Conservation genetics of traditional and commercial pig breeds, and evaluation of their crossbreeding potential for productivity improvement

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Abstract

The Food and Agriculture Organization have emphasised the importance of farm animal genetic diversity for the assurance of future global food security. Modern pig production has concentrated on a small number of commercialised breeds. This has significantly contributed to genetic erosion and loss of native breeds, deemed productively inefficient. It has been recommended to conserve the unique traits of traditional breeds as genetic insurance against future challenges. In order to ascertain the commercial viability of traditional breeds, genetic and productivity analyses were completed, using the Large White (LW) and Landrace (LR) as the commercial comparison.

Genetic diversity was assessed using a D-loop fragment of mitochondrial DNA for comparison between three purebred traditional breeds: Gloucester Old Spot (GOS), British Lop (BL) and Welsh (W), and commercial LW x LR. The traditional breeds greatly differed from the commercial hybrid, and possessed high variability at this genetic region. The BL and W demonstrated the greatest potential for crossbreeding to increase the diversity of commercial populations.

The crossing of LW x LR dams with GOS, BL and W terminal sires produced traditional crossbreds for comparison with LW sired crossbreds. Nuclear DNA diversity was assessed using a region of the iodothyronine deiodinase type 3 (DIO3) gene. This demonstrated that crossbreeding could improve future productivity, by utilising traditional variation to maximise heterozygosity in the progeny. The productivity assessment established that the traditional and commercial crossbreds performed comparably for most of the growth variables measured, however there were highly significant differences for birth weight, weaning weight, back fat and production length. The traditional crossbreds have shown potential for future application, with the W most suited for commercial production, due to the equivalence with the LW.

To conclude, the crossbreeding of traditional and commercial pig breeds is a viable genetic management strategy to conserve and genetically improve both groups.

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Abbreviations

ADG – average daily gain

AHDB – Agriculture and Horticulture Development Board

BL – British Lop

BL F_1 – British Lop crosses

BLPS – British Lop Pig Society

BLR – British Landrace

BLW – British Large White

BPA – British Pig Association

BPEX – British Pig Executive

DEFRA – Department for Food, Environment and Rural Affairs

DIO3 – Iodothyronine deiodinase type 3

EAAP - European Association of Animal Production

EUC – European Union Commission

F_1 – First generation

F_2 – Second generation

FAnGR – Farm animal genetic resources

FAO – Food and Agriculture Organization

GOS – Gloucester Old Spot

GOS F_1 – Gloucester Old Spot crosses

GOSPBC – Gloucester Old Spot Pig Breeders Club

IGF2 – insulin-like growth factor 2

ILRI – International Livestock Research Institute

LW – Large White

LW F_1 – Large White x Landrace crosses

LR – Landrace

LWLR – Large White x Landrace sows

LW x LR – Large White and Landrace hybrid

MS – Meishan

mtDNA – Mitochondrial DNA

NBA – number of piglets born alive

NGO – National Government Organisation

PWPS – The Pedigree Welsh Pig Society

PWSY – pigs weaned per sow per year

RBST – Rare Breed Survival Trust

W – Welsh

W F_1 – Welsh crosses

Chapter 1. Introduction

1.1. Global Food Security

During the last decades, the maintenance and management of genetic diversity within and between populations of domesticated livestock (Ligda and Zjalic, 2011), has become of foremost prominence for the economic and sustainable development of global agriculture (Food and Agriculture Organization (FAO), 2011a). At present, livestock production alone accounts for 43% of the world's total agricultural output (Hoffmann, 2011), which provides a diverse range of functional resources and serves as monetary assets, to safeguard the existence, well-being and livelihoods of humanity (Anderson, 2003). Correspondingly, the present global crisis being encountered by the human population is the future challenge of unstable food production (Cardellino, 2009), potentially resultant in the insecure availability, inappropriate utilisation and inaccessibility to safe, nutritive and affordable produce (Ruane and Sonnino, 2011). There has been an evident dramatic increase in the universal requirement for consumable livestock products (Mäki-Tanila and Hiemstra, 2010), distinctly concurrent with rapid growth throughout the world population, from the current 7 billion inhabitants to over 9 billion by the year 2050 (Thornton, 2010; Foresight, 2011).

There are numerous contributory drivers influencing the consumption trends of products derived from livestock (Haddad, 2005), specifically the changing dynamics of socio-economic development within different regions and countries of the developing world (Ruane and Sonnino, 2011). The impending stabilisation and predicted rise of income levels for impecunious inhabitants (Nonhebel and Kastner, 2011), has been indirectly initiated by strong economic growth across developing countries (Pilling, 2010), with predicted expansion at twice the rate of industrialised countries (Kearney, 2010). This has significantly impacted the migration flows of populations in poverty stricken areas, with a rapidly evident transition from rural to urban environments (de Janvry and Sadoulet, 2010), attributable to the prospect of employment and alternative income-earning opportunities (Satterthwaite *et al.,* 2010).

The universal demand for affluent agricultural produce, primarily consumable products of animal origin: meat and dairy (Nonhebel and Kastner, 2011), has driven the increased globalisation of international food systems (Senauer and Venturini, 2005), thus facilitating the creation of innovative opportunities in world agricultural trade for undeveloped countries (Woolverton *et al.,* 2010). The improved accessibility of smallholder producers to broader retail markets, worldwide distributors and foreign investors (Otte *et al.,* 2012), is permitting developing countries to become an integral component of the global export trade (Perry *et al.,* 2005; Chander *et al.,* 2011), owing to the specialised local production of premium agricultural products (McDermott *et al.,* 2010).

However, the rapid transference to urbanised living has had a profound effect on the composition of the diet (Msangi and Rosegrant, 2012), with a considerable nutritional transition from traditional, simplified diets of grains and vegetable staples (Ruel *et al.,* 2008), to the cumulative intake of varying luxurious animal-source products, vegetable oils and sugar-based foods (Popkin, 2006). This dietary modification and diversification is a result of the present global supply capabilities, extensive accessibility and lower domestic prices of food (Kearney, 2010), with an increasing reliance upon abundant importations from industrialised nations for affluent goods (Reilly and Willenbockel, 2010).

1.1.1. Intensification of Livestock Production

In order to accommodate for the production requirement to supply vast quantities of inexpensive animal-source produce worldwide (Merks *et al.,* 2012), the agricultural industries of further developed countries decided to enhance the level of food production output (Gerber *et al.,* 2010), through the progressive intensification and standardisation of the primary meat-producing livestock systems: bovine, ovine, swine and avian (Fraser, 2005). This has been attainable from the implementation of revolutionary management technologies, to minimise labour input and enhance reproductive efficiency (Gillespie and Flanders, 2010), and the worldwide dissemination of significantly improved livestock genetic material (Flint and Woolliams, 2008).

The remarkable achievement of increased output in commercialised meat, milk and egg production (Thornton, 2010), has been attributable to the selective genetic improvement and intensive utilisation of a diminutive minority of productively efficient, international transboundary breeds (Vicente *et al.,* 2008). Evidently, industrial livestock production functions as a significant contributor to world food supply, accounting for an estimated 63%, 79% and 10% of global pork, poultry meat and beef and mutton production (Hoffmann, 2011; FAO, 2012a). There is a higher demand of meat products from monogastric species (swine, poultry) (Costa *et al.,* 2010), and a prompt response to fulfil supply, owing to the growth in production output, rapidly escalating in comparison with that of ruminant species (cattle, goats, sheep) (Steinfield and Gerber, 2010).

1.2. The State of the World's Farm Animal Genetic Resources (FAnGr)

The growing demand for productively efficient genotypes, mainly in developed countries with modernised production systems (Valle Zárate *et al.,* 2006), has been facilitated by the ease of which contemporary livestock genetic resources can be globally exchanged (Hiemstra *et al.,* 2006), through various innovative, reproductive, biotechnological methods (Flint and Woolliams, 2008). However, the international exportation of commercial livestock genetic material is dominated by industrialised countries of the European Union (EU) and the United States of America, characterised by advanced breed development (Fujisaka *et al.,* 2011), and as of recently intensive gene trade flows have mainly occurred among northern countries (North-North) (Blackburn and Gollin, 2009; Blackburn, 2012).

The global reliance upon a significantly limited number of high-yielding breeds and lines (Williams, 2005), and the selective interchange of FAnGR (Biber-Klemm and Temmerman, 2011), has adversely contributed to recurring, irreversible erosion of genetic diversity in domestic livestock species (Simianer *et al.,* 2003; Groeneveld *et al.,* 2010). It has been reported that from the 6400 recognised farm animal species, an estimated 1000 have become inexistent within the last 100 years (Ramesha, 2011), with a further 21% of the world's livestock threatened with the risk of non-existence (McGowan, 2010),

conforming with the present degree of extinction, which is progressing at a rate of 1-2% breeds per year (Simianer, 2005).

1.2.1. Importance of Indigenous FAnGR

It is approximated that two-thirds of the worlds' livestock are located within developing countries (Nesamvuni *et al.,* 2010), which accounts for a considerable proportion of indispensable animal genetic resources (Hunlun and Ramsay, 2010). This is supported by Figure 1, which depicts that the highest concentrations of pigs are located in China and other Eastern Pacific countries, with several African countries (Uganda, Burkina Faso, Ghana, Nigeria, Togo), Central America and Brazil also having significant densities (Robinson *et al.,* 2014). Since the early 1970s, pig populations in developing countries have been increasing by 10% per year, which Forsberg *et al.,* (2005) attributed to the introduction of exotic breeds to improve the performance of indigenous pigs. For example, in Papua New Guinea, the pig population is estimated at 1.8 million; 1 million are indigenous, 0.8 million are exotic and their crossbreds, the growth of intensive commercial production and exotic x indigenous crossbreeding is threatening the survival of purebred indigenous pigs (Ayalew *et al.,* 2011). Similarly, in Bhutan, although 68% of the total pig population are indigenous, breeds are being faced with extinction, due to a fivefold population loss in the last two decades and numbers of exotic and composite breeds steadily increasing to improve pig production (Nidup *et al.,* 2011). It is projected that by 2030, the number of pigs in developing countries will have reached 761 million, accounting for 72% of the global total for meat production (FAO, 2003). These figures highlight the significance of developing countries towards global food security, but also the importance of maintaining pig genetic diversity for future production.

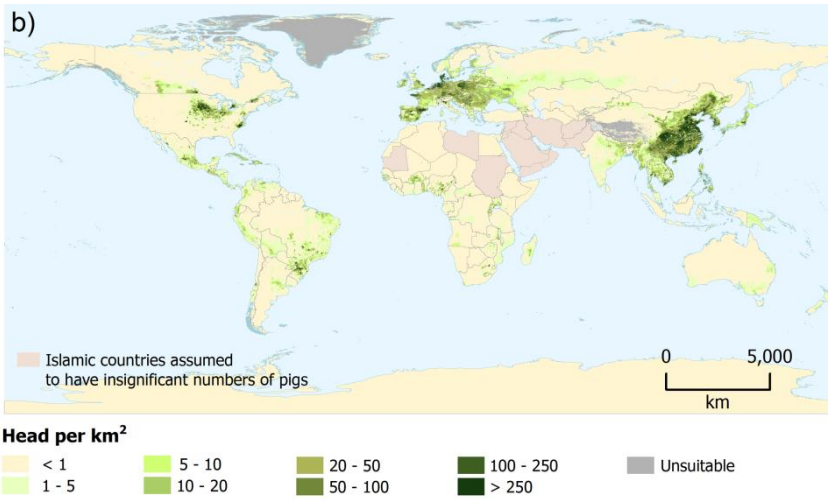

Figure 1. Global distribution of pigs (Robinson *et al.,* 2014).

Indigenous livestock play a vital role in supporting the livelihood maintenance of an estimated one billion inhabitants, those of which reside in the poorest countries throughout the developing world (Smith *et al.,* 2013). In rural communities, the keeping of livestock by smallholder producers is a customary practice to fulfil multiple livelihood functions (Madzimure *et al.,* 2010), mostly associated with socio-economic factors and socio-cultural values (Ngowi *et al.,* 2008). A sizeable proportion of the worlds' poorest people own some form of livestock, primarily for the benefit of non-income household commodities (Anderson, 2003), delivering not only food for home consumption (Chimonyo *et al.,* 2005), but the provision of non-food materials (wool, hides and skins), agricultural traction, waste by-products for crop production and a means of transportation (Anderson and Centonze, 2007; Ruane and Sonnino, 2011).

However, the rearing of livestock as a source of regular monetary income (Millar and Photakoun, 2008), obtained wholly from the sales of live animals, marketing food products or the lease of draught power services (Alary, 2011), operates as a critical component of employment generation and financial stability for the families of smallholder producers (Scarpa *et al.,* 2003). Numerous households also maintain small populations of various livestock species, purely to serve as a method of wealth accumulation and financial security (Randolph *et al.,* 2007), in the form of savings and insurance (Marshall *et al.,* 2011).

Livestock are regarded as valuable capital assets, which can be traded to significantly lessen the incidence of poverty within vulnerable communities (Perry and Grace, 2009).

In some regions and countries, livestock are not merely valued in terms of their monetary worth (Ashley and Nanyeenya, 2005), but for the creditable social status attained, denoted by the number, type and phenotypic characteristics of the species kept (Anderson, 2003). For example, in developing African countries, the ownership of large ruminants, primarily cattle, serves as respectable symbols of wealth, authority and cultural identity (Barnes *et al.,* 2012). Furthermore, the cultural values attached to livestock vary considerably in different parts of the world (FAO, 2007), whereas certain societies are traditionally bound to preserve specific breeding stock, customarily the superior males, until natural death (Anderson and Centonze, 2007), other communities present livestock as a gift for ceremonial events, and offer an animal for sacrificial purposes during religious rituals (Bettencourt *et al.,* 2013).

1.2.2. Threats to Indigenous FAnGr

The continual progression of international socio-economic dynamics: population growth, urbanisation, economic development and globalisation (Rege *et al.,* 2011), is rapidly revolutionising traditional smallholder production in developing countries, towards the application of standardised, industrial livestock systems, for the enhancement of animal-sourced food output (Simianer, 2005; Udo *et al.,* 2011). In order to achieve vast improvements in animal productivity, smallholder producers are focusing largely on the importation of high yielding, exotic livestock (Chimonyo *et al.,* 2005), which corresponds with the progressive global transfer from multi-purpose local to specialised international breeds (Tisdell, 2003), attributable to the perceived genetic superiority for performance-related traits (FAO, 2007). It has been identified that numerous governmental policies, from various food-deficit countries, favour the transition to intensive production systems and are endorsing the restricted utilisation of livestock genetic resources (Drucker *et al.,* 2001; Hoffmann, 2010a), as a faster means of increasing productive output for foods of animal origin, to secure the equilibrium between availability, accessibility and human need (Ruane and Sonnino, 2011).

Recent trends denote that a significant proportion of the global trade in contemporary livestock genetic material, has become dominated by the acceleration of gene flow transfer from developed to developing countries (North to South) (Gollin *et al.,* 2009; Hoffmann, 2010b). In consequence of this, local livestock species are being wholly substituted for non-native conventional breeds, which adversely endanger the survivability and/or elicit the irreversible loss of indigenous populations (Ajmone-Marsan, 2010).

However, some imported, exotic breeds lack the adaptive characteristics to cope with the local environmental stressors: climate, disease and dietary constraints, associated with harsh, tropical conditions (Mirkena *et al.,* 2010), which are commonly resultant in reproductive failures and low birth rates, deficiencies in productive performance and severely reduced survivability (Chimonyo *et al.,* 2005). Regardless of the abundant efforts to introduce and establish the utilisation of non-native breeds, it is well documented that the direct replacement of indigenous livestock has been invariably ineffective in several undeveloped countries (Philipsson *et al.,* 2011a), on account of the insufficient environmental adaptation, unsustainable importation and the unsuitability of the selected improved breeds to local production systems (Assan, 2013a).

1.2.3. Characteristics of Indigenous Livestock

Indigenous livestock possess the critical attributes of hardiness and adaptability (behavioural, physiological and morphological) to local environmental extremes (Chimonyo *et al.,* 2005), which facilitate the capacity to maintain survival, reproduce and thrive within resource-deprived systems (FAO, 2010), from the unique innate abilities of heat and nutritional tolerance and parasite, disease and stress resistance (Scarpa *et al.,* 2003). Haile *et al.,* (2011) have stated that the present selection and breeding strategies, to genetically improve the adaptive traits and productive viability of high-yielding exotic breeds, for practical application within developing countries, is not simultaneous with the continual climatic and environmental variations occurring worldwide. Therefore, it is imperative to conserve indigenous breed populations, in order to preserve and optimally utilise their unique adaptive qualities

(Barker, 2007), for probable incorporation within future exotic and native livestock breeding programmes. Indigenous breeds can be used as a form of genetic insurance against expected global modifications of production systems and environmental challenges (Thornton, 2010).

1.2.4. Crossbreeding for Genetic Improvement or Reducing Genetic Diversity?

On the other hand, it has been advocated that, as a consequence of the global food crisis, smallholder producers in undeveloped countries, should solely be concentrating their efforts on the genetic improvement of indigenous livestock (Assan, 2013b), in terms of enhancing the performance efficiency and productive output of the breeds reared (Bondoc *et al.,* 2010). To address this, numerous developing countries have been extensively implementing the crossbreeding of native and exotic breeds (Köhler-Rollefson *et al.,* 2009). In terms of pigs, mostly European pig breeds have been imported: Large White, Landrace, Hampshire, Duroc and Tamworth, for crossbreeding with indigenous pigs (FAO, 2009). Okoro and Mbajiorgu (2017) identified that crossbreeding indigenous Nigerian pigs with the Large White and Landrace, enhanced growth and conformation traits, as well as environmental adaptability in the crossbred progeny. Thus demonstrating the positive heterosis effect from the combination of resilience and fitness (indigenous) and production efficiency (exotic) (Leroy *et al.,* 2015). Hence, in some developing countries, crossbred livestock have become highly favourable in comparison to the original populations, owing to the improvement of progeny performance (Shrestha, 2005). However, it has been identified that the survival of purebred indigenous breeds can be reduced further, by the threat of complete replacement with exotic and native crossbreds (Anderson, 2003).

Furthermore, although crossbred livestock may demonstrate improved productive performance, the continuous upgrading of indigenous populations, through crossbreeding with exotic genotypes, has largely contributed to the genetic dilution of native animal germplasm, resultant in the progressive eradication of original breed adaptive attributes (Long, 2009; Berthouly-Salazar *et al.,* 2012). This has resulted in crossbred populations with heightened susceptibility to disease, impaired tolerance to climatic variations and incapability to thrive under severe nutritional stress (Mandakmale and

Kamble, 2005). An example of this lack of adaptation by the crossbreds, has been demonstrated in South Asian and West African countries, specifically Bangladesh and Nigeria (Madalena *et al.,* 2002), whereby traditional Zebu cattle have been crossed with the prevailing exotic dairy: Friesian, Holstein and Jersey, and beef breeds: Brahman, Hereford, Charolais and Simmental, with limited or negative sustained success (Jabbar *et al.,* 2010).

The forthcoming selection of exotic livestock, to be imported for indigenous crossbreeding programmes, should concentrate on appropriately matching suitable conventional genotypes to specific production systems and environments. This would optimise production efficiency, by improving environmental adaptability, therefore ensuring the prospective sustainability of utilising international breeds within developing countries.

1.3. Sustainability of Livestock Production

1.3.1. Intensification of Smallholder Agriculture

The gradual transformation towards sustainable intensification within smallholder systems, forms an integral component of the solution towards addressing global food security (McDermott *et al.,* 2010), from the recognition of which small-scale farmers contribute significantly to world food sufficiency, as they produce a substantial quantity of the food consumed in developing and emerging countries (United Nations Environment Programme, 2013). It has been identified that the prevailing mixed crop-livestock smallholder farming systems, produce the largest share of total global meat, 54%, and milk production, 90%, which demonstrates the crucial importance of safeguarding the future of developing country smallholder agriculture (Herrero *et al.,* 2009; Gerbens-Leenes *et al.,* 2013).

1.3.2. Conservation of FAnGr: FAO

The improvement of food production derived from livestock is not feasible without the conservation of FAnGR and their indispensable characteristics and traits (Wollny, 2003), owing to the notion of which a genetically diverse resource base is essential for the assurance of world food security (Philipsson *et al.,* 2011b). This concept was instigated by a report produced by the FAO: *The State of the World's Animal*

Genetic Resources for Food and Agriculture, following a global assessment of the roles, values, status and trends of FAnGR, which highlighted the importance of the livestock sector for food and livelihood security, the threats to genetic diversity and the capacity of countries to manage resources (FAO, 2007; Hoffmann *et al.,* 2011).

As a response to the report outcomes, the FAO developed the *Global Plan of Action for Animal Genetic Resources*, an internationally agreed strategic framework, adopted by 109 countries and implemented by national governments, for the sustainable use, development and conservation of livestock genetic resources utilised for food and agriculture (FAO, 2011). It has been identified that the conservation of indigenous livestock genetic resources is one of the vital foundations for ensuring sustainable agriculture and global food security, now and in the future (Sundar, 2011). Thus, it was stated by the FAO that increased attention and support was to be given to the sustainable use and development of indigenous breeds, particularly in local production systems of developing countries (FAO, 2007).

In 2015, *The Second Report on the State of the World's Animal Genetic Resources for Food and Agriculture* was published, serving as an update of the first report and focusing on the developments made since 2007 (FAO, 2015a). In brief, the report advised that genetic diversity remains under threat, with almost 100 of the world's livestock breeds becoming extinct between 2000 and 2014, a further 17% classified as at risk of extinction and 58% are of unknown risk status (FAO, 2016). The assessment of threats to FAnGr identified that the top two reported issues are indiscriminate crossbreeding and the introduction/increased use of exotic breeds: direct replacement of indigenous breeds (Paiva *et al.,* 2016). However, many countries have reported improved management of their FAnGr, through the implementation of national strategies and action plans: breeding programmes, animal identification, registration schemes, and the establishment of *in vitro* gene banks. Yet, progress is slow in some developing countries due to lack of financial resources, genetic improvement programmes and organisational structure to plan and implement breeding activities. The strategic priorities moving

forward heavily focus on: improving knowledge, strengthening the management of FAnGr and further development of breeding and conservation programmes (FAO, 2015a).

