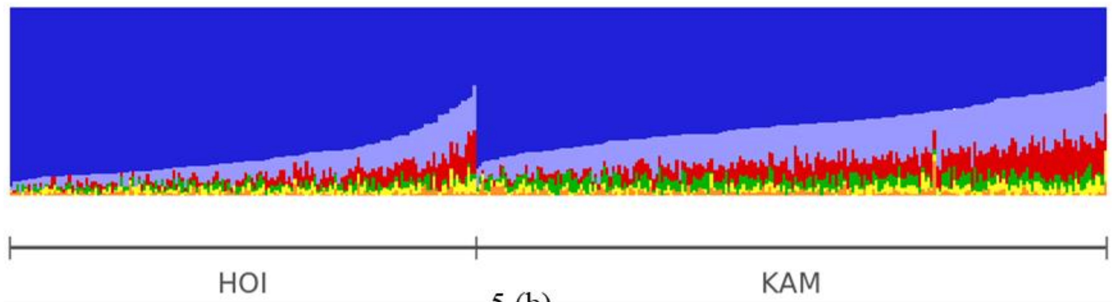


Figure 7. Multidimensional Scaling Analysis of Camborough® (CMB); Meishan (MS); Duroc (DRC); Uganda (Hoima (HOI); Kamuli (KAM): and Local (LOC)); Landrace (LR); Large White (LW); Iberian (IB); Saddleback (SB)and Large Black (LB). The first eigen vector separates the MS and IB from the rest of the population. The second eigenvector closely clusters LW and Uganda pigs and separates them from the rest.

We ran unsupervised analysis to infer ancestries of HOI and KAM pigs using various ancestral populations (K) without getting meaningful clusters at the lowest cross-validation error (CV) value. Therefore, we selected results at K=6 and visualized the results using POPHELPER (Francis, 2017). The LOC pigs (purple) represented the main ancestry which was also shared with Old British breeds. The modern European breeds contributed most of the ‘exotic’ ancestry in the Hoima and Kamuli pigs (Figures 5a and 5b).



5 (a)



5 (b)

Figure 8. (a) Ancestry pig populations for K=6: the modern European consists of Large white (LW; sky blue), Landrace (LR; red) and Camborough® (CMB; nearly half sky blue/ red). The old British breeds (SB: Saddleback: and LB: Large Black) share ancestries with the Iberian (IB), modern European and local Ugandan pigs (LOC). (b) The Uganda pigs Hoima (HOI) and Kamuli (KAM) have a dominant blue ancestry that we refer to as ‘local’ shared with the old British breeds. The modern European breeds contribute most of the exotic ancestry.

Results from using ADMIXTURE1.3 showed that modern European breeds (CMB, LR and LW) contributed on average 22.8% with a range of 2-50% of the ancestry while LOC contributed 69.2% (36.9-95.2%). The other 8.0% were contributed by DRC, IB and MS. We also found higher frequency of MS ancestry in LOC than in HOI or KAM pigs (Figures 5 (a) and 5 (b)). Note that ADMIXTURE1.3 did not separate the Old British breeds into a uniform cluster but linked it to various populations, notably to Iberian and Ugandan types.

5.4.3. Population structure and admixture analysis using CHROMOPAINTERv2, fineSTRUCTUREv4 and GLOBETROTTER

The fineSTRUCTUREv4 analysis identifies three main clusters based on the empirical c-value- HOI, KAM and LOC and the third cluster comprising international breeds (DRC, MS, IB, Modern European and Old British breeds). Considering that fineSTRUCTUREv4 did not identify clusters that differed much from our labeled data, we run 'as is' the data in GLOBETROTTER to identify and date the admixture. GLOBETROTTER identified a one-date-multiway (1-DMW) for HOI and a one-date (1-D) admixture event with two sources for KAM pigs. The GLOBETROTER inferred date and confidence intervals (95% CI) for HOI and KAM were 6.371 (3.543−7.311) and 4.719 (2.420−5.093) generations. We converted generations to years using a generation interval of 1.9 years (Welsh et al., 2010) and the present year as 2019 in the formula (Hudjashov et al., 2017):

$$Y = y — (1 + x) * g$$

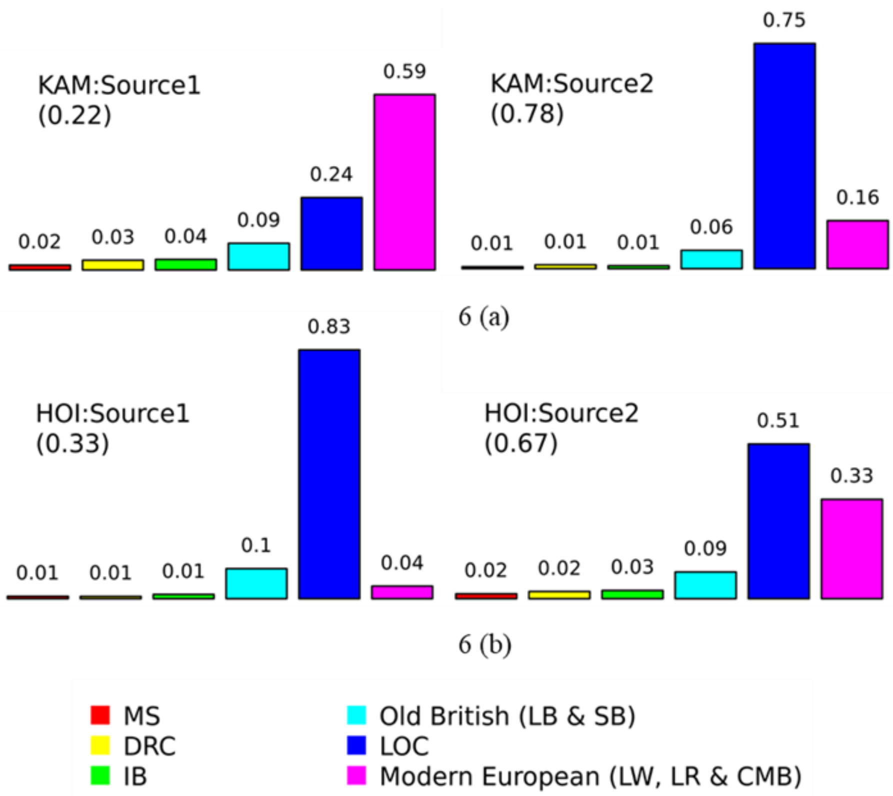


Figure 9. Proportions contributed by surrogate populations to the minor and major sources of admixture for (a) Kamuli (KAM) and (b) Hoima (HOI) pigs. The surrogate populations are:

Meishan (MS); Duroc (DRC); Iberian (IB); Large Black (LB); Saddleback (SB); local Ugandan (LOC); Large White (LW); Landrace (LR) and Camborough® (CMB). The numbers in brackets are the proportions each source contributes to the admixture in the target (recipient) population and they sum up to one. The numbers on top of the bars are the contributions of each surrogate population within each source and they sum up to one.

5.4.4. Autozygosity analysis of Uganda pigs

For a 50K SNP Chip, ROHs of length less than 2Mb may contain undetected heterozygotes and hence prone to false positives (Ferencakovic et al., 2013). Therefore, we reported inbreeding levels (FROH>2Mb) for ROH lengths greater than 2Mb. Only 348 of 381 pigs from Hoima and Kamuli districts, Uganda had at least one ROH>2Mb. The FROH>2Mb ranged from 0.000 to 0.363 with a mean of 0.043. The average ROH>2Mb length per animal was 3.6±1.9Mb and most pigs (81.6%) had at least one ROH >4Mb. The average FROH for ROH length of 4, 8 and 16 were 0.030, 0.013 and 0.007. The longest individual ROHs (>20Mb) were on chromosomes 4 and 14. The most inbred individual (FROH>2Mb = 0.363) had 129 ROHs, the longest individual ROH (28.9Mb), longest total length of ROHs (819.35Mb) for FROH >2Mb and was from Kamuli district (Figure 7 (a) and 7 (b)).

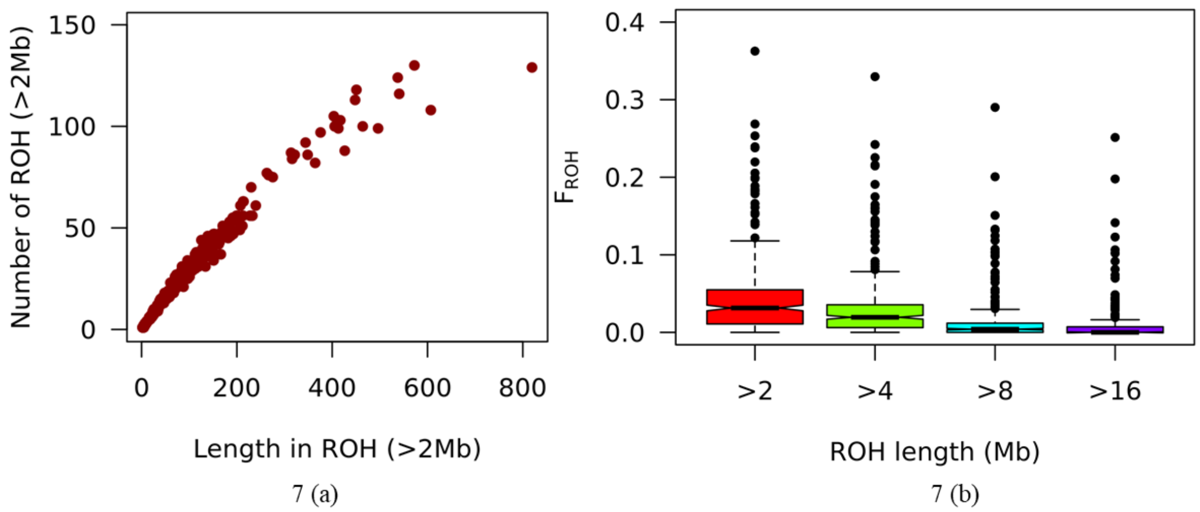


Figure 10. (a) Number of ROH distributed and along cumulative total ROH length on the pig genome in ROH. (b) Boxplot of FROH cutoffs of 2, 4, 8 and 16Mb for smallholder pigs from Hoima and Kamuli districts in Uganda.

5.5. Discussion

5.5.1. Breed composition of Uganda pigs

While we use the term LOC (local) to refer to pigs commonly considered to have been in Uganda for some time, we also note that no pig domestication event in Sub-Saharan Africa has been reported or supported by archeological or genetic evidence (Blench, 2000; Amills et al., 2013). Therefore, technically, indigenous Ugandan (Ugandese) pigs do not exist. However, we use the term local (LOC) throughout this paper to differentiate the resident population from exotic ones. We found what appeared LOC to relate more to ancestry contributions from black or belted old British pigs (Figures 5 (a) and 5 (b)). We also found signatures of MS in both the Uganda pigs as previously reported (Noce et al., 2015) and old British breeds. The MS signature in Uganda pigs is likely from an introgression through the old British breeds (Ramirez et al., 2009). We also observed a higher LOC ancestry in HOI than KAM pigs. This may be because Hoima is located further from Kampala, the capital of Uganda and a source of exotic pigs, than Kamuli. The local pigs of Uganda are not characterized and are only identified phenotypically according to the definition of African pigs by Blench (2000). It was difficult to find the local pigs especially where restocking programs had been or were operational. Our results complement previous findings and advocate for characterization and conservation of local pigs in Uganda.

The GLOBETROTTER analysis identified a one-date-multiway (1-DMW) admixture event for HOI pigs. The event involved mostly LOC and modern European breeds and dated the event to 2004 (95% CI: 2003-2010). In the case of Kamuli, a one date admixture event mostly involving modern European and LOC pigs was identified and dated to 2008 (95% CI: 2007-2012). These admixture dates imply recent introductions of exotic pigs in these areas, corresponding with varied 'on-the ground' activities that have been observed with the introduction of new pig breeds. Pigs have been distributed to Ugandan farmers through programs run by the government and non-government organizations (Ampaire, 2011; Tatwangire, 2013; Ouma, 2017). The inferred admixture dates coincide with the out scaling of National Agricultural Advisory Services (NAADS) programs in Uganda. The NAADS program essentially sourced and distributed farm inputs including pigs and other livestock to smallholder farmers (Benin et al., 2007; Ouma et al., 2015). Non-government organizations in Kamuli that also distributed pigs to smallholder farmers are Volunteer Efforts for Development

Concerns (VEDCO) (Ampaire, 2011), and Iowa State University-Center for Sustainable Rural Livelihoods (CSRL, 2021). Additionally, smallholder pig farmers in Uganda may also purchase pigs mainly from other nearby smallholder pig keepers or local markets (Ouma et al., 2015; Lichoti et al., 2016). These programs or farmers aim to improve productivity of pig herds through crossbreeding by distributing or purchasing pigs of commercial breeds including Landrace, Large White or Camborough®. The GLOBETROTTER and ADMIXTURE results together suggest the following. First, restocking programs have the potential to change the genetic constitution of smallholder pig herds. Second, the several admixture sources observed in the HOI and KAM pigs suggest indiscriminate crossbreeding (Greve, 2015) rather than for example a two- or three-way crossbreeding program. However, they could also suggest an ongoing upgrading of local herds given the proportionately higher frequency of the Modern European breed alleles.

5.5.2. Inbreeding levels of Uganda pigs

Using the porcine GGP 50K SNP Chip, we investigated the occurrence of ROHs and quantified autozygosity in pigs in Kamuli and Hoima districts of Uganda. In this study, we found the genomic inbreeding coefficient (FROH > 2Mb) to be 0.043 (0-0.363) for HOI and KAM pigs. The low FROH>2Mb indicates low inbreeding in the pig population. This is contrary to what has been previously reported (Tatwangire, 2014). Because of the very small herd size, sows are typically mated with village boars. Boar keepers usually source boars from outside the local area and the piglets received as payment for boar service are sold. Additionally, farmers with sows may source village boar service from sources outside their village depending on boar availability (Ouma et al., 2014; Lichoti et al., 2016). These scenarios suggest a low likelihood of mating related individuals, thus keeping inbreeding levels low. Somewhat higher inbreeding levels could be expected for households which own boars, but this a small minority. For instance, the most inbred individual (FROH>2Mb = 0.363) could be the offspring of full sib or parent-offspring mating. Also, events necessitating stock replacement, like African Swine Fever outbreaks (Lichoti et al., 2016; Ouma et al., 2018) would also lower inbreeding levels.

5.6. Conclusions

Smallholder pig production in Uganda is constrained by several factors, mostly related to pig health, nutrition and genetics (Ouma et al., 2015). Coupling genetic improvement with other appropriate management interventions would enhance productivity of smallholder pig herds. The results of this study showed that the contribution of Modern European ancestry did not exceed 50% for any of the animals sampled in Uganda. This was contrary to expectation, based on breed composition reported by smallholder farmers. The terms 'local', 'crossbred' and 'exotic' used in this context seemed to reflect farmer perception rather than actual breed history. The gradient of ancestries observed in the Hoima and Kamuli populations of this study is still big enough to investigate the effect of the proportion of Modern European ancestry on growth, health and reproduction of pigs in those areas. Longitudinal data for these traits for most of the animals in the current study is available and will be analyzed subsequently. Only then appropriate crossbreeding levels may be determined, and farmers advised about choice and sources of breeding stock.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

JS and KM conceived and designed the whole study. EO, JS and KM provided technical, administrative and logistic support. BMB oversaw the fieldwork, analyzed the data and drafted the manuscript. CL and CP provided genotype data through their companies. GM supported assembly of the data. BMB and JS analyzed the data. GM, KM, CL, and CP contributed to interpretation of data and all authors critically revised and approved the manuscript for submission.

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Data availability

The porcine 50k SNP chip data, including 50697 SNPs of 422 animals from Uganda included in this study was uploaded to DRYAD. The dataset has been assigned a unique identifier doi: 10.5061/dryad.4qrfj6q95 and is accessible via this temporary link: https://datadryad.org/stash/share/qKhv_9otEd2ivmo6TsIPuQHG30ZFg3BuSJjlg5SDj_M.