1.3.3. Conservation Programmes for Indigenous FAnGr

It has been established that conservation programmes and *in situ* and *ex situ* activities for indigenous FAnGR differ greatly worldwide (FAO, 2011), dependent upon the country, species of livestock and the stakeholders and organisations involved (Lauvie *et al.,* 2011). For example, all countries of the European Region have made significant progress, both individually and collaboratively, by employing national plans for the conservation of FAnGR (Ligda and Zjalic, 2011), which comprise of inventories, breeding schemes, cryopreservation activities and management strategies (Mäki-Tanila and Hiemstra, 2010). On the other hand, African countries remain lagging behind in terms of designing and implementing conservation programmes, despite the importance of the valuable biodiversity of their indigenous livestock (FAO, 2012b). It has been identified that, in many developing countries, this is attributable to the lack of financial support and trained personnel and poor distribution of information and appropriate resources, which are required by farmers to address the management of their FAnGR (Hoffmann *et al.,* 2011). However, the differences in progress achieved by developed and developing countries is not unexpected, given the governmental priorities and economic circumstances of areas within the developing world.

1.3.4. Differences in Criteria Used To Assess Conservation Status

Yet, there is a lack of uniformity in the decision making process for livestock conservation between countries (Blench, 2005), with no universally recommended criteria to rationalise which breeds are to be given priority for conservation (Simianer, 2005). Although, an important factor which is often taken into consideration is the degree of endangerment (DE) of livestock breeds, defined as being a measure of the likelihood that, under current circumstances and expectations, the breed will become extinct within a specified time period (Gandini *et al.,* 2004). There are three general approaches to estimate DE in use by the FAO, EU, the European Association of Animal Production (EAAP) and National Government

Organisations (NGO) (Boettcher *et al.,* 2010). The first approach evaluates DE broadly by major factors proposed to affect breed extinction risk: population size (number of breeding females and males), distribution (number of herds and size of geographical range), cultural, social and ecological farming context (existence of conservation activities, inclusion of breeding programmes and threats to genetic diversity) (FAO, 2007; Alderson, 2010). The second approach estimates extinction probabilities by projecting population size with demographic models to different time horizons. The third approach, focuses on the expected loss of genetic variation, expressed as cumulated inbreeding within a given time horizon, measured in terms of effective population size and species generation interval (Boettcher *et al.,* 2010).

However, each organisation has developed their own system to classify livestock breeds as to their DE, using a combination of the approaches described above, and varying assessment criteria (McManus *et al.,* 2013). The FAO and EU systems primarily focus on breeding population size, specifically the numbers of male and female animals, with numerical categorisation corresponding to risk status: critical, endangered and not at risk (Bahmani *et al.,* 2011). Whereas the EAAP system is concerned with the genetic characterisation of breeds: critically endangered, endangered, minimally endangered, potentially endangered and normal, by estimating the increase of the inbreeding level over a period of 50 years (Simianer, 2005) (Table 1). The NGO's define risk status of a breed by a combined evaluation of the main factors mentioned above; however there are modifications of the assessment criteria across different countries (Alderson, 2009). There is no standardised system stating which fixed criteria need to be assessed to measure the DE of each livestock breed. The discrepancies in definition and measurement of DE cause difficulty and confusion when comparing FAnGR data between systems, as the categorisation of breeds are based upon different factors, which provide conflicting and potentially misleading results.

There are several authors which propose different criteria should be included in the decision making process of prioritising livestock breeds for conservation. Halimani *et al.,* (2010) and Narloch *et al.,* (2011)

state that priority should be assigned to breeds whom possess unique adaptive and/or productivity traits of economic value, which could be of potential future benefit. Whereas, Hanotte and Jianlin (2005) and Ginja *et al.,* (2013) recommend that the genetic characterisation of livestock breeds is the most significant factor to consider, with those populations which have the largest within-breed diversity, and/or greater genetic distances between breeds, being of greater value to maximise future genetic diversity. Furthermore, it is understood that it is not feasible to save all existing livestock breeds, owing to the limited availability of financial resources (Blasco, 2008), therefore it is imperative that a standardised framework is developed so as to optimally allocate conservation funding based upon the DE and contribution value of a breed (Simianer, 2005).

Table 1. Criteria of the main systems for evaluation of the degree of endangerment. Adapted from Gandini *et al.,* (2004)

Criteria	EU	EAAP	FAO
Census	All EU countries	Per country	Per country
Overall population size			×
Population trend	×	×	×
Number of breeding males			×
Number of breeding females	×		×
Effective population size		×	
Generation interval	×	×	
Other		×	

1.3.5. Funding for Conservation Programmes

In developed countries, conservation funding is managed by governments and stakeholders, with financial support being provided to farmers rearing indigenous livestock, as an economic incentive to maintain traditional breed populations (FAO, 2007). However, the EU policies state that payment is only to be provided for those breeds involved in agri-environmental schemes and/or are classified endangered by the stipulated population thresholds, based on number of breeding females (Kleijn and Sutherland, 2003). In addition, in some developed countries, conservation activities are also provided and supported by NGO's, breed societies and charities (Ligda and Zjalic, 2011). For example, in the

United Kingdom (UK), the Rare Breed Survival Trust (RBST) operate *in-situ* and *ex-situ* conservation projects, animal recording/monitoring and breed support grants, to ensure the future survivability and genetic preservation of rare native livestock breeds (Rare Breed Survival Trust (RBST), 2012a). However, farmers associations and breed societies are not a common occurrence in many developing countries (FAO, 2007).

1.3.6. Methods for Assessing Genetic Diversity

Toro *et al.,* (2011) stated that one of the first steps in planning a conservation or selection scheme, for a breed, is to assess the current state and predicted changes of genetic diversity. The census size of numbers of breeding males and females is usually the only information available for most endangered livestock, often used to estimate effective population size: the number of individuals that would result in the same loss of genetic diversity, inbreeding or genetic drift if they behaved in the manner of an idealised population (Frankham *et al.,* 2010). In addition to counting within breed, demographic data, geographical distribution, production environment and morphological characteristics, are fundamental in assessing the biological diversity of livestock breeds (Groeneveld *et al.,* 2010). However, the development of DNA technology has enabled the analysis of breed diversity using various nuclear and mitochondrial genetic markers (Toro *et al.,* 2011).

Microsatellites: tandem repeats of short DNA sequences, are one of the most frequently used markers for within and between breed genetic diversity studies, due to their abundance, high polymorphism levels and co-dominant nature (FAO, 2007). The most common parameters for assessing within-breed diversity are: the mean number of alleles per locus (MNA), the average and expected heterozygosity (H_o and H_e) and testing for deviations from Hardy-Weinberg equilibrium (HWE) (Sheriff and Alemayehu, 2018). Microsatellites have been used extensively in cattle, sheep, goat, poultry and pig diversity studies (Groeneveld *et al.,* 2010). In pigs, they are often used in studies to address the biodiversity and conservation of commercial, indigenous and rare breeds (Nidup and Moran, 2011). For example, Cortes *et al.,* (2016), used a panel of 24 microsatellites, as recommended for genetic diversity studies by the

FAO, to analyse 45 local and commercial breeds from the Iberian Peninsula, Europe and America, in order to evaluate conservation priorities based on either genetic diversity within breed, between breed or both. Although, single nucleotide polymorphisms (SNPs): a position in the DNA of a species at which two or more alternative bases occur at appreciable frequency (Frankham *et al.,* 2010), have become increasingly popular for diversity analysis, due to their stable inheritance, widespread distribution, abundance in the genome and amenableness to high throughput automated analysis (Selvam *et al.,* 2017). Selvam *et al.,* (2017) used SNP markers within the Toll-like receptor 3, 5, 6, 9 and 10 genes, to analyse the within breed genetic diversity of the Kilakarsal and Vembur sheep breeds, associated with modified cellular immune response and an altered susceptibility to disease. Although not as common a method as microsatellites or SNPs, protein-coding genes have been used to explore functional portions of the genome (Chen *et al.,* 2007), examine intra and inter-species phylogenetics (Groenen *et al.,* 2012), identify novel polymorphisms and their association with specific diseases (Uchida *et al.,* 2014), and to compare genetic diversity for production (Deng *et al.,* 2015) and behavioural traits in livestock species (Lourenco-Jaramillo *et al.,* 2012). In pigs, the genetic diversity studies of protein-coding genes have focused on those associated with morphological, meat production, disease resistance and reproductive traits (Muñoz *et al.,* 2018). For example, Yang *et al.,* (2013) analysed the coding sequence of the toll-like receptor 5 (TLR5) gene in Western commercial and Chinese local pig populations to explore the genetic variation present and the association with susceptibility/resistance to disease.

Mitochondrial DNA (mtDNA) is another widely used genetic marker for animal population studies (Nabholz *et al.,* 2008). MtDNA is a double stranded, circular, haploid molecule, located in the mitochondria: cellular organelles responsible for energy production of eukaryotic cells (Frankham *et al.,* 2010). It contains a non-coding control region, including the unique displacement loop (D-loop), which is known to accumulate mutations particularly rapidly (Freeland, 2005). MtDNA is characterised by: small size, conserved gene arrangement (Galtier *et al.,* 2009a), high mutation rate (Hellberg, 2006), lack of recombination and maternal inheritance (Boore, 1999). These characteristics make mtDNA markers ideal for revealing and comparing genetic lineages both within and among populations, identifying

mitochondrial lineages, reflecting demographic effects and reconstructing phylogenetic histories (Freeland, 2005; Ladoukakis and Zouros, 2017). This is supported by Groeneveld *et al.,* (2010) whose review of genetic diversity in farm animals revealed that mtDNA markers have been used to establish origins, reconstruct domestication and differentiate populations of cattle, sheep, goats, pigs and chickens. The mtDNA D-loop region has been used extensively to assess genetic diversity of pig populations on a global scale (Fang *et al.,* 2006; Zhang *et al.,* 2016; Gvozdanovic *et al.,* 2018). For example, Zhang *et al.,* (2018) examined sequence variation in the mtDNA D-loop between the indigenous Bamei pig, and commercial Duroc, Landrace and Large White, to establish the Bamei's genetic diversity and degree of introgression with modern breeds.

At the molecular level, the genetic composition of a population is typically described using the frequencies of genotypes and alleles, proportion of polymorphic loci, observed and expected heterozygosity and allelic diversity (Frankham *et al.,* 2010; Toro *et al.,* 2011). In addition to these measures, haplotype diversity, nucleotide diversity, neutrality tests and quantitative gene variation, are commonly used in conservation genetics studies (Högland, 2009). When comparing populations, the fixation index (F_{ST}) is a widely used measure to quantify the genetic differentiation within and among populations, based upon the variation in allele frequencies (Freeland, 2005).

The major traits of livestock are quantitative: growth, production, reproduction and efficiency, which vary greatly amongst individuals (Hill, 2014). Quantitative genetics is the study of this variation, which models the inheritance and evolution of continuous phenotypic traits (von Cramon-Taubadel, 2016). The methods used to detect quantitative genetic variation include: assessing variation within and amongst populations, comparing inbred with outbred populations and determining resemblances amongst relatives (Frankham *et al.,* 2010). Phenotypic variation results from the segregation of alleles at multiple quantitative trait loci (QTL) and the interaction effect with the environment (Mackay, 2001). This is measured as an individual's phenotypic value, which is partitioned into the amount of variation due to genetic factors, and that due to environmental factors (Toghiani, 2012). The genetic variance is further

partitioned into additive genetic (adaptive evolutionary potential), dominance (deviations), and interaction (effects of outbreeding), variance (Frankham *et al.,* 2010). Heritability describes the properties of inheritance of quantitative traits, defined as the proportion of phenotypic variation due to the additive genetic variance amongst individuals (Whittemore, 1998). The heritability of a trait can be estimated from parent-offspring regressions (comparing phenotypes), with a value closer to 1 meaning genotypic variance is high and environmental variance is low, and the opposite for a value closer to 0 (Freeland, 2005). The genetic change in a population depends upon trait heritability and superiority of parental generation, which relates to the amount of additive genetic variation available (Whittemore, 1998). The heritability estimates can be used to determine the genotypic variance of QTL's, within and between populations, as a result of natural selection and genetic drift (Freeland, 2005). Ojeda *et al.,* (2011) studied a region on chromosome 4, the first QTL identified in the pig, shown to affect fat deposition and growth, comparing Asian, European, Mediterranean and international breeds, to gain insight into the evolutionary history of the species.

The most direct means for measuring genetic diversity is to determine the exact order of the nucleotide bases, within a DNA molecule, using DNA sequencing. This method can be used for analyses within and among populations and species (Frankham *et al.,* 2010). In addition to the sequencing of mitochondrial and nuclear genes, entire genomes have now been sequenced, with the pig genome being completed in 2012. This has revealed and confirmed the evolution of the porcine genome, population divergence and domestication of European and Asian breeds (Groenen *et al.,* 2012). Phylogenetics is the study of the evolutionary relatedness among populations and species. Molecular phylogenetics uses sequence data to infer these relationships, which is depicted in the form of a phylogenetic tree (Ziemert and Jensen, 2012). The tree positioning of a population or species is generally based upon the degree of relatedness and the extent of divergence from the common ancestor (Freeland, 2005). Phylogenetic trees have been used extensively in livestock genetic diversity studies, for example to show the genetic relationships among and between cattle breeds (Ndiaye *et al.,* 2015), the origination, migration and evolution of pig

populations (Yu *et al.,* 2013), and the identification of common ancestors, genetic relatedness and evolutionary distances between sheep breeds (Al-Atiyat and Aljumaah, 2014).

1.4. Livestock Production in the United Kingdom

1.4.1. Sustainable Agriculture

At present, the foremost approach being undertaken by the agricultural sector, in the UK, is centred on the sustainable development of contemporary livestock production (Hume *et al.,* 2011; Department for Food, Environment and Rural Affairs (DEFRA), 2012). The livestock industry aims to achieve this through effectively maximising animal performance (Gamborg and Sandøe, 2005; Crute and Muir, 2011), minimising negative environmental impacts and efficiently utilising and preserving functional genetic resources for potential future usage (Olesen *et al.,* 2000; Herrero *et al.,* 2009). Prioritising sustainable agriculture has been initiated by the emergence of a global food security issue (Godfray *et al.,* 2010a), with the UK alone forecasted to increase from 61 million to 70 million by 2030 (Technology Strategy Board, 2012). The prospective progression of the livestock industry is dependent upon the implementation of sustainable systems, to ensure equilibrium between the continual growth in demand for animal protein and the sufficient availability, access and affordability of livestock produce.

1.4.2. Consumer Requirements – 1950s to the Present Day

However, preceding the current challenges encountered by the agricultural industry, the former primary objectives of the livestock industry had remained constant for the past several decades (Moloney, 2002). The predominant focal points were the improvement of lean meat production efficiency (McClinton and Carson, 2000), and the enhancement of product quality (Edwards *et al.,* 2008a), to reduce the carcass fat quantity of food producing animals, particularly swine (Sellier *et al.,* 2010).

Since the 1950s, consumers have requested particular qualities in their food products, for example, specific fat composition (Williams, 2005), attributable to public opinion that pork has a relatively high saturated fat content (Alfonso *et al.,* 2010), which is considered as an unhealthy meat alternative and of an inferior quality, in comparison to poultry and beef (Rauw *et al.,* 2003). In response to growing public

demand for leaner pork (Hulsegge *et al.,* 2000), the breeding goals stipulated in the 1960s focused on the reduction of subcutaneous back fat, resultant from the introduction of specialised paternal and maternal lines (Gjerlaug-Enger *et al.,* 2012), for the provision of an improved quality product, incurred at the lowest feasible price by the consumer (Merks *et al.,* 2012).

Consequently, this initiated the subsequent stage of revolution for the UK pig industry in the 1970s (Woods, 2011), whereby the production of swine, intended for the commercial market, became intensified (Green, 2009), for the improvement of performance efficiency and maximisation of produce output, whilst simultaneously minimising production costs (Bishop and Woolliams, 2004). This became attainable through rapid progression in the enhancement of productivity: defined in agriculture as the effectiveness of productive effort, measured as the ratio of outputs to inputs (Brooks and Varley, 2003), particularly in terms of daily liveweight gain and pigs weaned per sow per year (van der Steen *et al.,* 2005). This was achieved by the scientific development and widespread availability of artificial insemination (Brassley, 2007). During this time, the pig breeding pyramid was introduced to select for particular characteristics and capitalise on hybrid vigour (Figure 2). At the top of the pyramid is the nucleus herd: purebred breeding stock (great grandparent), used to produce replacement breeding gilts and stud boars for the multiplier and commercial herds. The middle tier comprises the multiplier herds (grandparent): breeding and multiplying replacement gilts and boars to supply to commercial breeding herds. The third tier is the commercial (parent) herds: producing the slaughter pig from crosses between the terminal line sires and maternal line gilts and sows (BPA, 2016j). The genetic improvement of the UK pig industry has been continually dominated by a minority of distinguished international breeding companies (Cardellino and Boyazoglu, 2009), for the development and distribution of proprietary breeds and lines, through selective breeding for specific genetic traits (van Arendonk, 2011).

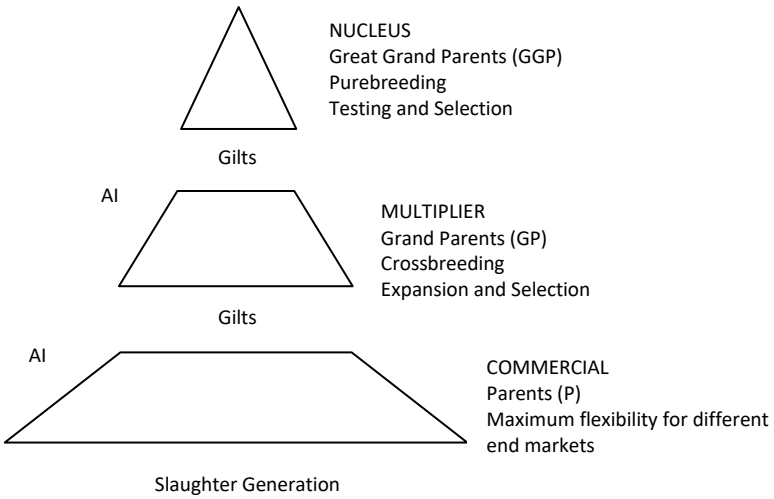

Figure 2. Pig Breeding Pyramid (Adapted from BPA, 2016j).

1.4.2.1. The Large White and Landrace

The Large White (LW), universally known as the Yorkshire, is stated as the most globally distributed of all the pig breeds and the leading source of genetic material of virtually all the commercial pig producing countries of the world (Figure 3) (British Pig Association (BPA), 2016a). The Large White is known to have originated from the north of England, predominantly Yorkshire, however the early ancestry is difficult to trace, but it is believed that the breed developed from the local Old English white breeds during the 19th century (Case, 2009). In comparison with a number of the other British breeds, the original Large White had very little genetic contribution from Asian pigs in the breed lineage (RBST, 2015a). The Large White demonstrated versatility as both a terminal sire: hardiness, growth, uniformity and quality, and dam line: large litter sizes, heavy milk production and excellent mothering ability, and by the end of the 19th century was rapidly being exported worldwide (Lewis, 2011: BPA, 2016a). The gene stock of the commercial Large White, held by breeding companies today, has been developed from the pedigree British Large White, first through selective breeding and later genetic selection to create synthetic lines with particular reproductive and/or growth performance traits. Although each company have created their own unique dam and sire breeding lines, they would have originated from regional lines of the purebred base population (Porter, 1993; Case, 2009).

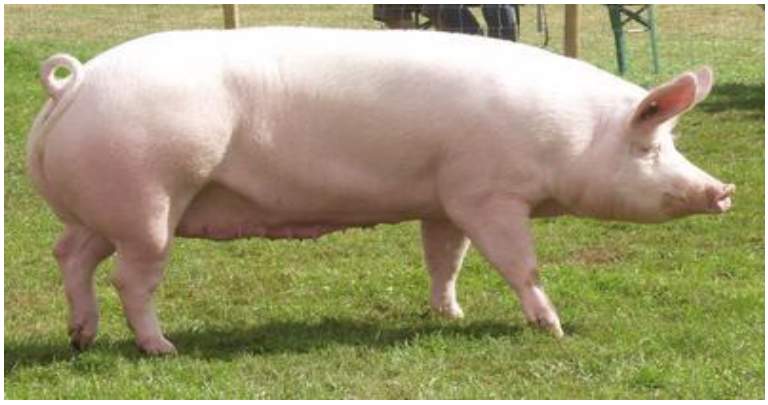

Figure 3. The Large White (RBST, 2015a).

It is claimed that the original Landrace breed was developed in Denmark, by crossbreeding British Large White's with native Danish pigs, with the aim of producing a more consistent bacon product for exportation. The Danish Landrace gained such a reputation for bacon production, due its body length, leanness and yield, that the breed was soon globally exported to improve the bacon market (Porter, 1993). The first Landrace pigs were introduced into Great Britain from Sweden in 1949, as anecdotal evidence suggests that the British pig was not meeting the requirements of the bacon market, for example leanness, uniformity and improved quality, at the lowest feasible price (BPA, 2016k). In 1950, the first UK pig testing scheme was created for daily liveweight gain and fat depths, to assess the Danish Landrace imports, and select only the superior individuals to form the basis of the British Landrace (BLR) breed (BPA, 2016b). Many countries developed their own national Landrace breed, by using the Danish as a base, crossbreeding with their indigenous pigs, and developing with 'improved' Landraces; meaning that several national Landraces owe their origins to more than one foreign Landrace (Porter, 1993).

Figure 4. The British Landrace (RBST, 2015b).