Chapter 6 Effect of proportion of Modern European ancestry on grower and sow performance of pigs in smallholder systems in Uganda

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6.1. Author summary

Uganda has the largest national pig herd and highest per capita pork consumption in East Africa. Pig production in Uganda is an important socio-economic activity that has grown over the last three decades. The national herd has increased from a few tens of thousands to millions of pigs distributed in more than a million households. Pork accounts for around 30% of the annual per capita meat consumption in Uganda. While the pigs are produced from both commercial and smallholder farms, it is the latter that holds the largest share of pork production. Smallholder pig production is poorly documented in terms of production statistics and this creates an information gap in policy and technical interventions. In 2017, the project "Sustainable intensification of the pig value chain in Uganda – for improved rural livelihoods and enhanced food security" (Uganda Pig Genetics Project-UPG) was launched under the leadership of the International Livestock Research Institute (ILRI). The project focused on identifying the most appropriate genetics for smallholder pig production in two districts of Uganda - Hoima and Kamuli. Studies were designed in the framework of this project to characterize and evaluate the smallholder pig herds. One of the studies focused on genomic characterization of the pig herds and traced their ancestry to Modern European (ME) and Old British pig breeds. The current study combines the genomic (proportion of ME ancestry) and longitudinal data from these pig herds to evaluate grower and sow performance. We found that ME was not a significant effect on body weight and total number of piglets born alive but was on total number of piglets weaned, with sows with relatively high proportion of ME (0.29-0.50) weaning around 3 piglets more than sows with low ME proportion (0.02-0.15). Cognizant of the function of both genotype and environment on performance, we hope that our results will inform the design of subsequent studies.

6.2. Abstract

Several factors including breed, lead to divergent performance of pigs for production and reproduction traits in different environments. A recent genomics study showed that Modern European (ME) pig breeds contribute to the ancestry of smallholder pigs in Hoima and Kamuli districts, Uganda. These pigs were also involved in a longitudinal study with several traits being recorded, including 540 body weights (WT) of 374 growing pigs, 195 records of total number of piglets born alive (TBA) of 157 sows and 110 total number weaned (TNW) records of 94 sows. Linear mixed effects models were used to test for the significance of environmental effects, including housing system, geographic location of the pig farm, season when the events

occurred as well as animal specific effects like age, sex, parity and farrow-to-weaning interval. Stepwise model reduction starting from models with all main effects and pairwise interactions was applied. The final models were then expanded to include proportions of Modern European (ME) ancestry for the subset of animals genotyped, following genomic ancestry analysis based on the Geneseek Genomic Profiler Porcine 50k SNP chip. For BW 94 records of 43 genotyped animals were available, TBA data included 135 records of 103 genotyped animals, for TNW the corresponding numbers were 80 and 67. ME ancestry proportions ranged from 0.02 to 0.50 and were categorized into three classes (low/medium/high ME) based on 33% quantiles. The effects of ME classes on BW and TBA were not significant. ME showed a significant effect ($\chi 2=10.3928$; $p=0.00554$) on TNW. Sows with high proportion of ME ($ME \geq 0.28$) weaned 2.4 piglets more than the low group ($ME \leq 0.15$), the medium ME group being intermediate with respect to TNW. This study used genomic data to investigate the effects of genetic ancestry on the performance of smallholder pigs in Uganda. The proportion of Modern European ancestry did not exceed 0.50, therefore not allowing comparison of local versus pure ‘exotic’ types of pigs. For the range of ancestries observed, which is the relevant one for current smallholder systems in Uganda, differences were small for body weight of growing pigs and number of piglets born alive, while higher proportions of Modern European ancestry resulted in significantly more piglets weaned. Availability of genotypes of a higher number of growing pigs would have been beneficial for drawing conclusions on the effect of ME ancestry on the growth rates of smallholder pigs in Uganda.

6.3. Introduction

Pork is an import source of animal protein and represents 30-40% of the meat consumed globally (FAO, 2014). The top pork producing countries in Africa include Nigeria, Malawi, Uganda (FAOSTAT, 2021). The national herd of Uganda is estimated at 4.2 million pigs (UBOS, 2020) and per capita consumption of pork is 3.4 Kg (FAOSTAT, 2018). Smallholder farmers represent majority of pig producers and pigs are kept for savings/ insurance and income (Babigumira et al., 2019). Small herds of variable size are kept from which piglets, slaughter animals or both are produced (Ouma et al., 2015; Ouma et al., 2017). Pig breeding is unstructured and services like Artificial Insemination are not commonly used. Most farmers rely on the services of a village boar for a fee to breed their sow (Dione et al., 2014). Performance traits related to reproduction (litter size), growth and disease resistance are important to smallholder farmers (Babigumira et al., 2019). All these constraints have implications on the performance of pigs in these typically low-input smallholder systems.

Previous studies on the performance of pigs in Africa have been under differing production conditions and have to a great extent relied on pig breed composition as reported by farmers or research stations, that is, local, crossbred and exotic (Adebambo and Dettmers, 1982; Affentranger et al., 1996; Ajala, 2007; Kagira et al., 2010; Muhanguzi et al., 2012; Greve, 2015; Dotché et al., 2020a). However, there is consensus that local pigs in Africa were introduced and are of European and Asian ancestries (Blench, 2000; Ramirez et al., 2009; Noce et al., 2015; Dotché et al., 2020b; Babigumira et al., 2021). To the best of our knowledge, the study by Babigumira et al. (2021) is the first in Uganda to both decipher and quantify the ancestry of smallholder pigs using SNP Chip data. Babigumira et al. (2021) analyzed the ancestries of Ugandan smallholder pigs, including Old British, Modern European, Iberian, Duroc and Chinese pigs as potential ancestral populations. The authors found that these pigs were mostly a mix of Old British and Modern European (ME) types. The current study was a follow on to the study by Babigumira et al. (2021). Both studies were conducted as part of a longitudinal survey of smallholder pig herds in the districts of Hoima and Kamuli, Uganda under a larger project. Here, we statistically tested the effects of ME ancestry (ranging 2-50%) on phenotypes recorded on these smallholder pigs in Kamuli and Hoima districts, Uganda. Our results highlight the role of the environment in the performance of pigs in smallholder herds and imply a holistic approach when intervening in smallholder pig production.

6.4. Materials and methods

6.4.1. Study sites and households

The study sites selected were Hoima and Kamuli districts, due to the importance of pig-keeping to smallholder livelihoods in these districts. Household selection proceeded as follows. For selected sub-counties within Hoima and Kamuli districts, a full list of pig keeping households was obtained in collaboration with the district extension staff. From here, 300 households were randomly selected and surveyed for key information on their household pig enterprise type, including main breed-type of pig kept (as local, cross-bred of local and exotic, and exotic), and type of pig-housing (as free-range, tethered versus housed). Households pig enterprises were then classified based on combinations of main breed-type kept and housing practiced (as local-tethered, cross-breed-tethered, exotic-tethered, cross-bred-housed, exotic-housed) with the final set of 200 project households purposively selected from these groups, such that each enterprise type had about an equal number of households. The 200 households were in 30 villages in 26 parishes across 8 sub counties in the two districts.

6.4.2. Ethics statement

This research received approval from the Uganda National Council of Science and Technology (UNCST), the Research Ethics Committee of the Vector Division of Ministry of Health (VCD-REC), Uganda; Research Ethics Committee (IREC), and Institute Animal Care and Use Committee (IACUC) of the International Livestock Research Institute (ILRI). Farmer participation in the study was voluntary.

6.4.3. Genotypes

The breed composition (genotypes) of the pigs were inferred by admixture analysis in a related study (Babigumira et al., 2021). Briefly, hair samples were taken from a random sample of smallholder pigs from 148 of the 200 smallholder households in the districts of Hoima and Kamuli and pigs phenotypically representative of 'local' pigs in the districts of Soroti, Kumi and Paliisa. Genotyping was done using the Geneseek Genomic Profiler Porcine 50k SNP chip and ancestry proportions were inferred by admixture analysis using ADMIXTURE 1.3 (Alexander et al., 2009). The pigs were found to have a mix of Old British and Modern European (ME) ancestries. Large White and Landrace pig breeds contributed most of the ME ancestry proportions, which were between 0.02 and 0.5 (Babigumira et al., 2021). .