New bloodlines were imported from Norway, in 1953 and 1980, to genetically broaden, further develop and establish the British Landrace (Figure 4) as a unique breed amongst the other Landrace breeds (BPA, 2016c). Although originally used for bacon and pork production, the British Landrace became widely recognised for its mothering attributes: high fertility, large litters, heavy milkers and ease of management, due to the docile nature of the breed (Lewis, 2011). The breed also demonstrated versatility for indoor and outdoor, intensive and non-intensive systems, making it suitable for commercial production (RBST, 2015b). Consequently, in the 1960s and 70s, it was identified that crossbreeding resulted in advantageous qualities, in breeding stock and progeny, from hybrid vigour. Hence, the reproductive traits of the British Landrace were amalgamated with the productivity traits of the British Large White, to produce first generation parent stock (BPA, 2016a). To further reproductive performance, the British Landrace has been heavily improved, using the European Landrace, to create the modern dam lines used by breeding companies today (BPA, 2016c).

1.4.3. Modern UK Pig Industry

As of December 2018, the British pig industry stood at 4.6 million for the total number of pigs, 1.4% lower than December 2017, predominantly due to a decrease in number of fattening pigs, with the female breeding herd comprising 406,000, 0.4% lower than the previous year, predominantly due to a decrease in the number of sows and gilts in pig. In 2018, roughly 10.5 million pigs were finished, which equated to 900,000 tonnes of pigmeat (DEFRA, 2018). The Agriculture and Horticulture Development

Board (AHDB) (2017a) reported that there are 30,000 premises with pigs on, 11,000 of which are for commercial pig farming. Approximately, 92% of production comes from 1600 assured farms, including 10 corporate companies, which account for 35% of the UK breeding herd. Indoor pig production is the norm for most global producers; however the UK is unusual in that outdoor pig production accounts for 40% (Driver, 2017a). In Denmark, the EU's main producer, 10% of their breeding herd is outdoors, whereas in Spain, the EU's second main producer, outdoor production is limited to traditional breeds, for example the Iberico, for niche market products (Lumb, 2013; European Union Commission, 2019). In contrast to the major EU countries, UK production systems are commonly straw based, with 40% weaners, 60% growers, 45% finishers and most of the indoor 60% pre-farrowing sows kept on straw, with the rest kept on indoor full or part slatted systems (Driver, 2017b).

It is expected that pig meat exports will significantly rise to 279,000 tonnes in 2019 (AHDB, 2019a). China has been the UK's largest buyer as of 2019, followed by Ireland, Germany and the Netherlands (King, 2019). However, pig meat imports are expected to drop slightly by 1% in 2019 to 1,053,000 tonnes, with Denmark as the largest supplier of pork and bacon/ham, Ireland for processed ham/shoulders and offal, and Germany for sausages (AHDB, 2019b). The UK retail trends remain steady, with AHDB (2019c) reporting no change in quantity of fresh and frozen pork purchased between March 2018-2019, whereas bacon decreased by 3% and sausages were up 1%.

1.4.4. Breeding Objectives and Strategies

During the last two decades, the breeding objectives of the porcine industry have expanded for the inclusion of reproductive: fertility and prolificacy (Merks, 2000), and productivity traits: growth rate and lean tissue percentage, in the dam and sire lines (Visscher *et al.,* 2000). The UK pig industry utilises productively efficient genetic lines, concentrated from a limited number of prevailing international breeds (Ollivier, 2009), intensively selected for economically important traits of: liveweight gain, feed conversion efficiency, carcass leanness and prolificacy (Kanis *et al.,* 2005). Additionally, commercial producers are continually adjusting their breeding strategies (Schwab *et al.,* 2010), simultaneous with

the industry shift towards the widespread implementation of a distinct three-way crossbreeding system (Figure 5) (Dekkers *et al.,* 2011), for the exploitation of specific paternal and maternal performance attributes, to enhance the heterosis, or hybrid vigour, exhibited by the progeny (Visscher *et al.,* 2000).

Heterosis is defined as 'the increase in performance of the offspring, compared to the average of the parents.' Heterosis tends to be largest for traits with low heritability: reproductive (litter size, weaning weight and piglet survival), but improvements can also be seen for moderately heritable traits: growth (average daily gain, slaughter age) (Clutter *et al.,* 2007; Walters, 2015). The crossing of two different breeds yields 100% heterosis (using the standardised scale); however the breed composition of the parent generation must be known. For example in a three way cross, the progeny of a (Landrace x Duroc) x Large White cross would show 100% individual heterosis, whereas the progeny of a (Landrace x Duroc) x Duroc cross would only show 50% individual heterosis, due to the same breed present in the dam and sire (Boddicker, 2015).

At present, the majority of the slaughter pig generation produced for the commercial pork market are derived from the hybridisation of the Large White and Landrace breeds (Litten *et al.,* 2004). This has continued through to the present day, with both breeds being intensively selected as dams and dam line sires for commercial breeding programmes, and the Large White as a terminal sire for pork production (RBST, 2015a; RBST, 2015b).

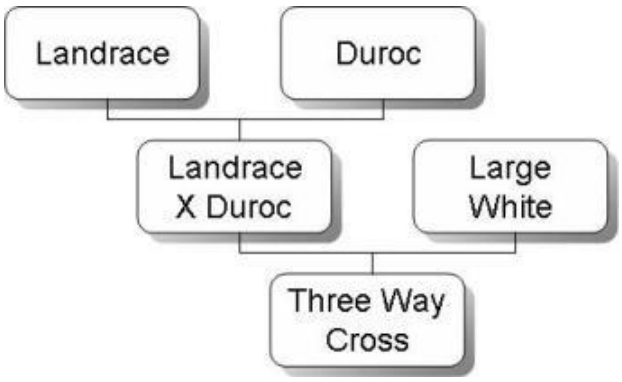

Figure 5. An example of a three way cross (BPA, 2016j).

1.4.5. Terminal Sire Breed and Lines

The growing demand for meat has driven the commercial pig industry to increase the output of saleable products, by continually improving the productive capacity of the slaughter pig (FAO, 2015b). The selection focus has largely remained the same: to further maximise lean growth, by optimising the daily liveweight gain, feed intake and conversion efficiency, for a rapid turnover of stock, from a reduction in the number of days to slaughter (Simpson, 2013). Modern terminal sire breeding programmes have already made significant progress in enhancing the lean tissue development and growth efficiency of finished pigs by 100% (Merks *et al.,* 2012), which has dramatically reduced total carcass fat from 40% to 20%, with a 75% decrease in subcutaneous fat (Kouba and Sellier, 2011).

It has been stated that the terminal sire breed or line is the primary factor influencing the productivity performance of pigs from weaning to finishing (Fabrega *et al.,* 2003; Latorre *et al.,* 2009). Although the Large White alone constitutes one third of the gene pool of slaughter pig stocks (Delgado *et al.,* 2000; Nidup and Moran, 2011), other terminal sire breeds and lines: Duroc, Landrace, Hampshire and Pietrain have become popular (Chen *et al.,* 2007). There was no available data on these breeds by number incorporated into slaughter crossbreds. The interest in new terminal sire genetics has developed from the identification of significant phenotypic differences (Bunter *et al*., 2008), between established and forthcoming European breeds and lines, in relation to slaughter pig performance efficiency and carcass characteristics (McCann *et al.,* 2008). The Duroc is renowned for fast growth rates, high lean: gain efficiency and valuable meat quality traits: favourable pH values, desirable meat colour and reduced drip loss (Kusec *et al.,* 2004). Similarly, the Hampshire exhibit rapid growth, resultant in reduced days to slaughter, robustness and increased carcass yield (British Pig Executive (BPEX), 2009). Whereas the Pietrain is noted for the production of heavy carcasses with improved composition: a high yield of lean meat and significantly low fat content (Whittemore *et al.,* 2003). The incorporation of the Duroc, Hampshire and Pietrain breeds and lines, primarily as terminal sires, within conventional UK crossbreeding programmes, has been progressively implemented to optimise the efficiency of mainstream commercial pork production (Ruusunen *et al.,* 2012).

In order to fulfil industry requirements, the leading breeding and genetics companies have also been using genetic markers to allow for the selection of terminal sires yielding more muscle mass, less fat deposition and rapid postnatal growth (Stalder *et al.,* 2011). This marker assisted selection has aided the identification of certain paternally imprinted genes, for example insulin-like growth factor 2 (IGF2) and retro-transposon like 1 (RTL1) which express positive effects upon progeny development, carcass leanness and uniformity (Yang *et al.,* 2009; Ruan *et al.,* 2013; Ding *et al.,* 2014). The incorporation of these genes is becoming of foremost importance, within terminal sire breeding programmes, to enable the optimisation of productivity and carcass composition in future slaughter generation pigs.

1.4.6. Maternal Dam Breeds and Lines

The hybridisation of the Large White, crossed with various Landrace strains (LW x LR), dominates almost all maternal lines utilised in intensive slaughter pig production within the UK (Notter 1999; Whittemore and Kyriazakis, 2006). This is owing to the fact that both breeds are equally renowned for their high prolificacy, ability to rear sizeable litters and improved piglet productivity (Bidanel, 2011). Breeding companies have remained focused on improving sow reproductive efficiency, using genetic selection and improvement (Roehe *et al.,* 2010), for economically important traits associated with fertility, litter size and pre-weaning viability (Foxcroft *et al.,* 2006). From 1970 to 2016, the commercial pig industry has successfully increased the indoor breeding herd average number of pigs born alive (NBA) per litter, by over three pigs, from 10.2 to 13.2 (Varley, 1988; AHDB, 2017b). This is 1.2 pigs more than the outdoor breeding herd average of 12 pigs born alive per litter (AHDB, 2017c). However, global variation between breeds and lines will occur, as each breeding company has different performance objectives, and thus selection criteria for their Large White and Landrace populations (Bergfelder-Drüing *et al.,* 2015). This statement is supported by two studies on NBA: Krupová et al., (2017) stated a minimal difference for NBA between the Czech Large White, 13.42, and Czech Landrace, 13.39, whereas Abell *et al.,* (2012) found that the Irish Landrace had 0.41 more NBA per litter than the Irish Large White. This increase in NBA has had a positive effect on pigs weaned per sow per year (PWSY): in 2010, the average indoor breeding herd were achieving 22.89 PWSY compared to 27.48 in 2018 (AHDB, 2019d), and the

average outdoor breeding herd have reached 23.59 PWSY in 2018, in contrast to 20.87 in 2010 (AHDB, 2019e).

1.4.6.1. Litter Size and Piglet Survival

Intensive selection for increased litter size has caused an unfavourable correlation between numbers born and piglet survival (Kapell *et al.,* 2009). Lund *et al.,* (2002) established a negative correlation of -0.39 between maternal genetic effects on total number born and piglet survival from birth to 3 weeks, and -0.41 between maternal and direct genetic effects on piglet survival from birth to 3 weeks in the Landrace. Although, these correlations were not similar in the Large White, the breed did show negative correlations between maternal and direct genetic effects on total number born (-0.47) and maternal genetic effects on total number born and direct genetic effects on piglet survival from birth to 3 weeks (-0.48). Krahn (2015) stated that piglet survival to weaning was significantly higher in litters with fewer piglets born alive, with a negative impact on survival as numbers born alive increased above 12. The uterine capacity of sows remains relatively unchanged, yet the component traits of ovulation rate and embryonic survival have positively responded to selection for large litter size, which has caused greater litter heterogeneity of piglet birth weight (Foxcroft, 2008). Calderón Díaz *et al.,* (2016) reported as litter size increases, birth weight decreases and the percentage of piglets with birth weight <1kg also increases. For example, a litter of 8 piglets had an average birth weight of 1.64kg, 0% of piglets <1kg and 13% of piglets <1.3kg, in comparison to a litter of 19 piglets which had an average birth weight of 1.18kg, 31% of piglets <1kg and 52% of piglets <1.3kg. In comparison to the stronger, heavier birth weight piglets, the light birth weight piglets are predisposed to higher pre-weaning mortality: total number of deaths divided by number born alive, slower lifetime growth rates: average daily gain and days to reach slaughter weight (Gondret *et al.,* 2005), and decreased meat-eating quality: lower tenderness, from enlarged myofiber cross-sectional areas in the muscle, lower lean meat content and fatter carcasses (Gondret *et al.,* 2006). The overall knock-on effects experienced by producers are depleted production output and efficiency, with severe economic losses from high piglet mortality, increased labour, complicated management and poor product quality (Campos *et al.,* 2011). It has

become apparent that if the reproductive focus of the pig industry is to enhance litter size beyond what is being currently achieved, then this needs to be accompanied with genetic selection for increased piglet survival.

1.5. Intensive Livestock Production and Traditional Breeds

1.5.1. The History of the Pig, Cattle and Sheep Industries

The contemporary artificial selection of the five mainstream porcine breeds and strains: Large White, Landrace, Duroc, Hampshire, Pietrain, has narrowed the availability of genetic resources and limited the diversification of traits (Ojeda *et al.,* 2011), which has continuously posed severe threats to the present existence of traditional pig populations within the UK (Buchanan and Stalder, 2011). Until the beginning of the 1930s, traditional purebred pig breeds were predominantly reared in small-scale, extensive pastoral systems (Hoffmann, 2011), with selection based on the utilisation of specialised breed-specific characteristics, to correspond with the diverse requirements of the past pork market (Notter, 1999).

The significantly negative decline in the population numbers of traditional breeds was largely attributable to the recommendations of the Howitt report of 1955 (Turner, 2010), which stated that the forefront of UK pig production should concentrate on the utilisation of only three commercial breeds: the Large White, British Landrace and Welsh (BPA, 2012). This was in relation to the development of the UK pig industry, following the end of the Second World War, by means of enhancing the productive efficiency of conventional bacon and pork pigs (Brassley, 2000), for the maximisation of produce output, in order to achieve equilibrium between industrial supply and market demand (Martin, 2009).

Incidentally, this trend radically descended to the cattle industry, whereby the importation of beneficially productive continental breeds, for example the Charolais, Limousin and Simmental, became the basis of post-war commercial beef production (Dohner, 2001). The integration of these prevailing European breeds, within contemporary beef production systems, followed similar principles to the breeding objectives of the swine industry (Porter, 2001), with emphasised selection for growth efficiency and carcass composition, relative to consumer satisfaction for vast quantities of lean meat at

stabilised prices (Wilson, 2011). This has carried through to the present day, with the number of dairy cross beef calf registrations continuing to grow: in 2016, the registrations totalled 583.9 thousand head, 10% more than 2015, and from January-September 2017, the registrations totalled 473 thousand head, 9% higher than the same period in 2016 (AHDB, 2018).

The UK sheep industry is renowned for its precedent stratified crossbreeding structure (Sargison, 2008), which previously utilised an extensive variety of multipurpose breeds and types, to contribute to the production of breeding stock for the slaughter generation (Lewis, 2004). In contrast to other livestock industries, the modification in the usage of different sheep breeds was largely driven by the regulations of previous economic policies (Yarwood and Evans, 2006), predominantly the introduction of the EU sheepmeat subsidy regime in 1980, which was resultant in considerable regional variations in breed structure and fluctuations in the population size of the UK industry (Ashworth *et al.,* 2000). Hence, this instigated the constructive improvement of meat-producing sheep breeds (McGuirk, 2000), observed by the widespread development of crossbred ewes (Leymaster, 2002), and the importation of phenotypically superior continental terminal sires, the Texel and Charollais, to enhance the conformation uniformity of slaughter lambs (Vipond, 2010). This was resultant in a concomitant rise in the utilisation of a minority of prevailing meat breeds (Simm *et al.,* 2001), within the diverse areas of the stratified system, for example, the hills: Scottish Blackface, Swaledale, longwool crossing breeds: Blue Faced Leicester, Border Leicester and terminal sires: Suffolk, Texel (Pollott and Stone, 2003). Thus, the pattern which was previously and is currently observed across the meat-producing sector of the livestock industry is the selective importation of productively efficient European breeds, owing to the possession of economically beneficial performance traits, which has been consequential in superseding the utilisation of traditional breeds.

1.5.2. Why Rare Breeds Are Rare

The inactive utilisation of traditional livestock populations has been additionally instigated by previous and present anecdotal evidence, which implies that indigenous breeds exhibit undesirable phenotypic

traits (Brandt *et al.,* 2010): inferior growth rates, inefficient feed utilisation, high content of back fat and mediocre carcass conformation, resultant in elevated production costs (Bonneau and Lebret, 2010). Hence, it was deemed that local breeds do not fit the productivity parameters of those breeds regarded as commercially efficient (Thornton, 2010), resultant in permanent detrimental impacts to breed resources and the population status of traditional livestock breeds (Sander-Regier, 2010). However, traditional cattle, sheep and pig breeds are becoming renowned for their unique physical features, reputable mothering attributes (Ciobanu *et al.,* 2001), environmental adaptability, aptness for alternative production systems (Caballero and Toro, 2002) and superiority of finished products (Edwards, 2005).

1.5.3. Traditional UK Pig Breeds

1.5.3.1. Selection of Breeds for this Study

The three traditional UK pig breeds, to be studied, were individually selected relative to the RBST numerical categorisation of registered breeding females, producing purebred offspring, differing in conservation status: vulnerable, at risk, minority and the historical connection, in terms of the effectual causes which threatened the existence of each breed. The RBST Watchlist is created using pedigree data from over 130 breed societies, in the form of annual male and female registrations, along with a multiplier to estimate the number of registered breeding females in the UK for each breed. However, the placement of a breed within the Watchlist can also be defined by additional variables of population genetic factors: inbreeding, genetic erosion and current trends in breed density and distribution (RBST, 2019).

The Gloucester Old Spot (GOS) and British Lop (BL) were selected as to represent two ends of the spectrum: in 2012, the GOS population were numerically the largest, whereas the BL population were numerically the smallest (RBST, 2012b). The Welsh (W) was selected to represent the median of the three breeds, and due to the past semi-commercialised nature of the breed (RBST, 2015c). This

encompassed the full range of pure, semi-commercialised and modern breeds and lines, allowing for the comparisons of hypothesised differing levels of genetic diversity and productivity.

1.5.3.2. The Gloucester Old Spot

The Gloucester Old Spot, commonly referred to as the 'Orchard Pig', is registered as one of the oldest spotted pedigree breed lines (European Union Commission (EUC), 2009), in the world, with records dating well before 1913, when the breed society was first formed (Gloucester Old Spot Pig Breeders Club (GOSPBC), 2012a). In 2016, the GOS were categorised as minority status: 500-100 recorded breeding females in 2016 (RBST, 2016) however in 2017, the GOS showed the most dramatic decline in traditional pig breed population numbers, leading the RBST to change the GOS to as 'at risk' status: 300-500 recorded breeding females (RBST, 2017a). This has remained the same for RBST 2018/2019 Watchlist (RBST, 2018), with the GOS in the 'of concern' category on the RBST Danger List 2018 (RBST, 2017b). There are presently 185 registered UK keepers of pedigree GOS, with the breed comprised of 15 female and 4 male bloodlines. In 2018, the BPA Bloodline Audit of GOS pedigree numbers showed a decline in the number of registered breeding sows from 785 (2017) to 702, and registered breeding boars from 185 (2017) to 172 (BPA, 2018a). However, the herd book registrations have increased from 377 in 2016, to 436 in 2017 (BPA, 2018b).

The GOS was developed in the Berkley Vale of Gloucestershire, and is believed to have originated from the crossing of the original Gloucestershire pig and the unimproved Berkshire (GOSPBC, 2012a). The breed has been exported overseas to create pedigree breeding groups, form modern commercial hybrids and to restock populations, since before World War 1 through to 1995. Although several attempts have been made to establish viable, pedigree populations overseas, the UK has only achieved this. However, in 1995, 20 unrelated animals were selected from three UK herds to form a breeding group in the USA, to maintain pedigree status and promote the breed: this population was used to establish the Gloucestershire Old Spots of America Inc. The increasing numbers of pigs and breeders in

the USA is such that if the UK population were reaching extinction, the pure American population could be reimported to restock and save the UK herd (GOSPBC, 2012b).

The breed is ideally suited for small scale, outdoor production, due to their hardiness, adaptability and foraging ability. GOS dams are noted for being docile, heavy milkers, with good maternal instincts (RBST, 2011a). The existence of the GOS was threatened following the end of the Second World War (GOSPBC, 2012a), subsequent to producers transferring to intensive production, with lessened interest in breeds suited for outdoor systems (Vicente *et al.,* 2008), ensuing severe critical breeding numbers of 120 sows (Fernandez *et al.,* 2011).

The stable regeneration of this breed has been the effect of specialist market demand for the reputable superior quality meat, produced by GOS (Bonneau and Lebret, 2010; RBST, 2011a), resultant in a marked improvement in population size, with the breed presently recorded as the largest, numerically, of all the pig breeds listed by the RBST.

Figure 6. Gloucester Old Spot (RBST, 2011a).

1.5.3.3. The British Lop

The British Lop is defined as Britain's rarest native pig breed (Figure 7) (Miller, 2012). In 2016, the BL was listed in the 'vulnerable' category: 200-300 registered breeding females (RBST, 2016), yet in 2017, the BL was moved to the 'endangered' category: 100-200 recorded breeding females (RBST, 2017a). This has remained the same for RBST 2018/2019 Watchlist (RBST, 2018), however the RBST Danger List 2018

show two pig breeds most likely to become extinct: the BL is one of the two, with just 161 breeding females left (RBST, 2017b). At present, there are 66 UK members breeding pedigree BL, with the breed comprised of 10 female and 7 male bloodlines (Upchurch, 2019), of which there were 150 registered breeding females and 50 registered breeding males in 2015 (Miller, 2016). The British Lop Pig Society uses Grassroots Pedigree Software to manage registered keepers and numbers of animals (Upchurch, 2019). This software also provides the opportunity to analyse DNA for parentage, identification of markers for functional genes and production of breed reports (Grassroots Systems Ltd, 2019).