6.4.4. Data collection

Data was collected on all pigs present within the project household at the time of the survey visit. Initially a pig census survey was performed (October to November 2018) with all pigs within the households tagged and demographic data on each pig obtained (including age, sex, breed, and for sows their parity, as per farmer recall), using a structured survey. From here the household pig herds were longitudinally monitored (December 2018 to March 2020). During the longitudinal monitoring, the households were visited 8 times, and information on their household pig enterprises, and pigs, recalled to the previous visit, again using a structured survey. Data captured during the longitudinal monitoring included (amongst others) farrowing and weaning events, health, nutrition (feeds and feeding practices), herd dynamics (entries and exits); pig transactions (sales and purchases), housing systems, morphometric and body weight measurements.

This study focused on analysis of growth and fertility traits. Body weight (WT) measurements were measured at birth, when possible, otherwise the birth date was recalled by the farmer and the weight of the pig measured during the visit. Pigs were weighed every subsequent visit until the animal exited the farm (through sale or death), or until the end of the survey. WT was measured using a digital weighing scale (Brand: Crane, range of measurement: 1-200kg and accuracy: 0.12kg). Heart girth (HG) and body length (BL) measurements were taken at the time of weighing each pig. Sow fertility data collected included farrowing and weaning dates, litter sizes at birth and at weaning. The data was entered into the Census and Survey Processing System (CSPro) (U.S. Census Bureau, 2012) and reposited in a SQL database on the ILRI data portal (Rutto et al., 2019).

6.4.5. Data analysis

We analyzed the influence of a range of effects (described below) on variation in growth and litter size of pigs All effects and their possible pairwise interactions were tested at a significance level of 0.05 by a linear mixed effects model using the lme4 package in R environment (Bates et al., 2014; R Core Team, 2020). Results from the lme4 packaged were visualized using the lmerTest R package (Kuznetsova et al., 2017). Least-squares means (LSM) were estimated and compared pairwise by Kenward-Roger method and Tukey p-value adjustment method for comparing multiple estimates using the lsmeans R package (Lenth, 2016).

6.4.5.1. Description of variables

Body weight (WT) and litter size at farrowing and weaning were continuous dependent variables. The independent variables of interest were housing system, geographic location of the farm, season, sex (for growers); farrow-to-weaning interval and parity (for sows). The pigs in each household were managed under one of three housing systems: free-range (only for growers), tethered, housed. The proportion of Modern European (ME) were inferred in a previous study (Babigumira et al., 2021) and were categorized into low, medium and high classes based on 33% quantiles. Season was defined as dry or wet based on the seasons of Uganda to which the month of farrowing (for sows) or weighing (for growers) belonged. Uganda majorly has two wet seasons: March to May and September to December (Caffrey et al., 2013; Mubiru et al., 2015). Parity was defined as "1" for a primiparous and "2+" for a multiparous sow. Farrow-to-weaning interval was a continuous variable computed in days and then categorized based on 33% quantiles. Age was a continuous variable while sex was a categorical variable (female or male). Genotypes were available on only 11.0 % of growing pigs with body weights (43 of 374) due to the inability to hair sample very young pigs and their absence at the next survey visit (e.g., due to sale or death). In contrast, 66% of sows were genotyped. The 43 genotyped growing animals with 94 records on WT were assigned to three ME classes on 33% quantiles (low $\leq$0.181, 0.181>medium< 0.280 and high$\geq$0.280). The sows were assigned to three ME classes based on 33% quantiles (low$\leq$0.153, 0.153>medium<0.289 and high$\geq$0.289).

The number of animals in each category of the variables is presented in table 1.

Table 18. Number of animals in each category of environmental and genetic effects

Characteristic	Levels	Sows (N)		Growers (N)
		Farrow	Wean	
Geographic location	Kamuli	91	61	319
	Hoima	66	34	55
Season	Dry	59	32	226
	Wet	107	67	254
Housing system	Housed	43	26	110
	Tethered	109	69	70
	Free-range	0	0	131
Parity	1	98	58	NA
	2+	77	43	NA
Sex	Male	NA	NA	172
	Female	157	95	191
ME	Genotyped	103	67	43
ME classes	Low	37	21	13
	Medium	34	24	13
	High	32	22	17
Farrow-to-weaning interval	Low	NA	35	NA
	Medium	NA	35	NA
	High	NA	38	NA

NA not applicable

6.4.5.2. Statistical models

A range of effects potentially affecting the traits under study, including geographical location, housing system and season, were included in the linear mixed statistical models employed. As only part of the animals with phenotypes were also genotyped for the prediction of levels of ME ancestry, the following strategy of analysis was employed:

First, mixed linear models with fixed environmental effects and all their pairwise interactions as well as the random effect of animal, accounting for repeated measurements, were tested. A stepwise procedure for model reduction was followed, excluding non-significant interaction terms one by one and then excluding non-significant main effects not involved in any of the interactions. Model reduction was based on Pearson's chi-square (χ^2) statistic with a threshold of p=0.05.

Second, the resulting model was then employed adding proportion of Modern European ancestry (ME: low, medium, and high) as well as its pairwise interactions with the other fixed effects in the final environmental effects model. Non-significant pairwise interaction terms of these environmental effects and ME were also excluded in a stepwise manner to arrive at the final model. Therefore, the results for the fixed environmental effects presented here are derived from the initial dataset with more observations while the effects of ME ancestry and its interactions come from the smaller dataset of genotyped animals. We run the final models fitting ME as a categorical variable as well as a continuous variable.

6.4.5.2.1. Grower performance

A total of 540 WT records from 374 animals with indicators of age, geographic location, sex, pig housing system and season were available. The number of animals with one, two, three and four records were 252, 83, 3 and five. For the 374 animals the ranges of WT, HG, BL and age were 0.7 to 49.0 Kg, 5.0 to 73.0 cm, 14.0 to 91.0 cm, and 7.0 to 210 days, respectively. The significance of the environmental effects on WT and all pairwise interactions were investigated using model (1).

$$WT_{ijklmno} = A_i + G_j + S_k + H_l + W_m + P_n + \text{all pairwise inteactions} + \varepsilon_{ijklmno} \quad \ldots\ldots\ldots (1)$$

Where; WT_{ijklmn} = body weight of the n^{th} animal; A_i = i^{th} age in days (covariate); G_j = j^{th} geographical location (j = Kamuli | Hoima); S_k = k^{th} sex (k = female | male); H_l = l^{th} pig housing system (l = free-range | tethered | housed); W_m = m^{th} season in which the animal's body weight was measured (m = dry | wet); P_n = n^{th} animal (random effect); ε_{ijklmn} = random residual effect.

6.4.5.2.2. Sow performance

The effect of season, geographic location of the farm, pig housing system and parity as fixed effects and the sow as a random effect on total number of piglets born (TBA) of 195 observations from 157 sows and on total number of piglets weaned (TNW) of 110 observations from 94 sows were investigated using model (2)

$$TBA_{ijkln}, TNW_{ijklmn} = S_i + G_j + H_k + P_l + I_m + AN_n + \text{all pairwise interactions} + \mathcal{E}_{ijkln}, \mathcal{E}_{ijklmn} \quad \ldots\ldots\ldots (2)$$

Where TBA_{ijkln} = total number of piglets born alive; TNW_{ijklmn} = total number of piglets weaned; S_i = i^{th} farrowing/ weaning season (i= wet | dry); G_j = j^{th} geographic location of farm (j= Kamuli | Hoima), H_k = k^{th} housing system (k= tethered | housed); P_l = l^{th} parity (l = 1 | 2+); I_m = m^{th} farrow-to-weaning interval (m = low | medium | high) (only for TNW); AN_n = n^{th} sow (n = 1…n); ε_{ijkln}, ε_{ijklmn} the random residual effect.

6.5. Results and discussion

6.5.1. Description of body weight and litter size

Most growing animals (92.5%) weighed less than 10kg (for HG, BL, and age less than 68, 79, and 200, respectively) due to heavier animals being sold from the household prior to the time of visits (Figure 1).

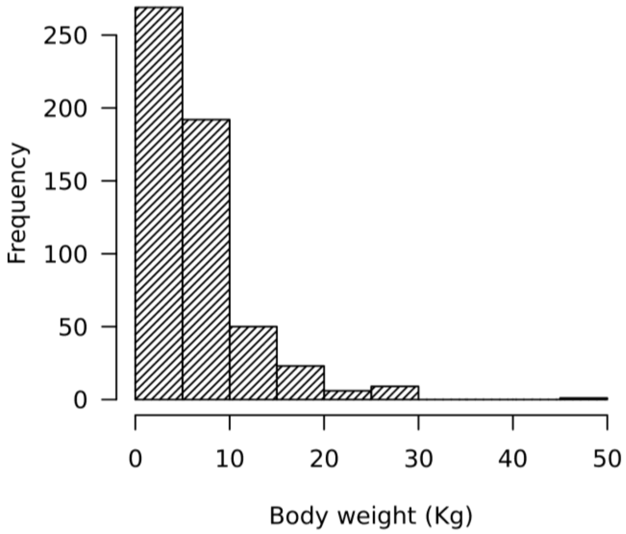

Figure 11. Distribution of body weight (WT) of growing pigs

The correlations between WT and the two morphometric measurements ranged from 0.74 to 0.92 (Table 2)

Table 19. Correlation between WT, HG and BL

	WT (Kg)	HG (cm)	BL (cm)
WT (Kg)	1.00		
HG (cm)	0.74	1.00	
BL (cm)	0.75	0.92	1.00

Note that the WT of eight animals with missing WT measurement but HG and BL measurements available was predicted using a multiple linear regression equation based on (3).

WT = -9.45091+ 0.40756× **HG** + 0.02152 × **BL** ……………………….……….……………. (3)

HG and BL explained 61% of the variation of WT (R-squared = 0.61)

The relationship between weight and age is shown in Fig. 2. The WT was very variable with age with some animals at either end of the spectrum. Variability in WT of growing pigs has also been reported in the Philippines (More et al., 1999), Kenya (Mutua et al., 2011b) and in commercial herds (López-Vergé et al., 2018).

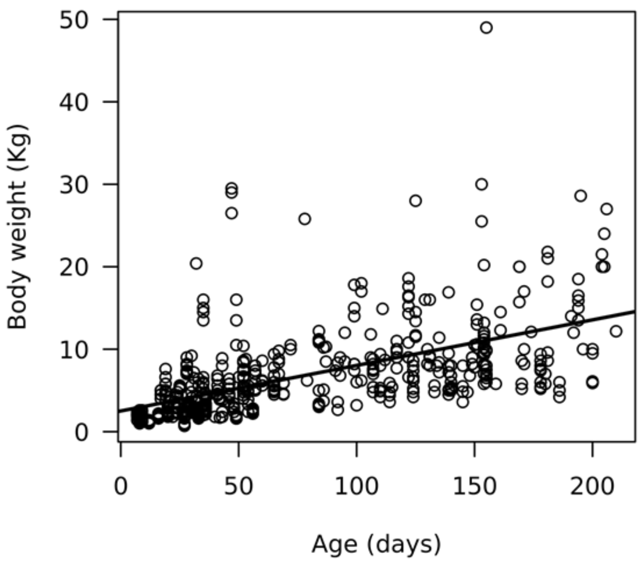

Figure 12. Weight-for-age of growing pigs

For sows, a total of 195 litters with a mean of 7.2±2.3 (1-13) had been farrowed by 157 sows between July 2018 and March 2020. The TBA values are comparable to that reported in India and Nigeria (Kumaresan et al., 2007; Abah et al., 2019) but lower than those reported in commercial herds in Uganda (Greve, 2015). A total of 110 litters of 94 sows had weaning records on total number of piglets weaned, season of farrowing, parity, geographic location of the farm and pig housing system practiced on the farm. The average size of weaned litters was 6.1±2.2 (1-11) piglets. The TNW values reported here are lower than those reported by Greve (2015). The litters were weaned between October 2018 and March 2020. The distribution of TBA and TNW are shown in Figure 13.

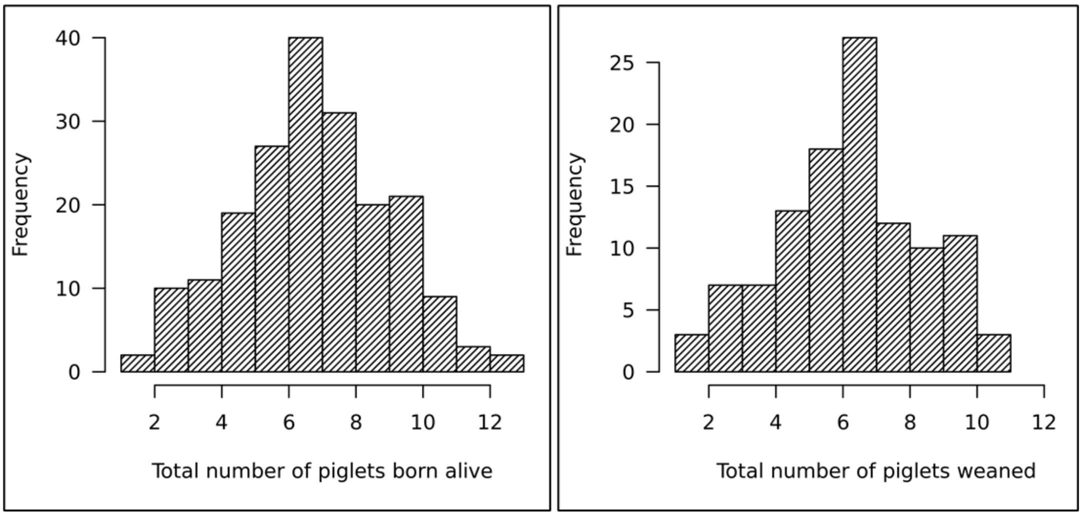

Figure 13. Distribution of total number of piglets born alive (TBA) and total number of piglets weaned (TNW).

6.5.2. Models including environmental effects

6.5.2.1. Grower performance

The final (reduced) model for growth performance contained the main effects and interaction terms presented in Table 20.

Table 20. significance of effects and interaction terms retained in the reduced model for WT

	χ^2	DF	Pr ($>\chi^2$)
Age	196.095	1	< 0.0001
Housing system	9.583	2	0.00830
Season	2.416	1	0.12011
Geographic location	0.629	1	0.42771
Age * season	17.751	1	0.00003
Age * geographic location	5.162	1	0.02308

The variances of the random effects namely animal and residuals were 7.762 and 11.521 respectively translating to a repeatability of 0.67 of the WT measurements. The average daily gain (ADG) derived from linear regression of weight on age was 55 g/day. Least square means for WT by housing system are presented in Table 21. Pairwise comparisons showed significant differences between housing systems (free-range vs housed).

Table 21. Least square means for WT by housing system

Housing system	LS mean	SE
Free-range	6.31[a]	0.52
Tethered	7.36[ab]	0.50
Housed	8.11[b]	0.42

[a,b] LS means not sharing the same superscripts are significantly different for WT.

Housing system was a significant effect on WT, and this could be attributed to intensified management of housed pigs. Pigs in Tanzania were found to gain between 68 when let to free-range and 72g/day when confined/ housed (Lipendele et al., 2015). The ADG reported in our study is close to those reported in Benin (Kouthinhouin et al., 2009) but lower than the 77 g/day that was reported for smallholder pigs elsewhere in Uganda (Lule and Lukuyu, 2017) and much lower than those reported for pigs in Kenya (Mutua et al., 2011b; Carter et al., 2013), Ghana (Darfour-Oduro et al., 2009), Zimbabwe (Chimonyo et al., 2010) and India (Kumaresan et al., 2007), the latter mostly derived from feeding trials. Smallholder pigs are fed energy rich but protein deficient crop residues comprising root tubers and their vines or leaves e.g., sweet potato and cassava (Carter, 2015). Feed shortages and poor-quality forages in the tropics contribute to slower pig growth (Mutua et al., 2012; Levy, 2014). Age (Carter et al., 2013) was found to have significant effect on WT as reported in our study.

6.5.2.2. Sow performance

6.5.2.2.1. Total number of piglets born alive

For TBA, the only significant effect retained was parity (χ^2= 5.8916; p=0.01521). The variance components for the random effects namely animal and residual were 0.728 and 4.294 respectively translating to a repeatability of 0.17. The least square means for TBA by parity are presented in Table 22. Pairwise comparisons showed significant differences between classes of parity (p=0.0173).

Table 22. Least square means of TBA by parity

Parity	LS mean	SE
1	6.85[a]	0.23
2+	7.62[b]	0.24

[a] LS means with different superscripts are significantly different for parity.

Multiparous sows farrowed 0.77 piglets more than their primiparous cohort. Litter size increased with each parity till around the fourth in a recent study of local and improved pigs in Benin (Dotché et al., 2020a).