The considerable decline in population figures was instigated by the implementation of the Howitt report in the 1950s (RBST, 2011b), and the confined locality of the BL, to its originating area of Tavistock in the West Country, which left the breed undiscovered by producers outside of the South West (Porter, 1987). The BL herds have become established in most parts of the UK: most are reared by a small number of dedicated breeders, for conservation purposes and/or niche markets (Kiddy, 2003). Thus, population size is steadily increasing, although not at a similar rate as that of other rare pig breeds, for example the GOS (The Ark, 2011). It has been suggested that this is attributable to the BL lacking the distinctiveness of colour or spots, in comparison to other rare breed swine, and the similarity to the conventional Landrace and Welsh, which has discouraged enthusiasts from rearing this perceived 'ordinary' breed (Dohner, 2001).

However, the BL is becoming highly populous for hobbyists and niche marketers, resultant from the breeds' suitability for small-scale and extensive outdoor production (Miller, 2012), due to their robustness and foraging ability (Hulme, 1982). In terms of reproductive ability, BL dams are recognised for docility, simple management, good maternal instincts and reputable prolificacy of 12-14 piglets per litter (Zhu *et al.,* 2008; York, 2010; RBST, 2011b). In addition, the BL could be utilised within commercial slaughter pig production, as they can be reared under intensive, indoor systems, grow efficiently, are less prone to becoming over fat and produce high quality, lean carcasses at conventional pork and bacon weights (Case, 2009; RBST, 2011b).

Figure 7. The British Lop (Farmers Weekly, 2009).

1.5.3.4. The Welsh

The Welsh is stated to be the most commercially developed of all Britain's traditional pig breeds (RBST, 2015c). From 2016-2018/2019, the Welsh has remained in the RBST 'at risk' category: 300-500 registered breeding females (RBST, 2016; RBST, 2018); however the RBST Danger List 2018 reported that the W breed are in decline (RBST, 2017b). There are presently 76 registered UK keepers of pedigree W, with the breed comprised of 26 female and 11 male bloodlines. In 2018, the BPA Bloodline Audit of W pedigree numbers showed a decrease in the number of registered breeding sows from 607 (2017) to 590, and registered breeding boars from 76 (2017) to 69 (BPA, 2018c). However, the herd book registrations increased slightly from 316 in 2016 to 337 in 2017 (BPA, 2018b).

It is said that the W pig can be traced back to a white, lop-eared breed, originating from the southern and western counties of the Principality of Wales, for as long as records exist (RBST, 2015c). The breed prospered during the post Second World War era, due to an increase in the supply and availability of animal feed, which led to remarkable growth of all breeds comprising the national pig herd (The Pedigree Welsh Pig Society (PWPS), 2014a).

In the 1950s, the demand for larger and leaner carcasses led to a breeder deciding to introduce the Swedish Landrace into the W herd book, for crossbreeding with the indigenous W. This created a fast growing, easily managed, commercial type pig, which became the foundation stock of the modern W breed (RBST, 2015c). As a result, the Howitt Report recommended that the future of the modern British

pig industry needed to focus on three main breeds, one of which being the modern W. Subsequently, the W became the third most numerous breed nationally, after the Large White and Landrace breeds, to be used in commercial pig production (BPA, 2016e). In spite of this, hybrid breeds became increasingly popular, simultaneous with the shift towards intensification, for the production of much leaner carcasses, causing a dramatic decline in the population figures of the modern Welsh breed (RBST, 2015c).

There has been resurgence in the keeping of W pigs, across the UK, from smallholders, hobbyists, but also farmers, keen to fill the niche markets for specialist pig meat products from traditional breeds (CALU, 2010). The W has become increasingly popular due to the productivity characteristics of the breed and the crossbreeding potential with commercial and rare breeds (BPA, 2016e; RBST 2015c). Alike the BL, the W dams are known for their maternal attributes, litter sizes averaging 11 (RBST, 2015c), and low piglet mortality, which are all desirable reproductive traits of the modern pig industry (PWPS, 2014b). In comparison with the GOS, the W are suited to all types of management system, can be reared more intensively, have fast liveweight gain, efficient feed conversion and produce lean carcasses, making them an ideal breed for commercial production (PWPS, 2014b). The key traits which have aided the revival of this breed are the selection for meat quality: sufficient back fat to retain traditional flavour, yet maintaining the leanness of the carcass, and the hardiness: adaptability to a diverse range of production systems (PWPS, 2014a). The PWPS is actively working to conserve, develop and market the pedigree Welsh pig as a commercially viable breed (PWPS, 2014b).

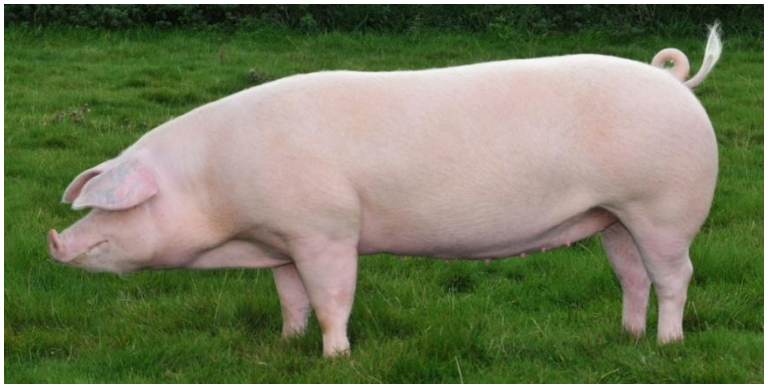

Figure 8. The Welsh (Countryfile, 2015).

1.5.3.5. British Large White and British Landrace

In 2013, the purebred British Large White, genetic founder of the commercial pig industry, was added to the RBST Watchlist, and listed as 'minority' status: 500-1000 registered breeding females (RBST, 2013). The BPA stated that this was due to the small number of breeders keeping pedigree British Large White's (BLW), and that there were only two or three large herds left of registered females (Anonymous, 2013). By 2018/2019, the BLW moved into the 'vulnerable' category: 200-300 registered breeding females (RBST, 2018), and the RBST Danger List 2018 reported that the BLW breed is in the 'of concern' zone of breeds at risk of extinction (RBST, 2017b). There are presently 55 registered UK keepers of pedigree BLW, with the breed comprised of 27 female (between 1-86 sows per line) and 17 male (between 0-16 boars per line) bloodlines. In 2018, the BPA Bloodline Audit of the BLW showed an increase in the number of registered breeding sows from 421 (2017) to 430, and registered breeding boars from 88 (2017) to 90 (BPA, 2018d). However, the herd book registrations decreased slightly from 285 in 2016 to 282 in 2017 (BPA, 2018b).

In 2015, the British Landrace (BLR) was also added to the RBST Watchlist, and categorised as 'vulnerable' status: 200-300 registered breeding females, following an application from the BPA for the breed to be accepted by the RSBT as a native, rare breed (RBST, 2015d). Since 2016, the BLR has been in the 'endangered' category: 100-200 registered breeding females (RBST, 2016; RBST 2018), with the RBST Danger List 2018 showing two pig breeds most likely to become extinct: the BL and the BLR, with just

138 breeding females left (RBST, 2017b). At present, there are 41 registered UK keepers of pedigree BLR, with the breed comprised of 40 female (between 0-23 sows per line), and 18 male (between 0-10 boars per line) bloodlines. In 2017, the BPA Bloodline Audit of the BLR showed a decrease in the number of registered breeding sows from 204 (2016) to 191, but an increase in registered breeding boar numbers from 34 (2016) to 41 (BPA, 2017). Also, the herd book registrations increased from 116 in 2016 to 126 in 2017 (BPA, 2018b).

1.6. The Future of Traditional Pig Breeds

1.6.1. Strategies for Survival

The future survival of traditional UK pig breeds is largely dependent upon population maintenance in hobbyist breeding and improvement of economic value for pork production. Hobbyists play an important role in the breeding and conservation of purebred traditional pig breeds. Native pigs are generally kept in small population sizes and reared under traditional practices, as companion animals, for showing and/or selling breeding stock (Weißmann, 2014). However, there have been recent fluctuations in numbers of registered keepers and pigs per bloodline, with decreases in the GOS, BL and W keepers and populations (BPA, 2016f; BPA, 2016g), perhaps as a result of personal and financial resources. Although, some smallholders have diversified into the rearing of traditional pigs for meat: supplying local butchers or marketing directly to customers from the farm gate and/or agricultural markets and shows (BPA, 2016i). In addition, The Gloucester Old Spot Breeders Club and The Pedigree Welsh Pig Society have received Traditional Specialities Guaranteed (TSG) status for the GOS and W breeds, which conserves their pedigree status, ensures production using traditional practices and provides product assurance (EUC, 2009; EUC, 2015). This not only secures production of purebred traditional breeds, from a conservation perspective, but also promotes their products to a wider audience, thereby increasing commercial value.

1.6.2. Improved Meat-Eating Quality

The pig and retail industries have observed a noticeable growth in consumer demand for meat and meat products from traditional breeds (Mathias *et al.,* 2010). This trend has been in response to increased consumer awareness concerning commercial livestock health and welfare (Guy *et al.,* 2002), product quality, safety and traceability and the environmental impacts of modern, intensive production systems (Kanis *et al.,* 2005). In addition, it has been identified that traditional breeds possess improved meat quality traits: darker colour, higher moisture content, greater pH, tenderness and high intramuscular fat content, which in combination are perceived to greatly enhance the eating quality of pork (Honeyman *et al.,* 2006).

Whereas, the selection pressure for improved lean gain in commercial breeds and lines has been negatively associated with a decline in meat quality (Lonergan *et al.,* 2001): a decrease in the overall firmness and cohesiveness of adipose tissue, caused by the targeted reduction and consequent structural alterations of carcass intramuscular and subcutaneous fat (Schinckel *et al.,* 2002; Kouba and Sellier, 2011). As a result, consumer preferences have been noticeably changing from lean to flavour and eating quality (Ciobanu *et al.,* 2001; Bentley, 2017), of which carcass fat is an important contributor to the palatability of pork (flavour, juiciness and tenderness) (Hamill *et al.,* 2013). Hence, the pig industry is being encouraged to include traits which improve eating quality: pH, colour, firmness, water-holding capacity, fat content, composition and uniformity, as selection criteria within breeding and genetic programmes (Ma *et al.,* 2013).

However, genetic improvement of meat quality in commercial breeds, as has been done with productive and reproductive traits, may reduce the opportunities of variation, from selection only occurring within the limited, modern gene pools. Traditional breeds are stated to produce meat of superior quality, to that of the commercial slaughter pig (Bonneau and Lebret, 2010), which suggests that they may confer different meat quality attributes to that of modern breeds. It is essential these traits are conserved, for

their potential future utilisation, to produce unique meat and meat products, supply a premium market and improve commercial meat quality.

1.6.3. Maternal and Paternal Survivability Traits

Instead of utilising traditional breed boars, the dams could be incorporated within commercial production systems, directly as a purebred animal or through the creation of a synthetic line: genetic improvement of the modern dam. Traditional dams are reputable for their reproductive qualities of prolificacy, maternal instincts and high milk production (Gillespie and Flanders, 2010), enabling the ability to rear average litters (10) of heavier birth weight piglets, with greater survivability to weaning (de Castro *et al.,* 2001). The maternal traits of traditional breeds, particularly survivability and mothering ability, could be genetically selected and incorporated to develop the modern dam, with the aim of decreasing perinatal mortality and increasing survivability to weaning (Zhu *et al.,* 2008). Alternatively, traditional dams could be crossbred with modern terminal sires, to ensure survival and utilisation of purebred maternal traits and improve productivity performance from the commercial breed (Weißmann, 2014).

However, recent studies have demonstrated the roles of paternally imprinted genes on the regulation of foetal growth and development and the effects on survivability during the pre-weaning period. It has been identified in pigs, that there is an association between piglet physiological maturation and survivability, from the expression of the terminal sire genotype during late foetal development. Leenhouwers *et al.,* (2002) demonstrated this positive correlation of which greater physiological maturity (full development) at birth promotes greater survivability to weaning. The targeted genetic improvement of piglet survival, both in maternal and paternal lines, is of foremost importance to achieve greater output of the sow herd (weaned pigs per sow per year) and increased financial return from more pigs sold.

1.6.4. Crossbreeding: Improving Traditional and Commercial Breeds

The crossbreeding of traditional and commercial pig breeds could be used not only as a conservation tool, but also as a means of genetic improvement for both groups. This strategy could address the anecdotal negative productive capacity of traditional breeds, and the limited range of genetic variation and poor meat-eating quality of commercial breeds (FAO, 2015b). So as to improve their commercial viability, the meat quality and adaptability traits of traditional breeds need to be retained, whilst improving their productive performance, with particular emphasis on growth, feed conversion efficiency and subcutaneous fat (Ligda and Zjalic, 2011). Whereas, the genetic diversity of commercial breeds needs to be enhanced, to enable the industry to tackle various emerging challenges: climate, disease, production requirements, resource availability and market demands (FAO, 2007; FAO, 2015b).

It has been advocated that crossbred progeny (traditional x commercial) exhibit significantly greater productive performance, than the purebred traditional, and improved environmental adaptability, compared to the commercial hybrid (Taneja, 1999; Shrestha, 2005). This demonstrates that the crossing of traditional and commercial breeds can achieve an amalgamation of both productive and adaptive traits, to benefit the performance and survivability of the resultant progeny.

In summary, this form of hybridisation between traditional and commercial breeds should be viewed as a means to productively improve and genetically preserve the beneficial characteristics of both groups, to ensure the sustainable development and genetic progression of future modern pig production.

1.7. Aims of this Study

The commercial pig industry is dominated by five productively efficient modern breeds and lines, which have narrowed the availability of genetic resources and limited the diversification of traits. It has been stated that a genetically diverse resource base is essential for the assurance of world food security and that the greatest genetic variation is found in traditional livestock breeds. Although populations of traditional breeds are conserved in the United Kingdom, there are limited studies assessing their genetic and productive potential for future needs. It is hypothesised that the traditional breeds will reveal high

levels of genetic diversity, whereas the commercial breeds and lines will show the opposite. This study will identify which traditional breed demonstrates the greatest genetic potential to broaden the diversity of modern breeds and lines. It has been said that purebred traditional progeny have poor birth to finish performance (anecdotal), and commercial hybrid progeny have decreased survivability to weaning from large litter sizes (objective): however both could be improved by the amalgamation of traits. This study will determine whether crossbreeding could produce a traditional x modern hybrid with greater survival and the ability to perform on par with the commercial slaughter pig. The overall aim of this study is to determine the viability of crossbreeding traditional and commercial breed pigs, as a genetic management strategy: conservation and improvement of productivity.

1.8. Research Objectives

The above aim will be achieved by fulfilling the following research objectives:

1. Assessing the within and between breed genetic diversity of three purebred traditional British pig breeds and the commercial Large White x Landrace, using mitochondrial DNA.
2. Assessing the within and between breed genetic diversity of three traditional British crossbreds, with the commercial crossbred sow and progeny, using a nuclear DNA region of the DIO3 gene.
3. Comparing the performance and carcass quality traits of three traditional British pig breed crosses, with the commercial hybrid slaughter pig, (Large White x Landrace) x Large White.

Chapter 2. An Assessment of Genetic Diversity Using Mitochondrial DNA

2.1. Global Outlook of the Pig Industry

To date it is approximated that there are over 730 pig breeds or lines globally (Chen *et al.,* 2007), of which 150 breeds have become extinct during the past 100 years (Scherf, 2000), and over a third of existent breeds are categorised as endangered or critically at risk of disappearance (Nidup and Moran, 2011). This decline in porcine genetic resources has been attributable to the commercial pig industry focusing on intensifying production to fulfil the increasing demand for pork from the growing global population (Thornton, 2010). Modern pork production is dominated by a small number of commercially efficient breeds (Ollivier, 2009), mainly the Large White and Landrace, intensively selected for advantageous performance traits: liveweight gain, feed conversion efficiency, carcass leanness and prolificacy (Kanis *et al.,* 2005). These traits are of significant importance to the pig industry, enabling the achievement of lean, high yielding carcasses, which are economical to produce, without compromising on product quality (Gjerlaug-Enger*et al.,* 2010).

The UK pig industry acted on the advice of the Howitt Report in 1955, which stated that the forefront of pig production should concentrate on the utilisation of only three commercial breeds: the Large White, British Landrace and Welsh (British Pig Association (BPA), 2012). In 1956, the sow and boar registrations revealed that 81% of the British pig breeds, including the Oxford Sandy and Black, Lincolnshire Curly Coat and Dorset Gold Tip, were in decline, following the implementation of the Howitt Report (Brassley, 2015). Subsequently, during the late 1950s to early 1970s, at least 6 British pig breeds became extinct: Cumberland, Dorset Gold Tip, Lincolnshire Curly Coat, Small Black, Small White and the Yorkshire Blue and White (Porter, 2011). Since the establishment of the Rare Breed Survival Trust in 1973, no native pigs have become extinct; however 11 breeds remain on the 'Watchlist' to monitor population size and threats (Rare Breed Survival Trust (RBST), 2016). However, the combination of the 1955 Howitt Report and the 20th century intensification of pig production, has resulted in the irreversible loss and threatened the existence of native, traditional breeds (Reid *et al.,* 2010), as past and present anecdotal

evidence implies that they do not fit the productivity parameters of modern, commercial breeds (Brandt *et al.,* 2010). Weißmann (2014) stated that traditional breeds are characterised by high fat content, low lean yield and inefficient feed conversion, which cannot compete with the fast growth, feed efficiency and lean meat content of today's modern breeds.

The global reliance on a limited range of genetic variability has considerably reduced the genetic diversity of the domestic pig (Simianer *et al.,* 2003; Groeneveld *et al.,* 2010), from small population numbers, presence of inbreeding, genetic drift and loss of favourable alleles, both in modern and traditional breeds (Fernandes *et al.,* 2010; Toro *et al.,* 2011). The continuous loss of genetic diversity can deleteriously lessen the opportunities to genetically improve livestock populations (Melka and Schenkel, 2010), which is prerequisite to the impending development of animal productivity, reproductive performance and survivability (Groeneveld *et al.,* 2010; Taberlet *et al.,* 2011).

2.2. Importance of Conservation

There has been a dramatic increase in the universal requirement for consumable livestock products (Mäki-Tanila and Hiemstra, 2010), distinctly concurrent with rapid growth throughout the world population, particularly in developing countries (Thornton, 2010). The consumption level of meat and dairy commodities is predicted to continually escalate (Marshall *et al.,* 2011), with projections of a 40 to 50% increase in demand by 2020-2030 (Green, 2009), rising to the requirement of 70 to 100% more food to be produced by 2050 (Godfray *et al.,* 2010b). The major determinant of prospective food production output and consumption volume is forecasted to be the unprecedented rise in global population numbers (Tomlinson, 2011), from the current 7 billion inhabitants to over 9 billion by the year 2050 (Foresight, 2011).

In order to ensure equilibrium between supply and demand for animal protein, the Food and Agriculture Organization (FAO) have been greatly promoting the preservation and development of traditional, indigenous breeds (Food and Agriculture Organization (FAO), 2015). Native breeds possess behavioural, physiological and morphological traits, enabling adaptation to harsh environments, which are of

significant importance to future livestock production (Melucci *et al.,* 2005). The FAO 2007 and 2015 reports on livestock biodiversity stated that a diverse genetic resource base is essential for increasing food security, adapting to present and future challenges: climate, disease, resource availability and market demands, and ensuring the sustainability of agriculture (FAO, 2007; FAO, 2015b).

2.2.1 Characteristics of Traditional Pig Breeds

Traditional breeds are characterised for morphological individuality in terms of coat colour and type, conformation and anatomical variations, for instance the British Saddleback pig has a black coat with a white band around the saddle (Case, 2009), although individuals can exhibit considerable variation in colour at other features: nose, hind limbs and tail, and band location (Wiener and Wilkinson, 2011). Coat colour is not a significant economic trait in pig production (McGlone and Pond, 2003); yet there is a strong preference for white coat colour in commercial European breeds: the Large White and Landrace. This is because European consumers prefer light-coloured meat from white pigs, as it is visually appealing (Hirooka *et al.,* 2002), however Japanese consumers prefer dark-coloured meat from black pigs, as it is considered healthier (Oh *et al.,* 2014). Yet, the external features of traditional livestock breeds can be productively beneficial, with regards to protection from potentially adverse weather conditions, for example dark pigmented livestock are less susceptible to sunburn (Chimonyo *et al.,* 2005), and thicker coated breeds are less inclined to lose condition, when exposed to harsh environments (Gillespie and Flanders, 2010).

Indigenous breeds are considerably adaptable to various geographical landscapes (Dalvit *et al.,* 2009), owing to the exhibition of effectual ranging behaviour and the instinctive coping mechanisms to manage social competitiveness for resources (Edwards, 2005). On the other hand, the advancement in the genetic composition of modern, commercial breeds has caused a limited physiological tolerance to changes in external temperature (Zumbach *et al.,* 2008), heightened susceptibility to disease and reduced performance after infection (Flori *et al.,* 2011). This has resulted in notable disparity in the immune capacity of different breeds (Mallard and Wilkie, 2007), particularly in terms of the humoral

immune response: differing levels of antibodies, levels of detectable disease and severity of symptoms, with two studies showing indigenous breeds having stronger resistance, to infection with porcine circovirus 2 and porcine reproductive and respiratory syndrome virus, than commercial breeds (Bulos *et al.,* 2016; Liang *et al.,* 2016). Liu *et al.,* (2010) conducted a comparative investigation on the immunity traits of the Large White, Landrace and a Chinese indigenous breed, Songliao Black, which indicated significantly higher disease resistance and greater immune capacity in the native breed, pre-and post vaccination with Classical Swine Fever, in comparison with the two commercial types. Hence, indigenous breeds are principally suited for extensive, outdoor production systems, as they acclimatise to a range of external environmental stimuli (Latorre *et al.,* 2009), with some localised traditional breeds associated with a single, treacherous environment, of which no other livestock breed or species could maintain survival (Fernandez *et al.,* 2011).