6.5.2.2.2. Total number of piglets weaned (TNW)

The non-significant interaction terms and main fixed effects were excluded stepwise from model (3). The significant main effects and interaction terms are presented in Table 23.

Table 23. Significance of fixed effects and their pairwise interaction terms on TNW

	χ^2	DF	Pr (>χ2)
Season	0.011	1	0.9166
Geographic location	3.486	1	0.0619
Housing system	5.584	1	0.0181
Parity	6.742	1	0.0094
Season: Geographic location	7.255	1	0.0071
Season: Parity	5.157	1	0.0232

Sows that farrowed in the wet season weaned 0.54 piglets less. The wet season rather than cold weather is associated with piglet mortality (Chiduwa et al., 2008). Multiparous sows weaned 1.6 piglets ($p=0.0013$) more and this is attributed to the improvement in mothering ability of the sow. The least square means of TNW by geographic location, housing system and parity are presented in Table 7. Pairwise comparison showed significant difference between different levels of each variable.

Table 24. Least square means for TNW by farrowing season, geographic location, and parity

Geographic location	LS mean	SE
Hoima	7.80^{a}	0.41
Kamuli	6.57^{b}	0.31
Housing system	LS mean	SE
Housed	7.74^{a}	0.43
Tethered	6.63^{b}	0.28
Parity	LS mean	SE
1	6.39^{a}	0.29
2+	7.98^{b}	0.42

^{a,b}LS means with different superscripts are significantly different for each variable.

6.5.3. Testing effects of proportion of Modern European (ME) ancestry

6.5.3.1. Grower performance

The analysis of the effect of ME classes on WT showed that ME was not a significant effect on WT (χ^2= 0.104, p=0.949) and none of the pairwise interaction terms of ME with the other main effects was significant (p= 0.083 or higher). Fig. 4 shows the least squares means and 95% confidence intervals of ME classes. Pairwise comparisons revealed non-significant (p<0.05) differences between the ME classes. Further analysis with ME as a regressor also revealed neither it (χ^2=0.001, p=0.973) nor its interactions with the other effects (p=0.489 or higher) in the model were a significant effect on WT.

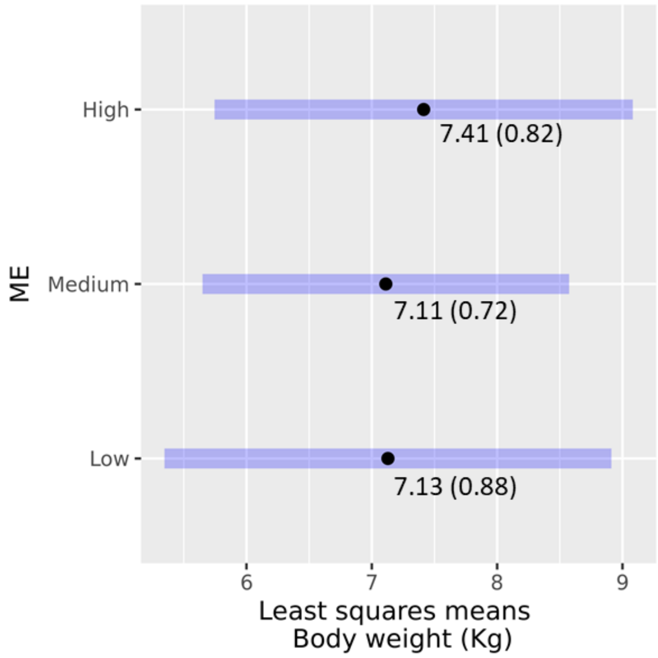

Figure 14. Effects of ME classes on WT, least square means (standard error) and their 95% confidence intervals. Horizontal bars indicate 95% confidence intervals

It is generally accepted that exotic pigs weigh heavier than their indigenous counterparts. However, we found no significant differences in effects of ME class on WT. Note that the number of animals as well of observations was small because only a small proportion of the growers were genotyped.

It is likely that ME effects were confounded by other effects such as housing system. Pigsties are usually provided by farmers capable of intensifying production, for example by using improved breeds and providing better management (Dione et al., 2014; Ouma et al., 2015).

6.5.3.2. Sow performance

6.5.3.2.1. Total number of piglets born alive (TBA)

As only parity was significant after reduction of model (3) with the full phenotype data, proportion of Modern European and its interaction term with parity were added for the analysis of data of genotyped animals. A total of 135 farrowing records that belonged to 103 genotyped sows were available for analysis. Neither ME (χ^2= 3.2163; p= 0.20026) nor its interaction with parity (χ^2= 0.64804; p= 0.64804) were significant effects on TBA. Least squares means of ME and their 95% confidence intervals for TBA are presented in Fig. 5. Sows in the ME medium and high groups farrowed 0.86 and 0.14 piglets more than those in the low group. A study in Cameroon that compared primiparous local versus exotic sows e.g., Large White, reported lower litter size for the local sows though the breed effects was non-significant. However, breed was a significant effect on litter size of multiparous sows (Kouamo et al., 2015). In our study, we found feed purchase not a significant effect on TBA. Quality and quantity of feed have an influence on how well sows perform in terms of litter size at farrowing (Kouamo et al., 2015; Dotché et al., 2020a).

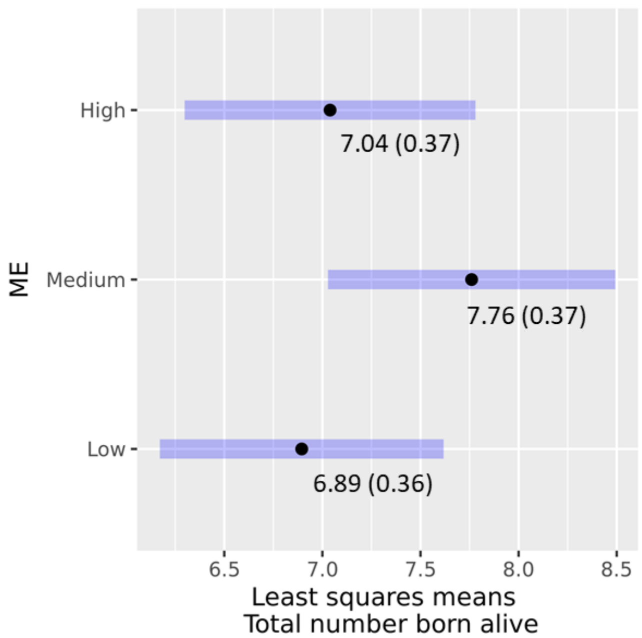

Figure 15. Effects of ME classes on TBA, least square means (standard error) and their 95% confidence intervals

6.5.3.2.2. Total number of piglets weaned (TNW)

For TNW, a total of 80 weaning records that belonged to 67 sows were available for analysis. ME was a significant effect (χ^2=10.3928; p=0.005537) on TNW as were the interactions between ME and geographic location (χ^2=6.8424; p=0.032673). The least squares means of

ME classes and their 95% confidence intervals for TNW are shown in Fig. 4. There was a clear ranking, with higher proportions of Modern European ancestry being associated with higher TNW. Pairwise significance testing indicated that medium levels of ME were significantly different from low ME. The LSMs for TNW by the interaction between ME and geographic location are shown in Table 8. The findings are similar to a study that compared local versus exotic pigs in Benin and showed the latter weaned more piglets (Dotché et al., 2020a). Crossbred pigs weaned around three piglets more than local pigs in a study in India (Nath et al., 2013).

Table 25. Least square means for TNW for the interaction between ME and geographic location and ME.