Many of the traditional pig breeds are renowned for exhibiting strong mothering ability (Walters, 2012) and reproductive attributes of improved fertility, enhanced prolificacy, greater progeny survivability and high milk production (Porter, 1993), in comparison to the conventional dam line: Large White x Landrace (Nissen and Oksbjerg, 2010). Yet, in the UK commercial pig industry, the only traditional breed to have been recently used for development is the Chinese Meishan. It is one of the most prolific breeds, with increased uterine capacity and placental efficiency, and thus larger litter sizes of 3-5 more piglets than the Large White and Landrace (Hernandez *et al.,* 2014). However, due to the poor growth rate and high carcass fat content of the Meishan, it has historically been amalgamated with the Large White or Landrace to improve the prolificacy of modern, commercial dam lines (Porter, 2011). The maternal traits of indigenous breeds could be exploited as sources of genetic variation (Gilbert *et al.,* 2010), to develop the concentrated reproductive traits currently presented by contemporary dams, by improving the behavioural and productive capabilities of future breeding lines (Zhu *et al.,* 2008).

The final products from traditional breeds are perceived to be of unique and superior pork quality, compared to commercial breeds, in terms of flavour and tenderness (Honeyman *et al.,* 2006). The main

factors affecting the eating quality and satisfaction of pork are tenderness, juiciness, flavour and ultimate pH. Lee *et al.,* (2012) found that pork from the Berkshire was tender, flavoursome and had a much higher pH in comparison with the pork from the Duroc, Yorkshire and Landrace. Some producers are able to exploit traditional breed meat and meat products in leading niche markets (Thompson *et al.,* 2007), for a 50% greater retail price than that of the commercial breed (Tomiyama *et al.,* 2010). Additionally, others have been subsidised an added premium per kilogram of deadweight, as a price incentive to encourage the production of traditional breeds (Wang *et al.,* 2011a).

2.2.2. Crossbreeding as a Conservation Tool

The practice of crossbreeding can be used to introduce varying desirable qualities into specific breeds and lines (Wiener and Wilkinson, 2011), with the purpose of increasing productive output, thus achieving breed improvement and amplifying the genetic diversification of phenotypic traits within a population (Ruusunen *et al.,* 2012). The crossbreeding of purebred indigenous livestock and imported exotic breeds, has been extensively implemented within numerous developing countries (Köhler-Rollefson *et al.,* 2009), to address the requirement for a sustainable increase in the production of consumable foods of animal origin (Age *et al.,* 2012). In managed crossbreeding programmes, genetic diversity is preserved from the prerequisite for a purebred population of native parent stock to be maintained (Tisdell, 2003), ensuring the conservation of indigenous farm FAnGR and the utilisation of individuals whom possess distinctive characteristics (Scholtz and Theunissen, 2010).

In the developing world, several smallholder producers concur that crossbreeding between exotic and indigenous breeds, produces crossbreds with significantly greater productive performance than the purebred native livestock, and improved environmental adaptability, compared to the imported non-native breeds (Taneja, 1999; Shrestha, 2005). This is owing to the exploitation of favourable attributes from the traditional indigenous and commercial exotic breeds, to maximise the hybrid vigour (heterosis) expressed by the crossbred progeny (Bishop and Woolliams, 2004), by means of achieving a preferred combination of adaptive and productive traits (van Arendonk, 2011). In order for this to successfully

occur, the gene pools of the exotic and indigenous parental generations would need to be effectively maintained, so as to ensure a continuous supply of first generation (F_1) progeny, to fully exploit the heterotic superiority of the first cross.

An example of this indigenous and exotic first cross has occurred in Vietnam, renowned for being one of the largest global pig producers, whereby high yielding exotic breeds: Large White/Yorkshire, Berkshire, Landrace, Duroc and Pietrain, have been imported since the early 20th century for crossbreeding with the more favoured, upgraded indigenous swine: I, Mong Cai and Lang Hong, as a form of genetic improvement and performance enhancement (Lemke *et al.,* 2005; Berthouly-Salazar *et al.,* 2012). In correspondence with this, it is has been specified that at present 56% of the 21.5 million swine reared in Vietnam are crossbred (FAO, 2007), which demonstrates the positive impact of introducing international genotypes on the growing pork market for lean meat production, whilst conserving the traditional FAnGR by means of successful crossbreeding (Herold *et al.,* 2010).

2.2.3. Crossbreeding: Additive vs. Non-additive

Crossbreeding programmes in pigs exploits between breed complementarity of additive genetic effects and heterosis produced by non-additive genetic effects (Visscher *et al.,* 2000). Additive genetic effect: the effect of two or more genes acting on the same trait, with their combined effect being equal to the sum of their individual effects. This is referred to as the breeding (parental) value for that trait (Bullock, 2010). The definition of which is the value of an individual as a contributor of genes to the next generation: transmitted directly from parents to offspring (Mishra *et al.,* 2017; Vitezica *et al.,* 2018). Non-additive genetic effect: the interactive effects of different alleles within loci (dominance), between loci (epistasis) and the environment (Rettew *et al.,* 2008). Heterosis is the result of non-additive genetic effects (Lalev *et al.,* 2014), and is measured as the amount by which the average productivity of the offspring exceeds the average of the parental breeds (Bullock, 2010). The greatest benefit from heterosis is observed for lowly heritable traits, for example reproduction, survival and overall fitness,

whereas additive effects are exploited to improve highly heritable traits for example growth and carcass composition (Freyer *et al.,* 2008; Yadav *et al*., 2018).

In pig breeding, pure breed improvement, at the nucleus level, utilises additive effects to achieve an increased frequency of allele combinations, which are favourable to improving the traits under selection. Whereas, the production of the parent generation utilises the non-additive effects of crossbreeding two or more breeds or lines: exploiting heterosis (increases heterozygosity) to directly improve reproductive traits (Visscher *et al.,* 2000). Similarly, the slaughter generation are produced via different crossbreeding strategies, most commonly the terminal system to utilise 100% of the hybrid vigour in the crossbred females and offspring, and capitalise on the productivity strengths of the purebred sire (Yadav *et al.,* 2018).

However, the advantage of hybrid vigour is confined to the F_1 generation, as the heterotic effect declines in subsequent generations, but the genetic improvement through generating heterosis, particularly for lowly heritable traits, is quicker than intensive selection (Shah *et al.,* 2017). Yet for highly heritable traits, genetic progress can be achieved more rapidly through intensive selection, rather than crossbreeding, due to greater accuracy in selection decisions (Bullock, 2010). Although, intensive selection for specific allele combinations, in the purebred population, can reduce variation (increased homozygosity), and potentially lead to fixation of alleles, which would work against hybrid vigour in the production of the parent and slaughter generations (Lim *et al.,* 2013). However, when parental breeds are crossed, favourable combinations of linked alleles affecting a trait can be broken apart during meiosis: recombination loss, causing reductions in the positive heterosis, and thus deteriorations in performance, in the resulting crossbreds (Freyer *et al.,* 2008).

Previously, breeding companies would improve by selection within the purebred generation, utilising the presence of additive genetic variance and opting for sires and dams of superiority: measured by the phenotypic variation for desirable traits (Whittemore, 1998). It is aimed that the additive genetic improvements made in the nucleus population, will be inherited by the multiplier, parent and slaughter

generations, regardless of hybridisation (Wakchaure *et al.,* 2015). Selective breeding programmes traditionally used estimated breeding values (EBV's) to predict an animal's genetic merit for a specific and/or set of traits, for example meat production; growth, meat quality and fat content, based upon individual performance (Parliamentary Office of Science & Technology, 2011).

However, molecular genetics has progressed from marker-assisted selection (MAS) and best linear unbiased predication (BLUP), to novel technologies of single nucleotide polymorphism (SNP) chips and genomic selection (Knol *et al.,* 2016). Genomic selection is based on the prediction of individual breeding value (GEBV), by combining all the SNP allele effects across the whole genome, with purebred selection based upon genotype rather than phenotype (Samore and Fontanesi, 2016). Most genomic selection procedures only consider the additive effects, however the inclusion of non-additive effects has become of interest as they may contribute to increasing the accuracy of predicting breeding values and selection response, and enhance non-additive genetic variation through the definition of appropriate crossbreeding or purebred breeding programmes (Varona *et al.,* 2018). In addition to genomic selection, breeding companies are including performance of the commercial crossbred progeny in the evaluation of the purebred nucleus, to increase prediction accuracy for crossbred productivity, by assessing inheritance of additive effects and measuring the effect of non-additive effects (Ibanez *et al.,* 2011). The combined approach of EBV's, GEBV's and performance measures, allows for improving the additive effects on traits, and inclusion of non-additive effects in selection decisions, to maximise the genetic effects in the crossbred generation.

2.2.4. Conservation of Traditional Breeds in the UK

In the United Kingdom, the Rare Breed Survival Trust (RBST) was established in 1973, for the purpose of preserving the existence and monitoring the viability of unique indigenous livestock genetic resources (Lauvie *et al.,* 2011). In order to achieve this aim, the RBST classifies the rare livestock breeds into five categories: critical, endangered, vulnerable, at risk and minority (Gandini *et al.,* 2004), primarily based upon the species and the total number of registered pedigree breeding females native to the UK

(Boettcher *et al.,* 2010). In recent times, the RBST has been established as the foremost national conservation programme in the UK, specifically for rare breeds (Ligda and Zjalic, 2011), as a result of their commendable achievement of which no native British livestock breeds have become extinct since the implementation of the non-governmental organisation (Alderson, 2001). The present circumstance of the traditional livestock sector is characterised by an extensive variety of mainly rare, regional breeds, predominantly reared by hobbyists in non-profit smallholdings (Hall, 2011), which are significantly limited in population size and breeding stock, with some threatened by the risk of extinction (Ollivier *et al.,* 2005).

The preservation of a purebred form of every indigenous UK livestock breed is regrettably unviable, owing to the limited availability of financial, physical and human resources (Gibson and Bishop, 2005), fluctuating profitability, corresponding to lack of breed competitiveness in commercial and/or niche markets (Pilling, 2010) and the impracticality of conserving highly endangered and prospectively inbred breeds in closed populations (Bennewitz *et al.,* 2008). The interbreeding of indigenous and commercial livestock could potentially facilitate the targeted genetic improvement of weakened commercial areas (mothering ability and meat quality) (Gourdine *et al.,* 2012), and alleviate the anecdotally adverse productivity characteristics exhibited by traditional breeds (Bonneau and Lebret, 2010). The coalition of breeds would ensure the conservation of genetic diversity (Wang *et al.,* 2011b), sustainable utilisation and continual improvement of contemporary and native FAnGR (Uimari and Tapio, 2011). However, there remains a lack of published studies analysing the heritability and potential dilution of productivity traits within an F_1 generation, formed through the merging of a commercial and traditional breed, particularly in the agricultural field of UK pig production.

2.3. Chapter Objective

The objective of this chapter is to assess the genetic diversity within and between three traditional British pig breeds and the commercial hybrid Large White x Landrace, using mitochondrial DNA as a

molecular marker. This assessment will determine the viability of crossbreeding traditional and modern pig breeds, as conservation tool, to maximise genetic diversity for the future.

2.4. Mitochondrial DNA – Form and Function

Mitochondria are double-membrane-bound organelles, found in the cytoplasm of eukaryotic cells. The most prominent function of mitochondria is to produce energy for the cell, in the form of the chemical adenosine triphosphate, through the process of oxidative phosphorylation (Chial and Craig, 2008). Unlike the other cellular organelles, the mitochondrion contains its own genome, genetically independent of the nuclear DNA, referred to as mitochondrial DNA (mtDNA). There are approximately 1000-10,000 copies of mitochondrial DNA in each cell (Yaping *et al.,* 1993). Structurally, the mammalian mitochondrial genome can range from 15-20 kb in length (species dependent) and is a covalently closed, double stranded, circular molecule, comprised of 37 genes which encode 13 polypeptides, 22 tRNAs and 2rRNAs (Wan *et al.,* 2004; Xie *et al.,* 2015). In addition, there is a single, non-coding region of approximately 1125 base pairs, termed the displacement loop (D-loop), which is located between the ribosomal RNA (12s rRNA) and cytochrome b (Cytb) genes (Figure 9) (Jain and Priya, 2015).

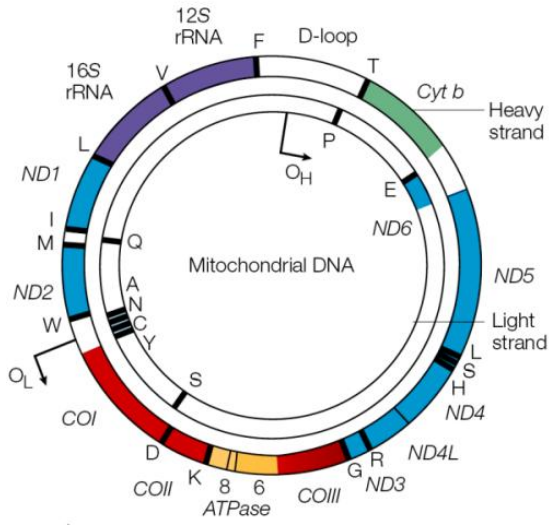

Figure 9. Functional structure of mammalian mitochondrial DNA (Sykes *et al.,* 2014).

The D-loop is also widely referred to as the control region of mtDNA (Pereira *et al.,* 2008). However, Doosti and Dehkordi (2011) clarified that the displacement loop occurs within the control region

segment, and although its function remains unknown, it has been discovered that it contains the regulatory elements for the replication and transcription of mtDNA molecules. In addition to the D-loop, the control region is flanked by two small sites; hypervariable region-1 (HV-I) and hypervariable region-2 (HV-II), the classification of which expresses the high variability of these regions. The mitochondrial genome has a much higher mutation rate than the nuclear genome, with the hypervariable sites stated to evolve at a 5-10 times faster rate (Srivastava *et al.,* 2015). Unlike the biparental inheritance of nuclear DNA, mtDNA is strictly maternally inherited as a haploid unit in most animal species (Chial and Craig, 2008).

2.4.1. Mitochondrial DNA as a Molecular Marker

Molecular markers are identifiable DNA sequences found at specific locations in the genome, which are inherited from one generation to the next. They are used as investigative tools for determining the genetic diversity and biodiversity of populations (Budimir *et al.,* 2014). These markers are classified into two types: mitochondrial and nuclear. Mitochondrial DNA is one of the most popular molecular markers, and has been used since the end of the 1970's. The mtDNA characteristics of maternal inheritance and lack of recombination provide direct genetic lineage of strongly conserved gene arrangements (Boore, 1999). Greater variation is found in mtDNA, because it has an effective population size that is one fourth that of nuclear DNA, from an increased mutation rate (Hellberg, 2006). The simple structure, size, high copy number and ease of amplification demonstrate mtDNA's convenience and feasibility to assay, in comparison with nuclear DNA (Galtier *et al.,* 2009a).

However, several studies have questioned the basic assumptions of three biological properties of mtDNA: clonal inheritance, nearly neutral mode of evolution and high mutation rate (Zhang and Hewitt, 2003; Rubinoff and Holland, 2005; Nabholz *et al.,* 2008; Galtier *et al.,* 2009a). One of the main arguments against using mtDNA is the mode of inheritance, as if the male and female history should differ, this would not be reflected in the overall species/population, as only the maternal lineage is considered (Zhang and Hewitt, 2003; Hurst and Jiggins, 2005). In addition, it has been long thought that

mitochondrial recombination does not occur; yet this has been identified in some animal species, specifically the mussel, lizard, fish and humans (Galtier *et al.*, 2009a). Secondly, it has been proposed that patterns of mtDNA diversity in animals are heavily influenced by adaptive evolution (Galtier *et al.,* 2009a). Bazin *et al.,* (2006) found the average within-species level of mtDNA to be similar across animal phyla, with the cause explained as recurrent selective sweeps, and a higher fixation rate of amino-acid substitutions in species with a large population size: not to be expected under the nearly neutral model. However, this was rejected by Nabholz *et al.,* (2008), whom stated that mammalian mtDNA appears little affected by frequent selective sweeps, and suggested purifying selection and genetic drift are the main determinants of mtDNA diversity. Lastly, it has been shown that mtDNA diversity is highly variable between mammalian orders and families, thought to be due to differences in mutation rate between lineages, yet the reasons for this occurrence remain unclear (Nabholz *et al.,* 2008; Galtier *et al.,* 2009a).

There are numerous applications of mtDNA, but it is commonly used for studies on species origination, genetic differentiation, intra and inter-species phylogenetics, population genetic structure and animal taxonomy (Yaping *et al.,* 1993; Rubinoff, 2006; Ebegbulem and Ozung, 2013), yet more recently has been branching into health, disease and ageing (Chial and Craig, 2008; Tao *et al.,* 2014). In terms of conservation genetics, mtDNA is a valuable tool in both captive and wild populations for estimating genetic diversity and relatedness between individuals, to reduce inbreeding and loss of genetic variation (Arif and Khan, 2009). Several studies in pigs have used the mitochondrial D-loop to establish the origins, genetic diversity and population structure of wild and domesticated indigenous and commercial populations (Grossi *et al.,* 2006; Alves *et al.,* 2010; Zhang *et al.,* 2016). For example, the Tibetan pig, indigenous to the Tibetan highlands, exhibits adaptability to extreme environmental conditions (high, cold climate, low quality pasture all year round); however the breed is at risk of extinction due to limited distribution areas (International Livestock Research Institute (ILRI), 2009). Yet, a mitochondrial diversity study revealed several unique haplotypes and high nucleotide diversity, demonstrating the value of this breed as a genetic resource and thus prioritisation for conservation (Jiao *et al.,* 2009).

2.4.2. Mitochondrial DNA Metrics

At the molecular level, genetic diversity is usually measured by the following metrics: the total and private numbers of haplotypes, proportion of polymorphic loci, gene diversity (*H*): the probability that two randomly chosen haplotypes are different, and nucleotide diversity: the average number of nucleotide differences per site between two sequences (π_n) (Toro *et al.,* 2011; Goodall-Copestake *et al.,* 2012). When estimating differentiation between populations, the most commonly used method is the F_{ST} (fixation index): the probability that two alleles drawn at random from within a subpopulation are identical by descent (Freeland, 2005). Lastly, when detecting natural selection, the most extensively used neutrality test is Tajima's *D*: compares the number of segregating nucleotide sites with the mean number of pairwise differences between two random sequences (Nielsen and Slatkin, 2013). Fu's *Fs* test: based on the haplotype (gene) frequency distribution, conditional on the value of theta, assuming that no recombination has occurred, was selected as it can be more sensitive to other tests in detecting demographic expansion (Ramirez-Soriano *et al.,* 2008).

The described metrics were selected because they have been considered suitable to assess and compare small, fragmented and large, inbred populations. There were numerous studies using the described metrics for mitochondrial DNA analysis, but specifically in indigenous and commercial pig populations, similar to this study. For example, Zhang *et al.,* (2018) used: number of polymorphic sites, number of haplotypes, nucleotide diversity, haplotype (gene) diversity and average number of nucleotide differences (Tajima's *D*), to compare the mitochondrial DNA D-loop sequences of indigenous Bamei pig (Qinghai Province of China) with commercial pigs: Duroc, Landrace and Yorkshire, for sequence variation and genetic diversity. On a global scale, Zhang *et al.,* (2016), examined sequence variation of the mitochondrial DNA D-loop in small indigenous and large commercial pig populations, using the same metrics to assess genetic diversity as stated above.

2.5. Materials and Methods

2.5.1. Sample Population

The sample population for this study was comprised of 99 individuals, separated into 4 breed groups: 24 Gloucester Old Spot (GOS), 25 British Lop (BL), 25 Welsh (W) and 25 Large White x Landrace (LW x LR). The three indigenous UK pig breeds, to be studied, were individually selected relative to the RBST numerical categorisation of registered breeding females differing in conservation status: vulnerable, at risk, minority and the historical connection, in terms of the effectual causes which threatened the existence of each breed. The rare breed and commercial pig keepers were sourced via a request sent in December 2011 to the secretaries of the Gloucester Old Spot Pig Breeders Club (GOSPBC), The Pedigree Welsh Pig Society (PWPS) and the British Lop Pig Society (BLPS), and five leading pig breeding and genetics companies. Due to the limited availability of the rare breed populations, location and willingness to participate; samples were taken from all pig keepers who responded to the request (27%). The rare breed GOS, BL and W boar semen, used for Chapter 4's study, was also sampled to represent the conserved rare breed population of the RBST. Samples were provided by two of the pig breeding companies (40%) to represent the commercial Large White x Landrace population. Further information for each breed group is in Appendix 1.

2.5.2. Sample Collection

Ethical approval was granted by Writtle College's Ethics Committee (Appendix 2). 20 hairs were taken from the back line of each pig, ensuring the hair follicles were intact, using sterile forceps. The hairs were put into individually labelled 2.0ml microcentrifuge tubes, and placed in an ice box for transportation. Samples were frozen upon return to the laboratory (0°C). DNA extraction was carried out following the manufacturer's protocol (QIAGEN): Purification of total DNA from nails, hair, or feathers using the DNeasy Blood & Tissue Kit (QIAGEN) and protocol 2: Purification of total DNA from animal sperm, using the DNeasy Blood & Tissue Kit (QIAGEN)).

2.5.3. Amplification and Sequencing

Genotyping of a fragment of the D-loop region was amplified using the pig specific primers MITL4 (5'-CCAAAAACAAAGCAGAGTGTAC-3') and MITH4 (5-'AGGGATTTTCAGTGCCTTG-3') to produce a 330-bp PCR product as published in Grossi *et al.,* (2006). Total volume of PCR mixture per reaction was 30µl consisting of: 1 x Q solution, 1 x PCR Buffer, 0.6µM dNTPs, 0.1µM Primer 18274F, 0.1µM Primer 18274R, 0.75 Units HotStarTaq Polymerase (QIAGEN), 20-50ng template DNA. A negative control was included for quality control purposes to monitor for contamination. PCR reactions were run using a S1000 Thermal Cycler (Bio-Rad) with the following conditions: 95°C for 5 minutes, then 34 cycles of 94°C for 30 seconds, 56.3°C for 45 seconds, 72°C for 1 minute, and 72°C for 10 minutes. Samples were prepared for sequencing in 0.5ml tubes of 30µl dilutions: 3µl of PCR product to 27µl of H_2O. Samples were sequenced at DNA Sequencing and Services at the University of Dundee, Scotland using the forward primer. For quality control, the process was repeated a second time.