ME	Geographic location	LS mean	SE
Low	Hoima	7.39[a]	0.98
	Kamuli	4.10[b]	0.96
Medium	Hoima	7.13[a]	1.20
	Kamuli	6.74[a]	1.24
High	Hoima	10.41[a]	1.55
	Kamuli	5.94[b]	0.54

[a,b]LS means with different superscripts in each ME category are significantly different

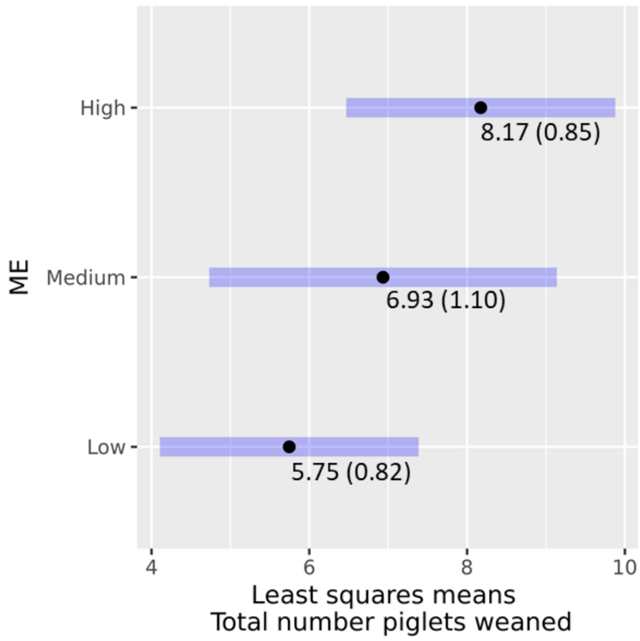

Figure 16. Effects of ME classes on TNW, least square means (standard error) and their 95% confidence intervals

Conclusion

Genetic and environmental factors influence phenotypes. In this study, we analyzed the effects of genetic ancestry of smallholder pigs in Uganda on growth and litter size traits. The variation in ancestry levels was limited, with none of the animals having more than 50% Modern European (Large White and Landrace) ancestry. The growth rates of pigs were extremely low, close to 55g per day for an age range from seven to 210 days. Further, while ME was not a significant effect on growth, growth was significantly affected by housing system. These findings underscore the role of appropriate management interventions for improved growth performance. Sow reproductive performance was influenced by parity for both TBA and TNW. Additionally, ME was a significant effect on TNW, such that sows with high ME ancestry weaned close to three piglets more than sows with low ME ancestry. These findings underscore the role of genetic improvement and appropriate management for improved litter sizes.

Author contributions

KM and JS conceived and designed the study. JS, KM, BL and EO provided technical, administrative, and logistic oversight. BM oversaw the field work and prepared the data for analysis. BM and JS analyzed the data. BM wrote the manuscript. All authors reviewed and accepted the manuscript for submission.

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Conflict of interest statement

The authors declare they have no conflicts of interest.

Chapter 7 General discussion and conclusions

Globally, pork is one of the most consumed animal source foods and therefore, a key contributor to food security (OECD, 2021). Traditional (also known as backyard or smallholder) producers account for around 40% of global pig production (Robinson et al., 2011) of which majority are in developing countries where pigs play several socioeconomic roles (Xayalath et al., 2020; Banda and Tanganyika, 2021). The importance of pig production in Uganda is reflected by the national herd (third largest in Africa and largest in Eastern Africa) and per capita pork consumption (highest in Eastern Africa). The common breed types in Uganda are local, crossbred, or exotic pigs. Smallholder farmers in Uganda complain about the inferior performance of local pigs for growth and reproduction traits (Ouma et al., 2015). On the other hand, local pigs are preferred because they are adapted to the challenges typical of low-input systems (Mbuza, 1995). Most interventions in pig breeding have focused on distributing improved pigs, that is, crossbred and/ or exotic breeds (Ouma et al., 2015). However, few studies have compared the performance of pig breed types in Uganda (Walugembe et al., 2014b; Greve, 2015). Further, most farmers in Uganda don’t keep records (Ampaire and Rothschild, 2010; Muhanguzi et al., 2012; Nabikyu and Kugonza, 2016) making performance evaluation difficult. Performance evaluation requires knowledge of both genotype and phenotype and genomics offers the opportunity to perform such analyses (Al Kalaldeh et al., 2021). Therefore, the aim of this thesis was to harness genomics as a decision support tool in smallholder pig production in Uganda. The objectives of this thesis were to 1) characterize the pig breeding practices of the farmers, 2) investigate the role of gender in trait and breed preferences of the farmers, 3) determine the breed composition of pigs kept by the farmers and 4) evaluate the performance of pigs kept by smallholders.

7.1. The production system

The production system was typical for smallholders with most farmers owning five or less acres (two or less hectares). Small herds with a median of three pigs under a mix of farrow-to-wean and farrow-to-finish systems (chapter 2) were observed, similar to what was reported in Vietnam (Lemke et al., 2006). In terms of herd dynamics, the small herd size may be attributed to death of animals from disease or sales (Dione et al., 2014). Events like African swine fever outbreaks trigger considerable herd size reduction through sales (Dione et al., 2014). The farmers usually restock their herds following losses (Lemke et al., 2006) through the purchase of piglets (Dione et al., 2017).

In terms of pig health, the common diseases and parasites were worms, fevers, diarrhea, and African swine fever (chapter 2). African swine fever is a highly fatal disease with a 77.5% fatality rate (Dione et al., 2014). Diarrhea is prevalent on smallholder farms in Uganda (Dione et al., 2014; Gertzell, 2020) and other tropical countries e.g., Philippines (Barnes et al., 2020), Kenya (Nganga et al., 2008) and South Africa (Munzhelele et al., 2017). Diarrhea leads to death or emaciation in piglets and growers (Gertzell, 2020). Deworming pigs has a positive effect on average daily gain (Kumaresan et al., 2009). Most farmers (>80%) relied on veterinarians for animal health care (chapter 2) and the most used veterinary inputs are anthelminthics (Dione et al., 2014; Kouam et al., 2018).

Most farmers used different crop residues to constitute feed rations (home mixed rations) for the pigs (chapter 2) similar to the situation in Kenya (Mbuthia et al., 2015b). The ingredients used by most farmers included maize bran, rice bran, sweet potato vines, cassava, swill and weeds (chapter 2) as previously reported in Uganda (Ouma et al., 2015). The brans (cereal residues) were purchased while the other ingredients were obtained from the farm (chapter 2) similar to elsewhere in Uganda (Pezo et al., 2014). Cereal-based commercial feed is hardly used by smallholder farmers in Sub-Saharan Africa because they are expensive (Githiga, 2013; Smale et al., 2013; Kanengoni et al., 2015). The nutrient composition of the feed varies with geographic location and this influences the ability for particular feed rations to meet the daily requirements of the pigs (Muthui et al., 2019). Further, seasonal availability of feed ingredients has implications for appropriate ration formulation (Carter et al., 2015). Feeding pigs on unbalanced feed rations affects growth and reproductive performance especially when crude protein levels are low (Kim et al., 2007; Carter et al., 2013; Gloaguen et al., 2014).

Pig housing (pigsty) was provided by few farmers (30%) (chapter 2) as most opt to tether their pigs (Kagira et al., 2010; Dione et al., 2014). However, pigsties may also be provided by higher percentages (98-100%) of smallholder farmers in Uganda (Muhanguzi et al., 2012) and Vietnam (Lemke et al., 2006). Smallholder farmers use locally available construction materials including cement, earth and wood (chapter 2) or wood/ bamboo (Lemke et al., 2006; Ahmed et al., 2017). Tethering is an outdoor system that predisposes the pigs to worm infestation (Tomass et al., 2013; Mbuthia et al., 2015b) and diseases like African swine fever (Dione et al., 2014) with negative effects on productivity (Stewart and Hoyt, 2006; Jenkins, 2007). Housed pigs are also affected by internal parasites particularly where worm control programs are irregular and general hygiene wanting (Kagira et al., 2017) as is the case in Uganda (Ouma et al., 2015).

Most farmers practiced a mix of farrow-to-wean and farrow-to-finish (chapter 2 and 3) while in Kenya, farmers were found to practice farrow to wean, porker to finisher, and a mix of these (Kagira et al., 2010). The pigs were kept for savings/ insurance and income from live animal sales (chapter 4) as reported in Kenya (Mbuthia et al., 2015b). The main pig products sold by the households were animals for breeding, fattening or slaughter with the latter being bought by traders (chapter 2). Smallholder farmers produce breeding, fattening and slaughter pigs (Tatwangire, 2014; Ouma et al., 2017).Traders will buy slaughter pigs from farmers in several villages and may play an important role in the spread of ASF (Lichoti et al., 2017).