2.5.4. Data Analysis

The first step was to check nucleotide quality at each site by viewing sequence chromatograms within FinchTV version 1.4.0. All 99 sequences were then loaded into ClustalX version 2.1. All sequences were then aligned in accordance with the 'multiple alignment mode', which is carried out by comparing all sequences to each other and identifying regions of similarity. The distances between each pair of sequences were calculated in accordance with the 'slow-accurate' alignment parameters, as it was the most appropriate method for short sequences (<1000 bp). Alignments were carried out with the default transition weighting of 0.5, as the sequences were from the same species, so were classed as 'closely related'. Although the mtDNA data to be analysed was non-coding, by default the programme assigns a protein weight matrix, therefore BLOSUM was selected, as it was the most applicable for evolutionary comparisons between closely related sequences. After the alignment, 10 sequences were removed: 1 GOS, 5 BL, 2 W and 2 LW x LR, due to poor sequence quality and lack of alignment. Once all four groups were re-aligned, the sequences were then loaded into MEGA version 7.0.14. to be edited, by manually cutting all sequences to an equal length. The resultant segment length for all 89 sequences was 201bp.

2.5.5. Statistical Analysis

The statistical analyses of genetic variability were: number of haplotypes, number of polymorphic sites, gene diversity (*H*) and nucleotide diversity (π_n) and genetic differentiation was F_{ST}.

DNASP version 5.10.1. was used to determine the number of private haplotypes within each group, shared haplotypes between the 4 groups, gene diversity, nucleotide diversity and number of polymorphic sites (Librado and Rozas, 2009). Gene diversity and nucleotide diversity were calculated using the formulas in Nei, 1987.

Arlequin version 3.5.2.2. was used to determine the transitions and transversions, F_{ST}, Tajima's *D* and Fu's *Fs* test (Excoffier *et al.,* 2005). Pairwise F_{ST} were used as short-term genetic distances between populations, in accordance with the formula in Reynolds *et al.,* (1983). The statistical analyses of neutrality completed were Tajima's *D* and Fu's *Fs* tests. Tajima's *D* was calculated using the formula in Tajima, 1989. Fu's *Fs* test was calculated using the formula in Fu, 1997.

A phylogenetic tree was created using MEGA version 7.0.14. Preliminary trials of distance (UPGMA, Neighbour-Joining and Minimum Evolution) and character based (Maximum Likelihood - ML and Maximum Parsimony - MP) methods, identified ML as the strongest statistical method. This was because the percentage of branches which clustered together was greater than the application of other methods. The ML method searches for the evolutionary model that has the highest likelihood of producing the observed data (Brinkman and Leipe, 2001). In comparison, MP disregards evolutionary models and minimises the amount of change (Strickler, no date) and the distance based methods disregard the characters, assume evolutionary rates are constant and are more sensitive to systematic errors (Scott and Gras, 2012). The data was then analysed by the Model Selector, in MEGA, to identify the best fit substitution model. Models with the lowest Bayesian Information Criterion (BIC) score are considered to best describe the substitution pattern (Nei and Kumar, 2000).

From the 24 different nucleotide substitution models tested, the Hasegawa-Kishino-Yano (HKY) model was selected as the best model for the data presented, as it had the lowest BIC score. The HKY model recognises that in animal mtDNA, transitional nucleotide changes arise at greater frequency than transversional changes, and that the substitution frequencies of the base pairs are unequal (Hasewaga *et al.,* 1985). The Model Selector also advised the application of a discrete Gamma Distribution of 5, to allow for the non-uniformity of evolutionary rates among sites (Kumar *et al.,* 2016). A Maximum Likelihood heuristic method was applied to increase consistency, robustness and to lower variance in estimation (Strickler, no date). The Nearest-Neighbour-Interchange heuristic method was applied to improve the likelihood of a given tree. This algorithm functions by searching through the tree topologies, interchanging the neighbouring branches and discarding and retaining trees of 'better fit', until a tree with the highest likelihood is reached (Tamura *et al.,* 2013). The initial tree for Maximum Likelihood was automatically created using the Maximum Parsimony method. Sundberg *et al.,* (2008) stated that the performance of heuristic methods for finding Maximum Likelihood trees could be improved by using Maximum Parsimony as an initial estimator.

To ensure the reliability and repeatability of the Maximum Likelihood tree produced, the statistical confidence of each node was estimated by 1000 bootstrap resamplings of the data (Tamura *et al.,* 2013). The sequence for the most recent common ancestor was sourced from the GenBank: Sus scrofa scrofa mitochondrion, complete genome (Accession: KP301137), and was used as the root sequence.

2.6. Results

Marked differences between the traditional breeds: GOS, BL and W, and the commercial LW x LR were discovered from the measures of genetic diversity for the D-loop fragment of mtDNA. From the 89 sequences analysed, 35 haplotypes were identified, with the GOS and W demonstrating the highest haplotype variation and uniqueness. Despite a smaller sample population for the BL, the total and number of private haplotypes was greater, in comparison to the LW x LR. Gene diversity was highest amongst the traditional breeds, with the W exhibiting a very high level, and the lowest in the

commercial LW x LR. However, nucleotide diversity was greatest in the GOS and lowest in the LW x LR, correlating to the differences in number of haplotypes per group. All 4 groups exhibited both transitions and transversions, with the GOS having the largest, and the LW x LR having the smallest numbers (Table 2).

Table 2. (Gene) measures of mtDNA genetic diversity. *n* is the number of individuals, *H* is gene diversity and π_n is a measure of nucleotide diversity.

	Gloucester Old Spot (GOS)	**British Lop (BL)**	**Welsh (W)**	**Large White x Landrace (LW x LR)**
N	23	20	23	23
No. of haplotypes (*h*)	13	9	13	8
Private haplotypes	11	8	11	4
H	0.846 ± SD (0.071)	0.842 ± SD (0.061)	0.874 ± SD (0.060)	0.526 ± SD (0.126)
π_n	0.030 ± SD (0.008)	0.013 ± SD (0.003)	0.023 ± SD (0.006)	0.008 ± SD (0.002)
No. of polymorphic sites	46	16	30	20
Transitions (ts)	29	14	26	9
Transversions (tv)	8	4	6	2

There was no significant differentiation between the BL and W. However, there were significant differentiations between all the other breeds, particularly comparisons between the traditional and commercial groups (Table 3).

Table 3. Measures of population differentiation using F_{ST}. (*) indicates statistical significance $p < 0.05$.

	Gloucester Old Spot (GOS)	**British Lop (BL)**	**Welsh (W)**
British Lop (BL)	0.231 (*)	-	
Welsh (W)	0.233 (*)	0.024	-
Large White x Landrace (LW x LR)	0.044 (*)	0.318 (*)	0.288 (*)

There was only 1 haplotype common in all 4 groups, haplotype 11, which was observed in 1 GOS, 7 BL, 8 W and 1 LW x LR. There were 4 other haplotypes shared between some groups: haplotypes 3, 7, 16 and 30. Haplotype 3 was observed in 1 GOS and 1 W. Haplotype 7 was observed in 9 GOS, 1 BL and 16 LW x LR. Haplotype 16 was observed in 3 BL and 1 LW x LR. Haplotype 30 was observed in 3 W and 1 LW x LR (Table 4).

Table 4. mtDNA haplotype frequencies occurring in all four groups.

Haplotype number	Gloucester Old Spot (GOS)	British Lop (BL)	Welsh (W)	Large White x Landrace (LW x LR)
H1	0.043	-	-	-
H2	0.043	-	-	-
H3	0.043	-	0.043	-
H4	0.043	-	-	-
H5	0.043	-	-	-
H6	0.130	-	-	-
H7	0.391	0.050	-	0.696
H8	0.043	-	-	-
H9	0.043	-	-	-
H10	0.043	-	-	-
H11	0.043	0.350	0.348	0.043
H12	0.043	-	-	-
H13	0.043	-	-	-
H14	-	0.050	-	-
H15	-	0.200	-	-
H16	-	0.150	-	0.043
H17	-	0.050	-	-
H18	-	0.050	-	-
H19	-	0.050	-	-
H20	-	0.050	-	-
H21	-	-	0.043	-
H22	-	-	0.086	-
H23	-	-	0.043	-
H24	-	-	0.043	-
H25	-	-	0.043	-
H26	-	-	0.043	-
H27	-	-	0.043	-
H28	-	-	0.043	-
H29	-	-	0.043	-
H30	-	-	0.130	0.043
H31	-	-	0.043	-
H32	-	-	-	0.043
H33	-	-	-	0.043
H34	-	-	-	0.043
H35	-	-	-	0.043

For the neutrality tests, Tajima's *D* and Fu's *Fs*, was negative for all 4 groups. There were statistical significances in the Tajima's *D* test for the GOS, BL and W groups, and in the Fu's *Fs* test for the LW x LR group (Table 5).

Table 5. Results of Tajima's D and Fu's Fs neutrality tests. (*) indicates statistical significance $p < 0.05$.

	Gloucester Old Spot (GOS)	**British Lop (BL)**	**Welsh (W)**	**Large White x Landrace (LW x LR)**
Tajima's *D* test	-1.556 (*)	-1.739 (*)	-1.769 (*)	-1.321
Fu's *Fs* test	-1.702	-2.578	-3.591	-2.998 (*)

The commercial and traditional populations have mainly remained clustered together in 8 distinct clades (Figure 10). The GOS at the bottom of the tree, followed by the LW x LR, then a second group of GOS, followed by a small group of BL, then a large group of W, with the final part of the tree being interspersed with W and BL towards the top. There are 7 exceptions; BL 48 034, LW43 049, GOS41 048, GOS21 023, GOS35 043, LW41 050 and LW41 051. The nodes have yielded confidence levels between 51-75%.

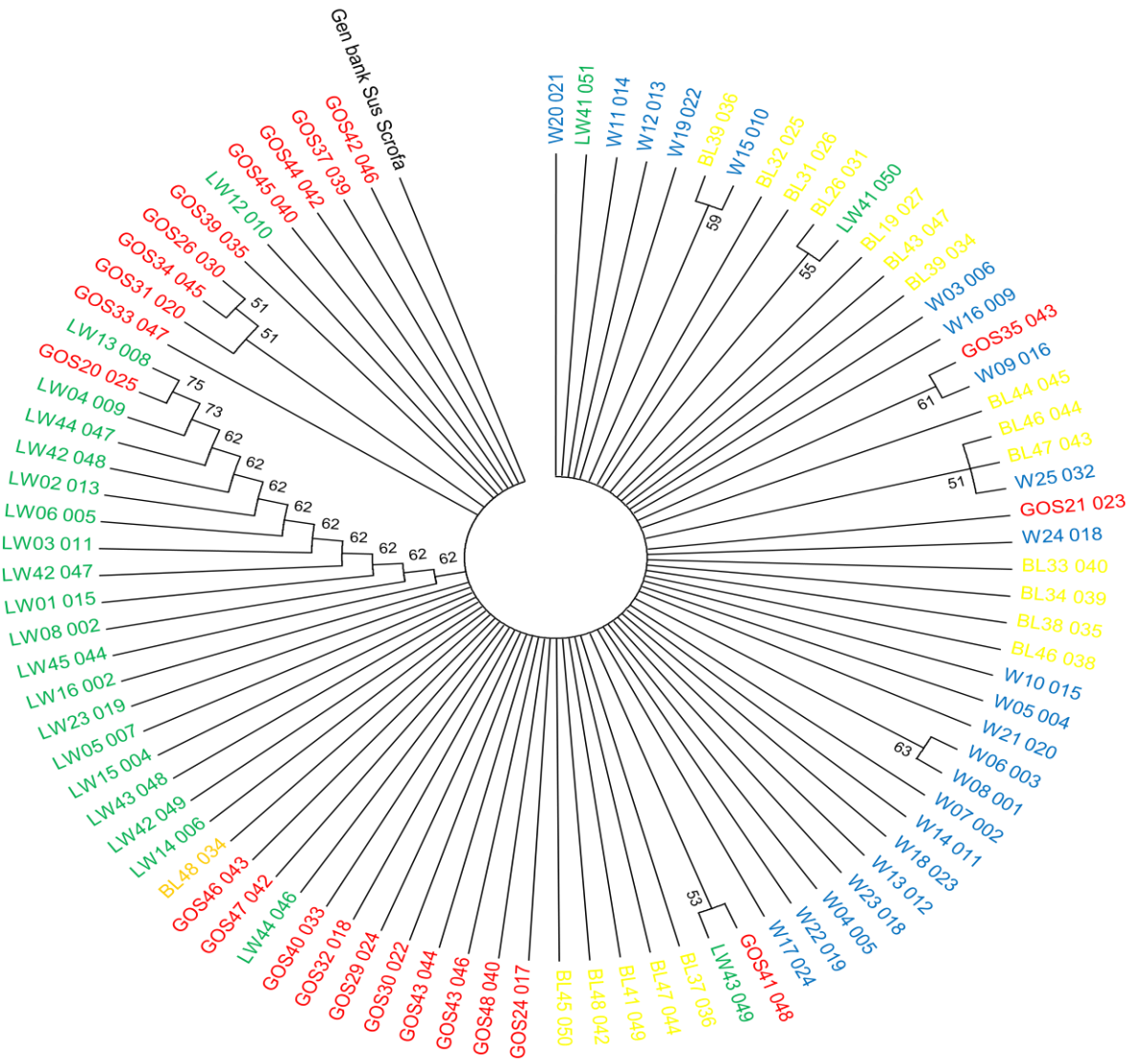

Figure 10. Phylogenetic analysis by Maximum Likelihood Method based on the Hasegawa-Kishino-Yano model. Percentage of replicate trees are shown next to the branches (1000 bootstrap replications). Initial tree for the heuristic search were obtained by applying the Maximum Parsimony Method. Red – GOS; Yellow – BL; Blue – W; LW x LR – Green.

2.7. Discussion

There are evident differences between the traditional breeds: GOS, BL and W and the commercial LW x LR, with regards to the levels of mtDNA diversity within the D-loop fragment investigated.

2.7.1. Haplotype Diversity

The traditional breeds demonstrated the greatest haplotype variation, with 13 haplotypes identified in the 23 W, 13 in the 23 GOS and 9 in the 20 BL, whereas the commercial LW x LR displayed the lowest count with only 8 haplotypes. Moon *et al.,* (2015) have observed low haplotype diversity in contemporary pig breeds: Large White and Landrace, which is considered to be as a result of intensive artificial selection within modern breeding programmes. However, Bosse *et al.,* (2015) said that commercial breeds have greater haplotype diversity than their wild counterparts, from the introgression of Asian haplotypes during domestication. Interestingly, haplotype 11 is present in all three traditional and the one commercial population suggesting a shared common ancestor (Bosse *et al.,* 2014). Yet, the definitive origin of, and the extent to which Asian pigs have contributed genetically to, the domestic pig is still being researched (Frantz *et al.,* 2015).

The low haplotype count of the commercial group could be attributed to relatedness of individuals within the Large White and Landrace populations (Moon *et al.,* 2015). In contrast to the results of this study, traditional pig breeds are stated to have low haplotype diversity, caused by inbreeding, relatedness between individuals and small population numbers (Molnár *et al.,* 2013; Zhang *et al.,* 2016). Yet, several mtDNA variation studies have demonstrated high and unique haplotype diversity in indigenous livestock species. Gorkhali *et al.,* (2015) discovered that of the 111 individuals studied, no haplotypes were shared, from the 64 identified, between the four breeds of indigenous Nepalese sheep, demonstrating their widespread distribution, lack of interbreeding and high levels of mtDNA haplotype diversity. Whereas a study on the newly classified, yet endangered breed of indigenous Chikso cattle, identified 13 haplotypes within the breed, 11 of which were Chikso-specific and 1 of which was only shared between the indigenous Asian cattle breeds, showing the genetic differentiation from the European breeds Kim *et al.,* (2013a).

2.7.2. Heterozygosity

The heterozygosity differences between breed groups were not statistically tested. The heterozygosity differences per breed group represent the individuals sampled for this study, not the breeds as a whole. The traditional W exhibited the greatest level of heterozygosity (0.874 ± SD 0.060), whereas the commercial LW x LR displayed the lowest level of the 4 groups (0.526 ± SD 0.126). The high heterozygosity of the W breed could be as a result of the historic mixing of the Swedish Landrace and the indigenous W in the 1950s, to create the modern W (Porter, 1993). The low heterozygosity of the LW x LR breed could be attributed to the commercial nature of genetic isolation and the intensive selection for productivity, at the expense of natural adaptations for survival (ILRI, 2011).

The result for the W was expected to be lower, as it was once a semi-commercialised breed, however they were not rigorously selected in the same way as the LW x LR, and suffered a population decline following intensification of the industry (The Pedigree Welsh Pig Society (PWPS), 2014a). The W population numbers have steadily recovered, with an estimated 850 registered breeding pedigree pigs in 2016 (British Pig Association (BPA), 2016f). This could justify the high heterozygosity level of the W group, as it has been identified that as population size increases, as does the amount of genetic variation, from reduced relatedness between individuals and introduction of new lineages (Ortego *et al.,* 2007). This could also account for the high heterozygosity level of the GOS group (0.846 ± SD 0.071), as they are numerically the largest of all the traditional pig breeds and have the most stable bloodlines (BPA, 2016g).

However, this does not answer the result for the BL group, as the breed is rarest of all the native pigs (British Lop Pig Society (BLPS), 2014a), yet had a marginally smaller heterozygosity level (0.842 ± SD 0.061) than the GOS group. Although it is predicted that reductions in population size negatively impact genetic diversity, not all small populations will show decreased genetic diversity. It has been said that breed maintenance and/or development can result in genetically diverse, yet small populations, despite periods of decline (Torres-Florez *et al.,* 2014). This could explain the result for the British Lop group; as

there was a large purebred population pre-war, which narrowed during the war, however was maintained by 11 breeders, and has been steadily maintained from 1975 to the present day (BLPS, 2014a).

Druml *et al.,* (2012) have proposed that the large founder gene pool, controlled breeding programmes and increased population sizes are responsible for the high levels of heterozygosity in European commercial pig breeds such as the LW and LR. Although the population sizes of the LW and LR are numerically large, intensive selection and artificial breeding strategies can lead to undesirable losses of genetic diversity, increased inbreeding and high levels of homozygosity with detrimental consequences on productivity (Zanella *et al.,* 2016). This is supported by Zhang and Plastow (2011) whom discovered that in comparison with their wild counterparts; European commercial pig breeds (Large White, Landrace, Hampshire, Duroc) have much lower heterozygosity levels, with an average of 0.570, which is similar to the result of the LW x LR group of 0.526.

2.7.3. Nucleotide Diversity

The GOS displayed the highest level of nucleotide diversity (0.030 ± SD 0.008) and number of polymorphic sites (46), whereas the commercial LW x LR presented the lowest nucleotide diversity (0.008 ± SD 0.002) and polymorphisms (20) of the 4 groups. Both results are consistent with the high haplotype count of the GOS group (13) and low haplotype count of the LW x LR group (8).

The low nucleotide diversity of the commercial group could be as a result of the breeding of highly productive, yet genetically concentrated terminal sires and dam lines, which has lead to the fixation of desirable alleles through artificial selection (Ramírez *et al.,* 2009). However, Bosse *et al.,* (2012) stated that in their study nucleotide diversity was higher in European domestic breeds compared to the European wild boars, which again was attributed to the speculative hybridisation with Asian pigs during domestication. This is supported by Ojeda *et al.,* (2008), whom stated that nucleotide diversity was low in the European wild boar, due to a population bottleneck, followed by an expansion, prior to domestication. Yet, a study on indigenous Indian cattle identified high nucleotide diversity in all 11

breeds, which was suggested to be because of the extensive management practices of traditional livestock breeding systems (Sharma *et al.,* 2015). This could explain the high nucleotide diversities of the traditional pig breeds of this study, as they are commonly reared for preservation and high quality produce on small-scale, indoor/outdoor, pastoral farms (Lewis, 2011).

The high nucleotide diversity of the GOS could be attributable the population size, with 1053 breeding females and 174 males recorded in 2016 (BPA, 2016g). Additionally, the breeding system encouraged by the GOSPBC aims to increase genetic diversity by identifying unrelated stock and practicing line breeding (Gloucester Old Spot Pig Breeders Club (GOSPBC), 2012c).

Although the W exhibited the greatest level of heterozygosity, the result for nucleotide diversity was less (0.023 ± SD 0.006) than that of the GOS (0.030 ± SD 0.008). This could be associated with the semi-commercialised nature of the breed: the selective breeding for particular carcass, meat qualities and eating traits (European Union Commission (EUC), 2015), and/or the smaller population numbers of 590 breeding females and 114 males. Additionally, although there are 26 female bloodlines, registered sows are in decline with a 2.8% loss from 2017 to 2018, 30% are of the bloodlines: Lucky Girl, Nina or Theresa, and 3 bloodlines are very vulnerable to extinction. The boars have had a 5.5% increase in registered numbers from 2017 to 2018, however two bloodlines: Arthur and Ivor are at risk with low numbers (BPA, 2018c).

Lastly, the result for the BL was the lowest of the traditional breeds (0.013 ± SD 0.003), yet was greater than that of the LW x LR. In comparison with the GOS and W groups, the low nucleotide diversity of the BL group could be attributed to a population bottleneck, experienced in the 1950s, following the publication of the Howitt Report (RBST, 2011b). Whilst the breed has been slowly stabilising, the BL remains the rarest of all the native UK pig breeds, with the smallest population size of 150 breeding females and 50 males recorded in 2015 (Miller, 2016). Additionally, although there are 10 female bloodlines, a third of the population are of the bloodline Harmony. Whilst the BL has the smallest population of the 4 groups studied, the higher nucleotide diversity than the modern LW x LR could be

due to the extensive nature of the breed: stable bloodlines, limited selective breeding and rare presence in commercial production.

2.7.4. Transitions and Transversions

It is well established that transitional nucleotide changes (purine to purine or pyrimidine to pyrimidine) occur with greater frequency than transversional changes (purine to pyrimidine or pyrimidine to purine) in mammalian genomes. This universal bias is primarily due to the biochemical structure of the nucleotide bases and the chemical properties of complementary base pairing (Yang and Yoder, 1999; Rosenberg *et al.,* 2003).

All groups demonstrated greater transitions than transversions, which agrees with the transitional mutation pattern found within mammalian mtDNA. The GOS displayed 29 ts to 8 tv, followed by the W with 26 ts to 6 tv, then the BL with 14 ts to 4 tv and lastly the LW x LR with 9 ts to 2 tv.

2.7.5. Genetic Differentiation

The greatest breed genetic differentiation (F_{ST}) was between the native BL and the commercial LW x LR groups (0.318). This demonstrates that there were extremely low levels of gene exchange during the development of the Yorkshire breed from the 18th century onwards (Porter, 1993; Scali *et al.,* 2011). The confined geographical locality and independence of the BL breed society would also explain the large differentiation between the two populations (Porter, 1987). The F_{ST} (0.288) results between the modern W and the conventional LW x LR were quite surprising, on account of the past semi-commercialised nature of the W breed (PWPS, 2014a). However, although the modern W prospered during 1950-1980s (BPA, 2016e), this result could suggest that genetic introgression of the W into the LW and LR for breed improvement was rare.

On the other hand, there was moderate genetic differentiation (0.044) between the traditional GOS and the commercial LW x LR. This is supported by Porter (1987; 2011) who states that the Large White and

Landrace were both improved with the GOS, due to the breed's docility, prolificacy and quality of bacon and hams.

However, it was the comparison of the BL and W groups which demonstrated little genetic differentiation (0.024). This could be attributed to various reports which suggest that the Welsh and old English Lops are of the same type and origins. The Old Glamorgan Pig Society, Welsh Pig Society and Long White Lop-Eared Pig Society merged during 1922-1926 to form the National Long White Lop-Eared Pig Society. Although the Welsh Pig Society and National Long White Lop-Eared Pig Society (British Lop Society from 1969) separated in 1928 (Porter, 1987; BLPS, 2014a), the amalgamation of societies demonstrates the little genetic differentiation between the BL and W. This is further strengthened by the overall topology of the phylogenetic tree (Figure 10), with the commercial LW x LR and traditional GOS grouped at the base, and the traditional BL and W interspersed at the top.

The F_{ST} (0.231) of the GOS and BL and F_{ST} (0.233) of the GOS and W are quite similar, showing large genetic differentiation between the populations. This could have been caused by geographical location, the tradition of purebred populations and selection for improvement within the breeds (Porter, 2011).

2.7.6. Neutrality Tests

All 4 groups exhibited negative results for Tajima's *D* and Fu's *Fs* neutrality tests. The negative values of the Tajima's *D* test indicate a presence of rare alleles at high frequencies, which can be caused by population growth, selective sweep or positive selection (Stajich and Hahn, 2004). Similarly, the negative values of Fu's *Fs* test indicate an excess of recent mutations, which can be caused by expansion in population numbers and/or selection (Alexandrino *et al.,* 2002).

The significantly negative Tajima's *D* results of the GOS (-1.556), BL (-1.739) and W (-1.769) indicate an excess number of rare alleles compared to what would be expected under neutrality, which implies a demographic expansion, following a genetic bottleneck (Sharma *et al.,* 2013). The recent population fluctuations of the GOS, BL and W have mainly been driven by trends in consumer demand for

traditional, rare breed meat and meat products, and thus the number of registered traditional livestock breeders/keepers (BPA, 2016h). However, the non-significant negative result of the LW x LR (-1.321) could be attributed to strong selective sweep for favourable traits, triggered by intensive selection for improved phenotypes, within the modern pig industry (Chen *et al.,* 2007). This is supported by Ojeda *et al.,* (2008) whom stated that the strong negative values for modern pig breeds: Large White, Duroc and Hampshire, were as expected for a classical selective sweep.

The negative, but not significant, Fu's *Fs* results of the GOS (-1.702), BL (-2.578) and W (-3.591) indicate an excess of rare haplotypes compared to what would be expected under neutrality, which again implies demographic expansion. The negative value of the LW x LR (-2.998) indicates an excess of recent mutations, which again implies strong selective sweep within the commercial pig population (Joshi *et al.,* 2013). Yet, the results of the three traditional breeds for Tajima's *D* are significant, but non-significant for Fu's *Fs* test, and the commercial breed results are significant for Fu's *Fs* test, but non-significant for Tajima's *D.* It has been suggested that Fu's *Fs* test is a more sensitive indicator of population expansion and selective sweep than Tajima's *D* (Li *et al.,* 2015). Therefore, as both neutrality tests demonstrate negative values, it can be surmised that the three traditional breed populations have undergone expansions, and the commercial population has experienced selective sweep.

2.8. Conclusion

Traditional pig breeds have been recognised as a valuable future genetic resource from the possession of unique behavioural, physiological and morphological traits: maternal qualities, adaptation to harsh environments and disease resistance. There are presently limited to no studies assessing the genetic diversity of traditional British pig breeds, and comparing this with the commercial European hybrid. However, the analysis of genetic diversity, within the mtDNA D-loop fragment, and comparisons of population differentiation in this study revealed marked differences between the traditional and commercial breeds. The three traditional breeds all presented high levels of genetic diversity, with the greatest overall in the GOS, followed by the W and the BL, whereas the commercial LW x LR

demonstrated the opposite results. This was further supported by the population differentiation results, which identified the BL and LW x LR as the more distantly related breeds, followed by the W and the GOS. Traditional and modern pig breeds could potentially be amalgamated, to ensure sustainability and improve production, by maintaining the valuable characteristics of both. The BL and W demonstrated the greatest potential for genetic conservation to benefit the LW x LR. Although the GOS demonstrated high levels of genetic diversity, there was only moderate genetic differentiation between the GOS and LW x LR. However, this study highlighted the conservation value of all three traditional breeds: providing genetically diverse populations, to maximise opportunities for the commercial pig industry in the future.

Chapter 3. Assessing the Impact of Crossbreeding on Nuclear DNA Diversity

3.1. The Consequences of Increased Litter Size

Over the past few decades, the global pig industry has strived to increase the number of piglets born alive and number of piglets weaned per litter, to maximise profitability by improving the reproductive efficiency of the sow (Knox, 2013). In order to achieve the above goal, pig breeding and genetics companies have strongly selected for litter size within commercial dam lines (Whittemore and Kyriazakis, 2006). From 1970 to 2016, the average number of pigs born alive per litter has increased over a full three pigs, from 10.2 to 13.2 (Halley and Soffe, 1988; Agriculture and Horticulture Development Board (AHDB), 2017b). However, numerous studies have demonstrated a negative genetic correlation between selection for larger litter sizes and piglet survival (Knol *et al.,* 2002; Wolf *et al.,* 2008; Kapell *et al.,* 2011). This can be confirmed by the increased pre-weaning mortality rates in the UK, from an average of 10-13% in 2010 (AHDB, 2010), to an average of 16-20% in 2016 (Scotland's Rural College, 2016). The two major causes identified as higher numbers of low birth weights piglets (< 1.2 kg) and increased within litter variability in birth weight (Wolf *et al.,* 2008; Zindove *et al.,* 2014). Lower birth weight piglets are at greater risk of pre-weaning mortality from inadequate energy reserves, low colostrum intake, poor thermoregulation and direct competition to functional and productive teats (Milligan *et al.,* 2002; Souza *et al.,* 2014). Cabrera *et al.,* (2012) demonstrated that the combination of these factors not only led to elevated mortality but slower postnatal growth and a compromised immune system.

3.1.1. Effects on Latter Stages of Production

Pig producers commonly use the number of pigs weaned per sow per year (PWSY) as a benchmarking tool to measure the efficiency and productivity of their breeding herds (Koketsu *et al.,* 2017). In the UK, producers of indoor sows are currently achieving an average of 26.4 PWSY and for outdoor sows, an average of 22.5 PWSY (Davis, 2016). It has been shown that large birth weight variation within litters can have significant effects on the latter stages of production: weaning, growing, finishing and slaughter

(Wittenburg *et al.,* 2008). Milligan *et al.,* (2002) and Quesnel *et al.,* (2008) found that litters with more variable birth weights, low individual birth weights and greater numbers of litter-mates were more likely to have high variation in weights at weaning. Uniformity in weaning weight is desirable for producers, as it results in easier management of the growing-slaughter stages and greater efficiency of producing a high-quality product (Taylor and Roese, 2006). Additionally, piglets of lower birth weight develop poorer carcass composition: higher fat and lower lean deposition, and lower meat quality: tenderness and water holding capacity, in comparison to piglets of medium and heavy birth weights (Rehfeldt *et al.,* 2008; Wittenburg *et al.,* 2008).

3.2. Improving Piglet Survival

3.2.1. Management Techniques

The profitability of a pig herd is significantly impacted by the survival of piglets/litters through to weaning (AHDB, 2010; Roy *et al.,* 2014). In order to increase piglet survivability, during the critical 72 hours after birth, management strategies focused on maximising colostrum intake and minimising heat loss are implemented (Muns Vila, 2013). The most standard practices include cross-fostering: equalising numbers, standardising weights and ensuring sufficient teats, by transferring piglets between sows/litters (Deen and Bilkei, 2004; Douglas *et al.,* 2014a), split suckling: splitting litters into two groups of light and heavy birth weight piglets and rotating teat access for a predefined time (British Pig Executive (BPEX), 2012), and the manipulation of the piglet's micro-environment: provision of bedding materials, heat lamps or mats and/or a heated creep area (Wiegert and Estienne, 2015).

In order to improve viability and increase average daily gain to weaning, the nutritional intervention of creep feeding: feeding a solid diet to piglets, while they are still suckling the sow, to prepare their digestive system for weaning, is commonly implemented from day seven of age (BPEX, 2013). However, the newest management technique, to accommodate for surplus or low viability piglets, is an artificial rearing system called Rescue Decks: specially designed, fully slatted, heated and lit units, positioned

above farrowing crates, offering artificial milk and water to up to 12 piglets aged 3-28 days (Baxter *et al.,* 2013).

Although the management techniques mentioned have shown to have the greatest influence on reducing pre-weaning mortality (Muirhead and Alexander, 2013), it has been stated that the mortality reduction limit through these means has been reached, and any future improvements in survivability will need to be achieved in combination with breeding and genetics (Roehe *et al.,* 2010).

3.2.2. Crossbreeding to Improve Productivity

The practice of crossbreeding is widespread in livestock production: used to exploit diversification by combining desirable characteristics of many breeds or targeting a particular trait to maximise hybrid vigour, thus achieving significant increases in productive output (Wiener and Wilkinson, 2011; Ruusunen *et al.,* 2012). As discussed in Chapters 1 and 2, traditional breeds are reservoirs of genetic diversity, developed historically to suit a regional market/system (British Pig Association (BPA), 2016h), whereas modern breeds have been intensively selected for productive efficiency to fulfil global demand (Kanis *et al.,* 2005). However, crossbreeding the two extremes could result in greater diversity of functional and production traits, enabling breed improvement in response to future changes in: climate, disease, production requirements, resource availability and market demands (FAO, 2007; FAO, 2015b). There are numerous studies demonstrating the beneficial effects of crossbreeding traditional breeds with their commercial counterparts to improve their overall productivity (Berthouly-Salazar *et al.,* 2012; Hailu, 2013; Weißmann, 2014). For example, the Boer goat has been used extensively across developing countries to enhance the productivity of local breeds for meat production, with significant improvements observed in the crossbred progeny of greater birth, weaning and finished weights and average daily gains. The positive heterosis effect for the production traits is attributed to the large genetic distances between the two breeds crossed (Assan, 2013c).

Traditional breeds are renowned for their survival attributes: instinctiveness, hardiness, heat and nutritional tolerance and parasite, disease and stress resistance (Scarpa *et al.,* 2003; Moonga and Chitambo, 2010). Yet, there are very few studies demonstrating how these traits could be utilised to improve the environmental adaptability of commercial breeds and increase their productivity: survival rates. Although, Olson (2011) described the importance of *Bos indicus* breeds in the production of crossbred cattle for commercial beef in Florida, as they inherit the adaptability to extreme environmental conditions. In addition, a recent study by Wilkes *et al.,* (2017) identified that crossbreeding with indigenous Mongolian sheep breeds significantly increased productivity (liveweight gain) and improved adaptation to winter climates in the crossbreds. Thus, functional traits can be positively conferred to commercial breeds, supporting the notion of which production traits i.e. survivability, of traditional breeds will also be of benefit.

3.2.3. Past Genetic Improvement using Traditional Breeds

Since the late 1980s, pig breeding and genetics companies have investigated and developed, with some having produced synthetic lines, the Chinese Taihu breeds, particularly the Meishan (MS), to improve prolificacy and piglet survivability (McLaren, 1990; Porter, 1993). These traditional breeds are reputable for producing large litters of light birth weight piglets with very low rates of mortality, in comparison to the high mortality and within-litter weight variation of the intensively selected Large White (LW). It has been stated that, in Meishan litters, this is due to the physiological maturity of the piglets at birth, attributed to the prenatal adaptations of the liver, increased body lipids, vascularity of the placenta and homogeneity of individual birth weight (Fainberg *et al.,* 2012; Voillet *et al.,* 2014; Hong *et al.,* 2016).

Behaviourally, it has been reported that the Meishan has a lower incidence of crushing than the commercial hybrid dam, from the innate characteristics of increased time spent nest building pre-farrowing and lying post-farrowing, fewer postural changes throughout lactation and greater piglet contact (Minick *et al.,* 1996; Farmer *et al.,* 2001). Additionally, number of functional teats equates to milking ability, the optimal number of teats is 16; yet the commercial average is currently 12-14

(Muirhead and Alexander, 2013), whereas the Chinese Taihu breeds have an average of 16-18 teats (McLaren, 1990).

An early study in 1987 identified that Meishan (MS) x LW F_1 sows produced large numbers of piglets born alive: up to four more live than the purebred LW sow, the MS x LW progeny grew at the same rate as the LW, and the MS x LW back fat levels were between those of each breed (Porter, 1993). Similarly, Wolter *et al.,* (2000) established that Meishan F_1 crossbred dams could significantly improve reproductive and litter productivity traits; but the growth performance and carcass quality of their progeny was considerably poorer than that of the commercial hybrid. This demonstrates the reproductive capacity of traditional dams and their potential for genetic selection and/or crossbreeding, yet they require productive development to be considered for further commercial application. However, due to the considerable genetic improvements made in commercial dam line (LW x LR) productivity, an alternative strategy to consider would be that of selection for increased survivability in terminal sire lines.

3.3. Paternal Imprinting: DIO3

Recent studies have demonstrated the important role of paternally imprinted genes on placental development, embryonic and foetal growth and survival (Yang *et al.,* 2009; Qiao *et al.,* 2012; Oczkowicz *et al.,* 2015). In mammals, a small number of genes are marked with their parental origin, which results in either maternal-specific or paternal-specific mono-allelic expression: imprinted genes (Li and Sasaki, 2011). The process of genomic imprinting is achieved by silencing one parental allele via DNA methylation of CpG-islands and histone modifications at imprinting control regions (Pervjakova *et al.,* 2016). The repressed allele is methylated, whereas the active allele is unmethylated (Bajrami and Spiroski, 2016). The life cycle of imprints involves erasure during early germ cell development, establishment later in the development of sperm or eggs, transmission to the zygote through fertilisation, maintenance during embryonic development and returning to erasure in the germ cells of the embryo (Reik and Walter 2001; Abramowitz and Bartolomei, 2012; Li and Sasaki 2011). The

mechanisms to 'read' the imprint can involve different aspects of gene regulation: promoters, enhancers, silencers, insulators, boundary elements and antisense transcripts (Reik and Walter, 2001). If the paternal allele is expressed, the maternal allele is imprinted (silenced) and vice versa. For example, the paternally expressed IGF2 gene and maternally expressed H19 gene share enhancers and their reciprocal imprinting controlled by a CTCF insulator protein: an element that blocks enhancer and promoter interactions when placed between them (Abramowtiz and Bartolomei, 2012). On the maternal chromosome, the presence of CTCF blocks the enhancers from interacting with IGF2 promotors: inactivates gene, the enhancers drive activity from H19 instead. On the paternally inherited chromosome, the CTCF cannot bind, due to DNA methylation in the male germline, the enhancers drive activity from the IGF2 promotors and secondary methylation silences the paternal H19: IGF2 gene expressed (Bartolomei and Ferguson-Smith, 2011; Barlow and Bartolomei, 2014).

It has been shown that the iodothyronine deiodinase type 3 (DIO3) gene has central importance in the modulation of the thyroid hormone: encodes for a selenoenzyme which catalyses the conversion of the prohormone thyroxine (T4) and bioactive hormone (T3) into biologically inactive metabolites (Hernandez, 2005; Charalambous and Hernandez, 2013). This enzyme is highly expressed in the pregnant uterus, placenta, foetal and neonatal tissues, hence it is assumed that DIO3 maintains the appropriate levels of thyroid hormone, during each stage of development, to prevent premature and/or overexposure to adult levels (Martinez *et al.,* 2014; National Center for Biotechnology Information, 2017). It has been discovered that DIO3-deficient mice exhibit reduced fertility, growth retardation, immunodeficiency, impaired neurological and endocrine functions and low neonatal viability (Hernandez, 2005; Charalambous and Hernandez, 2013). Therefore, it has been suggested that DIO3 plays a critical regulatory role in mammalian growth and development, particularly during the embryonic, foetal and early postnatal stages (Coster *et al.,* 2012; Oczkowicz *et al.,* 2015).

The DIO3 gene is located in the evolutionary conserved DLK1-DIO3 imprinted domain, which also contains another two paternally expressed imprinted protein-coding genes; Delta-like homologue 1

(DLK1) and Retrotransposon-like gene (Rtl1/Mart1) (Edwards *et al.,* 2008b), and multiple maternally expressed imprinted non-coding RNA genes, for example; gene 3 (Gtl2/Meg3), gene 8 (Rian/Meg8), PEG11-antisense gene (PEG11AS) and micro-RNA containing gene (MIRG) (Magee *et al.,* 2011). In pigs, the DIO3 gene is intronless, has one exon and is located in the DLK1-DIO3 imprinted domain on chromosome 7 (Qiao *et al.,* 2012).

DIO3 is generally considered to be expressed preferentially from the paternally inherited allele; however studies have shown repression of the maternal allele is not complete, with tissue-specific biallelic or maternal expression reported in the placenta and regions of the brain in mice (Medina *et al.,* 2012). Yet, in the pig, high paternal expression of DIO3 has been identified in several embryonic and foetal tissues, for example liver, uterus, kidney, heart and small intestine (Qiao *et al.,* 2012), and in the live tissues of 2 month old piglets, for example skeletal muscle, heart, spleen, lung, stomach and brain (Yang *et al.,* 2009). Yang *et al.,* (2009) identified DIO3 A744C polymorphism (AY533208), however the genotypes were not significantly associated with any carcass traits. Whereas, Qiao *et al.,* (2012) found significant associations between a DIO3 single nucleotide polymorphism (SNP) A/C 687, and carcass and meat quality traits. The genetic variation analysis revealed the Chinese indigenous breeds having higher frequencies of the C allele, associated with an increase of fat deposition traits and a decrease of muscle traits compared to the commercial breeds, with the predominant A allele presenting opposite effects.

The relationship between imprinted genes and economically important production traits has been further demonstrated in cattle and sheep. In sheep, the DLK1-DIO3 imprinted domain, located on chromosome 18, contains the 'callipyge' (CLPG) mutation, a single A to G substitution, which causes postnatal increased muscle growth, along with reduced total fat content, in heterozygous offspring (Yang *et al.,* 2009; Magee *et al.,* 2011). In cattle, the DLK1-DIO3 imprinted domain, located on chromosome 21, contains the CLPG_1 SNP, orthologous to the sheep mutation, which has displayed similar phenotypic associations as described above (Magee *et al.,* 2011).

In addition, Coster *et al.,* (2012) and Oczkowicz *et al.,* (2015) have identified further polymorphic site within the DIO3 gene, which are hypothesised to be associated with the regulation of female fertility, litter size and/or early embryonic survival. Coster *et al.,* (2012) identified the SNP ASGA0037226 as being closely linked to DIO3 and showing a significant imprinting effect on the total number of piglets born, suggesting the two have a combined effect on litter size. This is further supported by Oczkowicz *et al.,* (2015), revealing significant associations between the two DIO3 polymorphisms studied, rs80999359 and rs80983654, and several reproductive traits, for example number of piglets born alive, number of piglets at 21 days and period between parities. As the studies on the DIO3 gene in the pig are few and broad, further research is necessary to clarify the role and effects of this gene on productive and reproductive performance, as it appears a promising target for future genetic selection.

In the mouse, DIO3 has also been shown to be of importance to embryonic growth, foetal development and postnatal survival (da Rocha *et al.,* 2008), as hormone modulation contributes to metabolic and environmental adaptation, thus aiding the transition from foetal to postnatal life (Labialle *et al.,* 2014). This is supported by Hernandez *et al.,* (2007) and Charalambous *et al.,* (2012) whom have suggested that DIO3 may regulate adipocyte proliferation and stimulate cell differentiation, to develop brown adipose tissue for energy metabolism and homeostasis. As piglets are born with limited reserves of fat and glycogen, this gene demonstrates potential for future selection, as increasing brown adipose tissue could improve thermoregulatory ability and energy storage, resulting in greater chances of survival (Hales *et al.,* 2014).