7.2. Pig breeding

The genotype of an animal contributes to its overall performance. The breed types kept by most farmers were local and crossbred. Breeding animals were selected from among those born in the herds and/ or purchased from other smallholder farmers (chapter 3). Albeit only around 25% of the farmers had tried to improve their herds through selective breeding (chapter 2). Small herds offer limited choice when selecting candidates and practices like castration of male animals to control breeding (Nath et al., 2013; Dione et al., 2014) make the choice base narrower. Inaccessibility and unavailability of breeding animals are important constraints to genetic improvement of these smallholder pig herds (chapter 2). The costs of maintaining breeding animals are prohibitive and therefore, only a few farmers keep them (Dione et al., 2014; Lichoti et al., 2016). Breeding animals purchased from other farmers are an important source of replacement stock (Lemke et al., 2006). These transactions are based on friend- and/ or kinships that are often within the village (Lichoti et al., 2016). Most of the farmers were aware of sources of breeding animals within the village or in a village within their district (Chapter 3). The small herds make it uneconomical to keep boars (Wabacha et al., 2004a) and therefore, most farmers with sows used the village boar service (chapter 3). Smallholder farmers usually pay for boar service in-kind (piglet) when the sow farrows (Dione et al., 2014). Pig artificial insemination was not used by any of the farmers (chapter 3) and while few centers provide the service (Makerere University, 2017), it is generally unavailable in Uganda (Worsley, 2013). Artificial insemination has the advantages of disseminating desired germplasm and reducing the risk of disease transmission between farms (Morrell, 2011). Artificial insemination (AI) in pigs has been implemented in other developing countries like India to address challenges of boar unavailability and improve grower and sow performance

(Kadirvel et al., 2013; Singh and Mollier, 2020). However, AI should be supported by a breeding program that strategically involves the community of pig farmers (Wurzinger et al., 2011). The farmers in the study area preferred exotic over crossbred over local (chapter 4) even though most kept either local or crossbred animals (chapters 2 and 3). Further, the traits important to these farmers were related to growth, disease resistance and reproduction (chapter 4). The smallholder farmers represent most of the producers and end users of the pigs in the smallholder value chain (chapter 2). These farmer-to-farmer linkages could form the reticulum for a community-based breeding program. However, pigs in Uganda are poorly characterized which is why we conducted a genomic characterization and evaluation of the herds (chapters 5 and 6).

As indicated in the previous paragraph, few farmers keep boars and rely on village boar service. Therefore, it is the responsibility of the farmers to detect heat in sows/ gilts. Most of the farmers were conversant with heat detection by observing for vulva changes (chapter 3). Training the farmers in other heat detection methods such standing heat would reduce the risk of missed heat considering that poor heat detection has been reported as one of the reproductive management challenges faced by farmers elsewhere in Uganda (Gertzell et al., 2021). Accurate heat detection is important because it reduces the incidence of poor sow reproductive performance manifested by low levels of farrowing and small litter size (chapter 2 and 3). The number of piglets weaned per sow per year is a good index of sow reproductive performance (Dial, 1992). The farmers complained about delayed return to estrus postweaning (chapter 3) which has multifactorial origin including poor heat detection. However, the small number of farmers that reported repeat breeding as a sow reproductive problem (chapter 3) supports the hypothesis that the farmers are conversant with heat detection. Sows in smallholder pig herds have been reported to have long farrowing-to-weaning and inter-farrowing intervals (Lañada et al., 1999; Wabacha et al., 2004b) which could delay return to estrus. While record keeping is important for breeding and general management of the pigs, very few farmers in the study kept records or identified their animals (chapter 3). Practicing record keeping and accurate heat detection was found to improve inter-farrowing intervals in pigs (Lañada et al., 1999).

7.3. Genomic characterization and evaluation

The performance (phenotype) of an animal is determined by both the genotype and environment. The origin of pigs in Africa is enshrouded in mystery given that no domestication event occurred there (Blench, 2000) and the pigs are poorly characterized (Amills et al., 2013). Nevertheless, it is common to refer to pigs in Africa as indigenous (local), crossbred or exotic

(Blench, 2000). The history of pigs in Uganda dates to the colonial era when breeds like Large White, Large Black and Berkshire were introduced (Montgomery, 1921; Prosser, 1936; UGANDA, 1940). The national pig herd has since then grown from a few tens of thousands in 1961 to over four million animals in 2019 (UBOS, 2020; FAOSTAT, 2021). While reference is made to indigenous pigs in Uganda (Mbuza, 1995; Ssewannyana and Mukasa, 2004), their origin remains unclear. Such references are also common for pigs in other parts of Africa (Adebambo and Dettmers, 1982; Ncube et al., 2003; Abdul-Rahman et al., 2016). Recent studies based on molecular markers pointed to European and Asian ancestries for African pigs (Ramirez et al., 2009; Mujibi et al., 2018) and in the case of Uganda, Indian ancestry as well (Noce et al., 2015). These results concur with historical accounts of the Indian Ocean Trade and colonial eras. Our results (chapter 5) showed that the ancestry of the pigs was predominantly a mix of Modern European (Large White and Landrace) and Old British (Saddleback and Large Black) breeds. Small signatures of Duroc, Chinese and Iberian breeds were detected in the ancestry of the pigs. The Chinese ancestry was most likely through introgression given that Modern European breeds were developed using Chinese pigs (Larson et al., 2005; Ramirez et al., 2009). It was surprising that the Modern European ancestry of the pigs hardly exceeded 50%, implying no pure exotic pigs in the smallholder herds. Further, the level of inbreeding based on runs of homozygosity (ROH) in the pigs was very low (average F_{ROH}=0.043) (Chapter 6). This low F_{ROH} was surprising because it is often assumed that smallholder pigs are inbred due to mating of close relatives (Ssewannyana and Mukasa, 2004; Worsley, 2013; Tatwangire, 2014). This might be expected considering the small herds, few farmers that keep boars and those who provide boar service (chapter 2). The observed low levels of inbreeding can be explained by different scenarios. Outbreaks of diseases of high mortality rate like African swine fever will reduce the herd size if not wipe out the entire herd (Dione et al., 2014; Chenais et al., 2017). Given that farmers source pigs through village-level farmer-to-farmer linkages (chapter 2; Lichoti et al., 2016), such an outbreak within the village would require them to source replacement stock outside the village leading to herds with unrelated individuals. Boar service providers also source for pigs through village-level networks and will look for replacement stock outside the village (Lichoti et al., 2016). Most farmers with sows produce piglets for use as breeding animals or fatteners and these are usually sold to other farmers (chapter 2 and 3). This lowers the chance of mating between parents and offspring or between siblings.

Performance evaluation of smallholder pigs in developing countries like Uganda is difficult because no breeding structures exist. Further, animal identification and record keeping are hardly practiced by the smallholder farmers (chapter 3; Muhanguzi et al., 2012). Having determined the breed composition of pigs in these smallholder herds (chapter 5), we incorporated longitudinal phenotype data collected on the animals in a genomic evaluation of grower and sow performance (chapter 6). Cognizant of the trait preferences of the farmers (chapter 4) we assessed growers on their body weight (WT) and sows on litter size at farrowing and weaning. We were interested in testing the effect of proportion of Modern European ancestry (ME; chapter 5) because Large White and Landrace have been bred for superior performance in the traits under study. Although higher ME proportions were associated with better performance, ME was not a significant effect on WT and total number of piglets born alive (TBA). However, ME was a significant effect on total number of piglets weaned (TNW) and higher ME levels were associated with higher TNW values.

7.4. Concluding remarks and future research perspectives

This doctoral thesis has attempted to tell the pig breeding story of smallholder farmers in Uganda using genomics. The absence of animals with more than 50% ME ancestry is an important finding considering the breed preferences of the farmers (exotic > crossbred > local). Given the challenges in the production system e.g., African swine fever, these breed proportions are more likely a consequence of natural rather than artificial selection. Another important finding are the low levels of inbreeding of the pigs. While we have attempted to explain this occurrence, its etiology remains largely unclear. Studies that focus on the gene flow in these herds (within and between villages) could provide more insight into the underlying mechanisms. We expected significant effects of ME on all three traits. Our results could be influenced by the small sample size of genotyped animals and other factors. Overall, this study demonstrated the potential of genomics to support livestock breeding and conservation programs in smallholder systems in developing countries. However, while the ever-reducing genotyping costs point to a bright future, phenotyping costs remain high and require institutional reinforcement. Development of low-cost phenotyping tools and their implementation in a structured way will go a long way in ensuring appropriate management of livestock genetic resources in developing countries.

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