3.3.1. Using Protein-coding Genes to Analyse Genetic Diversity

Protein-coding genes have been used for various mammalian genetic studies on the examination of intra-species phylogenetics, genetic diversity and functional genomic differences, identification of novel polymorphisms and mutations, and the development of genetic maps (O'Brien *et al.,* 1999; Bonde *et al.,* 2012). Although, mitochondrial DNA is generally chosen for the analysis of genetic diversity, due to the characteristics of high variability and mutation rate (Galtier *et al.,* 2009a), it has been identified that in

protein-coding genes, the sequence divergence within species is sufficient for analysis, and the rate of evolution is generally high (Palys *et al.,* 2000).

It has been shown that protein-coding genes can be used to identify genetic variants for specific disease, behavioural, phenotypic characteristics and production traits, which demonstrate potential for inclusion within future selection strategies. For example, a fragment of the interferon-induced guanylate-binding protein 1 gene (GBP1), key to protective immunity, was explored in wild (Hungarian, Chinese), domestic (Iberian, Hungarian, Romanian, Chinese) and commercial pig breeds (Pietrain, Large White, Landrace), which found that a sizeable proportion of genetic diversity in wild and domestic species, is not present in commercial breeds for this gene (Chen *et al.,* 2012). Whereas, in cattle, the tyrosine hydroxylase (TH) and dopamine β-hydroxylase (DBH) genes were sequenced to assess the genetic variation between the *Bos taurus* and *Bos indicus* breeds for temperament differences, which revealed significant differences in the intra and inter-population haplotype distribution, and the future selection potential for behavioural phenotypes (Lourenco-Jaramillo *et al.,* 2012). Whilst a recent study genotyped three codons in the prion protein gene (PRNP), to analyse genetic diversity in 34 Czech Republic sheep breeds, which displayed the positive effects of the national scrapie resistance breeding programme on significantly increasing resistant, and decreasing susceptible, haplotypes and genotypes (Stepanek and Horin, 2017). In addition, both of these studies discovered novel haplotypes in native breeds (Chen *et al.,* 2012; Stepanek and Horin, 2017), demonstrating their conservation value for future selection, and validating the use of protein-coding genes as a surveillance tool to monitor genetic diversity for specific genes.

3.3.2. Nuclear DNA Metrics

The metrics used to measure nuclear DNA genetic diversity were exactly the same to those described in 2.4.2 for mitochondrial DNA, as the literature stated that, despite their differences, they could be used for both independently and for comparison. For example, in a genetic diversity study of the Toll-like receptor 5 among Chinese local breeds, Chinese wild boar and Western commercial breeds, nuclear SNP's were analysed using haplotype diversity, nucleotide diversity, number of polymorphic sites and

transitions and transversions, and tested for deviation from neutrality using Tajima's *D* (Yang *et al.,* 2013). Similarly, Mujibi *et al.,* (2018) genotyped local African: Busia, Homabay, wild African: warthogs, bush pigs, the commercial Yorkshire, Duroc, Large White cross, Landrace and European wild boar, using nuclear SNP's, for genetic diversity, genomic structure and perceived tolerance to African Swine Fever. The metrics used for assessment included: number of haplotypes, heterozygosity, number of polymorphic sites and F_{ST}. In terms of studies comparing genetic diversity between indigenous and commercial pigs, using both mitochondrial and nuclear markers, the same metrics have been applied for analysis. For example, Ji *et al.,* (2011), used the metrics of number of haplotypes, nucleotide diversity and F_{ST}, to compare the mitochondrial and nuclear genetic diversity of East Asian wild boars and domestic pigs. Therefore, it was chosen that the same metrics would be used for both mitochondrial and nuclear DNA analysis, as supported by the literature, to determine if there were any similarities or differences between them, mainly on account of the mode of inheritance.

3.4. Chapter Objective

The objective of this chapter is to assess the within and between breed genetic diversity of three groups of traditional x commercial progeny, and one group of commercial crosses, using a nuclear DNA region of the DIO3 gene. This will analyse the effect of crossbreeding on nuclear DNA diversity and identify whether traditional crosses exhibit greater variability for this gene. A nuclear marker was selected for comparison with mitochondrial DNA, to assess the impact of inheritance on genetic diversity: maternal vs. biparental.

3.5. Materials and Methods

3.5.1. Sample Population

The sample population for this study was comprised of 110 individuals: 94 crossbred slaughter progeny (24 Gloucester Old Spot crosses (GOS F_1), 22 British Lop crosses (BL F_1), 24 Welsh crosses (W F_1), 24 Large White x Landrace crosses (LW F_1)), and 16 maternal sows.

The pigs were reared at Sturgeons Farm of Writtle College in Essex, United Kingdom. A total of 167 slaughter progeny were bred from 18 commercial Large White x Landrace (LW x LR) sows. The sows were divided into 6 groups: A, C, D and E consisted of 14 second parity sows, Groups B and F consisted of 4 gilts (Appendix 3).

The 4 terminal sire breeds used were: Gloucester Old Spot (GOS), Welsh (W), British Lop (BL) and a Large White (LW) synthetic line. The rare breed semen was imported from a sole supplier, Deerpark Pedigree Pigs of Magherafelt, Northern Ireland, who during 2013-2014 kept 2 GOS (Forthill Rufus 367 and Forthill Rufus 456), 1 BL (Bezurrell Charles 10) and 1 Welsh (Tates Victor 24) stud boars. Due to the limited number of rare breed stud boars for commercial application, semen was sent based on boar availability and working condition: health status and physical soundness. The commercial breed semen was obtained from 4 Large White boars at one of the leading pig breeding and genetics companies.

Each traditional breed cross was conducted 4 times, as was the control commercial cross, in order to reduce variability and increase the significance of the results (Appendix 3). In addition, it was decided with the Pig Unit Manager that it was only feasible to produce 16 litters: 4 of each breed, due to limited finishing pig space. The 16 litters were produced through the crossbreeding of: (LW x LR) x GOS, (LW x LR) x W, (LW x LR) x BL and (LW x LR) x LW.

3.5.2. Rearing System - Birth to Weaning

Six piglets were randomly selected from each litter; this number was chosen as it was half of the average litter size (12), which allowed for sows with lower numbers born alive and pre-weaning mortality. One day post-farrowing, the weight and sex of each individual were recorded. Each piglet was ear tagged and assigned a number for ease of identification between litters and breeds (Blue – W F_1, Red – GOS F_1, Yellow – BL F_1 and White – LW x LR F_1). There were no differences in the housing: finger-bar farrowing crate, environmentally controlled rooms (16°c) and enclosed creep area with heat lamp (30°c), or management: twice daily feeding following the Stotfold lactation feed scale and routine litter tasks, such as iron injecting, tail docking and teeth clipping, of the sows and piglets from birth to weaning.

3.5.3. Sample Collection

Ethical approval was granted by Writtle College's Ethics Committee (Appendix 2). 2cm of tail were collected from each piglet, as a by-product of routine tail docking using a gas operated tail docker. The tails were put into individually labelled 2.0ml microcentrifuge tubes, and placed in an ice box for transportation. On return to the laboratory, a 5% dimethyl sulfoxide-salt solution was added to the tubes for tissue preservation. 20 hairs were taken from the back line of each sow, ensuring the hair follicles were intact, using sterile forceps. The hairs were put into individually labelled 2.0ml microcentrifuge tubes, and placed in an ice box for transportation. Hair and tissue samples were both frozen (0°C). DNA extraction was carried out following the manufacturer's protocol (QIAGEN): Purification of total DNA from nails, hair, or feathers using the DNeasy Blood & Tissue Kit.

3.5.4. Amplification and Sequencing

Genotyping of a fragment of the DIO3 gene was amplified using the pig specific primers ACF (5-CATCATCTACATTGAGGAAGCC-3') and ACR (5-'CAGAGCCCACCAAGTTCAGTC-3') to produce a 372-bp PCR product as published in Qiao *et al.,* (2012). Total volume of PCR mixture per reaction was 30 µL consisting of: 1 x Q solution, 1 x PCR Buffer, 0.6µM dNTPs, 0.1µM Primer F, 0.1µM Primer R, 1.75mM $MgCl_2$, 0.75 Units HotStarTaq Polymerase (QIAGEN), 20-50ng template DNA. A negative control was included for quality control purposes to monitor for contamination. PCR reactions were run using a S1000 Thermal Cycler (Bio-Rad) with the following conditions: 95°C for 5 minutes, then 34 cycles of 94°C for 40 seconds, 59.2°C for 40 seconds, 72°C for 45 seconds, and 72°C for 10 minutes. Samples were prepared for sequencing in 0.5ml tubes of 30µl dilutions: 3µl of PCR product to 27µl of H_2O. Samples were sequenced at DNA Sequencing and Services at the University of Dundee, Scotland using the forward primer. For quality control, the sequencing and some PCR reactions were repeated a second time at NewGene, Newcastle upon Tyne.

3.5.5. Data Analysis

Data was analysed as per the protocol described in Chapter 2.5.4. After the alignment, 6 sequences were removed: 1 GOS F_1, 3 BL F_1, 1 W F_1 and 1 LW F_1 due to poor sequence quality and lack of alignment. The resultant segment length for all 88 sequences was 288bp.

3.5.6. Statistical Analysis

The intra and inter-population methods used were as per the statistical analyses described in Chapter 2.5.5. In addition, Fu and Li's *D* and *F* and Fay and Wu's *H* neutrality tests were completed in DNASP version 5.10.1. Fu and Li's *D*: the differences between $\eta_{e,}$ the total number of mutations in external branches of the genealogy, and η, the total number of mutations, and Fu and Li's *F*: the differences between $\eta_{e,}$ the total number of mutations in external branches of the genealogy, and π_n, the average number of nucleotide differences, were calculated using the formulas in Fu and Li, 1993. Fay and Wu's *H* statistic: the differences between two estimators of θ: θ_π, the average number of nucleotide differences between pairs of sequences, and $\theta_{H,}$ an estimator based on the frequency of the derived variants. Where θ_L is the mean number of mutations accumulated in each gene since the most recent common ancestor. The normalised *H* statistic is the scaled version of the *H* statistic. It was calculated using the formula in Zeng *et al.,* 2006. The sequence for the most recent common ancestor was sourced from the GenBank: *Sus scrofa* iodothyronine deiodinase 3 (DIO3) (Accession: NM001001625.2), and was used as the outgroup sequence for these tests.

3.6. Results

Variability within and between the traditional crossbreds: GOS F_1, BL F_1 and W F_1, and the commercial LW F_1 and LWLR sows were discovered from the measures of genetic diversity for the region of the DIO3 gene (Table 6).

From the 103 sequences analysed, 37 haplotypes were identified, with the GOS F_1 and BL F_1 both demonstrating the greatest haplotype variation: total and private numbers. Whereas, the haplotype variation observed in the LWLR sows was three times smaller. This was closely followed by the $W_{1,}$ with

only one haplotype greater than the LWLR sows. The BL F_1 displayed the greatest gene diversity, followed by the GOS F_1, LW F_1, LWLR sows and W F_1. However, nucleotide diversity was greatest in the GOS F_1, followed by the BL F_1, LW F_1, W F_1 and LWLR sows. All 4 groups exhibited both transitions and transversions, with the GOS F_1 having the largest, and the LWLR sows having the smallest numbers (Table 6).

Table 6. (Gene) measures of nuclear DNA genetic diversity. *n* is the number of individuals, *H* is gene diversity and π_n is a measure of nucleotide diversity.

	Gloucester Old Spot cross (GOS F_1)	**British Lop cross (BL F_1)**	**Welsh cross (W F_1)**	**Large White cross (LW F_1)**	**Large White x Landrace sows (LWLR)**
N	23	19	23	23	15
No. of haplotypes (*h*)	12	12	5	8	4
Private haplotypes	11	11	4	7	3
H	0.779 ± SD (0.091)	0.836 ± SD (0.087)	0.324 ± SD (0.124)	0.526 ± SD (0.126)	0.371 ± SD (0.153)
π_n	0.028 ± SD (0.006)	0.015 ± SD (0.003)	0.009 ± SD (0.005)	0.013 ± SD (0.006)	0.003 ± SD (0.002)
No. of polymorphic sites	35	27	25	31	6
Transitions (ts)	26	15	22	25	6
Transversions (tv)	10	12	4	7	1

There was no significant differentiation between the GOS F_1 and LWLR sows, the BL F_1 and LW F_1, the W F_1 and LW F_1 and the W F_1 and LWLR sows. However, there were significant differentiations between the GOS F_1 and all the crossbreds; the BL F_1, and W F_1, and LWLR sows; and the LW F_1 and the LWLR sows (Table 7).

Table 7. Measures of population differentiation using F_{ST}. (*) indicates statistical significance $p < 0.05$.

	Gloucester Old Spot cross (GOS F_1)	**British Lop cross (BL F_1)**	**Welsh cross (W F_1)**	**Large White cross (LW F_1)**
British Lop cross (BL F_1)	0.089 (*)	-		
Welsh cross (W F_1)	0.087 (*)	0.042 (*)	-	-
Large White cross (LW F_1)	0.086 (*)	0.011	0.004	-
Large White x Landrace sows (LWLR)	0.083	0.075 (*)	0.009	0.029 (*)

There was only 1 haplotype common in all 4 groups, haplotype 2, which was observed in 11 GOS F_1, 8 BL F_1, 19 W F_1, 16 LW F_1 and 12 LWLR sows (Table 8).

Table 8. DIO3 haplotype frequencies occurring in all four groups.

Haplotype number	Gloucester Old Spot cross (GOS F_1)	British Lop cross (BL F_1)	Welsh cross (W F_1)	Large White cross (LW F_1)	Large White x Landrace sows (LWLR)
H1	-	-	-	-	0.066
H2	0.478	0.421	0.826	0.699	0.800
H3	-	-	-	-	0.006
H4	-	-	-	-	0.006
H5	0.043	-	-	-	-
H6	0.043	-	-	-	-
H7	0.043	-	-	-	-
H8	0.043	-	-	-	-
H9	0.043	-	-	-	-
H10	0.043	-	-	-	-
H11	0.043	-	-	-	-
H12	0.087	-	-	-	-
H13	0.043	-	-	-	-
H14	0.043	-	-	-	-
H15	0.043	-	-	-	-
H16	-	0.053	-	-	-
H17	-	0.053	-	-	-
H18	-	0.053	-	-	-
H19	-	0.053	-	-	-
H20	-	0.053	-	-	-
H21	-	0.053	-	-	-
H22	-	0.053	-	-	-
H23	-	0.053	-	-	-
H24	-	0.053	-	-	-
H25	-	0.053	-	-	-
H26	-	0.053	-	-	-
H27	-	-	-	0.043	-
H28	-	-	-	0.043	-
H29	-	-	-	0.043	-
H30	-	-	-	0.043	-
H31	-	-	-	0.043	-
H32	-	-	-	0.043	-
H33	-	-	-	0.043	-
H34	-	-	0.043	-	-
H35	-	-	0.043	-	-
H36	-	-	0.043	-	-
H37	-	-	0.043	-	-

Tajima's *D* was negative for all 5 groups and significant for all apart from the GOS F_1. Fu's *Fs*, test was positive for the W F_1 and LW F_1 and negative for the GOS F_1 and LWLR, and significant for the BL F_1. Fu and Li's *D* was negative for all 5 groups and significant for the W F_1 and LW F_1. Fu and Li's *F* was negative

for all 5 groups and significant for the W F_1 and LW F_1. Fay and Wu's *H* was negative and significant for all 5 groups (Table 9).

Table 9. Results of Tajima's *D*, Fu and Li's *D* and *F*, Fay and Wu's *H* and Fu's *Fs* neutrality tests. (*) indicates statistical significance $p < 0.05$.

	Gloucester Old Spot cross (GOS F_1)	**British Lop cross (BL F_1)**	**Welsh cross (W F_1)**	**Large White cross (LW F_1)**	**Large White x Landrace sows (LWLR)**
Tajima's *D* test	-1.030	-1.768 (*)	-2.292 (*)	-2.127 (*)	-1.766 (*)
Fu and Li's *D* test	-1.331	-1.770	-3.510 (*)	-3.160 (*)	-1.956
Fu and Li's *F* test	-1.518	-2.055	-3.691 (*)	-3.347 (*)	-2.180
Fay and Wu's *H* test	-3.836 (*)	-2.029 (*)	-1.804 (*)	-2.910 (*)	-2.322 (*)
Fu's *Fs* test	-0.726	-3.705 (*)	1.776	0.175	-0.533

3.7. Discussion

There is considerable variability for this nuclear DNA region of the DIO3 gene within and between the traditional: GOS F_1, BL F_1 and W F_1, and the commercial LW F_1 crossbreds and LWLR sows.

3.7.1. Haplotype Diversity

Two of the traditional crossbreds demonstrated the greatest haplotype variation, with 12 haplotypes identified in the 19 BL F_1 and 12 in the 23 GOS F_1, followed by 8 in the 23 commercial LW F_1, then 5 in the 23 W F_1 and the lowest count with only 4 haplotypes in the 15 commercial LWLR sows.

The high haplotype counts of the BL F_1 and GOS F_1 could be attributed to the historical background of the breeds: until the 1930s they were developed with particular characteristics fitting local needs, populations declined as pig production progressed towards intensification, although some breed numbers/lines were preserved by hobbyists/smallholders/niche producers (BPA, 2016h). Thus, in comparison to their modern counterparts, traditional populations are more genetically diverse, having retained a larger proportion of their original characteristics. There are several studies comparing the haplotype diversity of traditional, modern and commercial livestock breeds, often with the traditional

exhibiting the greater of the three (Ginja *et al.,* 2009; Koseniuk and Slota, 2016; Novák *et al.,* 2017). For example, Liu *et al.,* (2015) compared a coding region of the melanocortin receptor 1 (MCR1) in native Tibetan and commercial Landrace pigs, finding higher haplotype diversity in the Tibetan, for the weather protective dark coat colour, as a result of differing population dynamics and artificial selection for white coat colour in the Landrace.

However, 19 of the W F_1, 16 of the LW F_1 and 12 of the LWLR were characterised by haplotype 2. The result for the W F_1 was surprising, as although the original breed was developed for commercial use during the 1950 – 1980s, it did not progress in the same capacity as the LW and LR to the modern day (The Pedigree Welsh Pig Society (PWPS), 2014a). Although, the genetic advances made and the decline in W pig numbers from the 1980s would have presumably decreased genetic diversity, thus reflecting the small number of haplotypes. This interpretation is consistent with that of the Turopolje pig, an indigenous Croatian breed, which was numerous and widespread, accounted for 20% of all pigs reared and had been introgressed with European breeds, however in the 1950s saw a dramatic population decline, due to changes in production systems and consumer interest, to approximately 250 individuals. Harcet *et al.,* (2006) identified low genetic diversity at 10 microsatellites and no differences in the mitochondrial D-loop sequences of the Turopolje pigs sampled, which was attributed to the severe demographic bottleneck experienced in the mid 20^{th} century. Whereas, the results for the LW F_1 and LWLR were to be expected as the modern breeding practice of intensive selection, within a closely related gene pool, has resulted in reduced genetic variation (Moon *et al.,* 2015).

In addition to breed, the differing haplotype diversity was also considered to be an effect of the traditional and commercial crossbreeding. The large number of crossbreds and maternal sows characterised by haplotype 2, infers a shared ancestral haplotype and close relatedness between breeds (Vandenplas *et al.,* 2016). This is supported by Kim and Rothschild (2014), whereby the frequency of haplotypes in Kenyan crossbred dairy cattle, was dependent on the frequency of haplotypes in their ancestral breed. Haplotype 2 is of high frequency in W F_1 and LW F_1 populations, indicative of

homozygous parent/s and sharing of the same haplotypes. This is supported by the haplotype results for the LWLR maternal sows, only sharing the one common haplotype with all the crossbred progeny. It was expected that the commercial dams' within-breed diversity would be low, due to their close genetic relatedness and phenotypic comparability (Buchanan, 2000). Therefore, any between-breed differences observed would be due to the effect of the boars introducing new variation. The number of haplotypes of the LW F_1, is almost double that of the W F_1. It is suggested that this could be due to greater number of terminal sires used to produce the crossbreds: 1 W boar and 4 LW boars. However, only 1 BL and 2 GOS were used, with larger numbers of haplotypes identified in their crossbreds, which demonstrates that these three sires may be heterozygous, with greater variability for this gene.

3.7.2. Heterozygosity

Consistent with the haplotype diversity results, two of the traditional crossbreds exhibited the greatest levels of heterozygosity, BL F_1 (0.836 ± SD 0.087) and GOS F_1 (0.779 ± SD 0.091), followed by the commercial LW F_1 (0.526 ± SD 0.126) and LWLR (0.371 ± SD 0153), and lastly the traditional W F_1 with the lowest level (0.324 ± SD 0.124).

Although numerically the rarest of the native breeds studied, the high heterozygosity of the BL F_1 could be attributed to the historical factors of the breed: geographical isolation, selection for regional priorities and maintenance of purebred populations, resulting in genetically distinct individuals and lines (British Lop Pig Society (BLPS), 2014b). Yet, it is generally assumed that small population size can lead to low genetic diversity, and the contrary for large populations (Torres-Florez *et al.,* 2014). However, Osei-Amponsah *et al.,* (2017) identified that the endangered Ashanti Dwarf Pig of Ghana showed considerable variation for the MC1R gene: coat colour in comparison to domestic pigs. Similarly, greater heterozygosity was found in *Bos indicus*; Thai native White Lamphun and Mountain cattle, for the heat shock protein 90-kDa beta gene (HSP90AB1): heat stress, compared to *Bos taurus*; crossbred Holstein Friesian cattle (Charoensook, 2011). Both these studies demonstrate the phenotypic and physiological

diversity of indigenous livestock, and support their conservation of favourable alleles for the improvement of commercial breeds in the future.

The crossbreeding of two separate breeds has been shown to increase heterozygosity in the F_1 generation, from differences between the parental gene frequencies (Trail and Gregory, 1981; Nitter, 1999). This is supported by Lymbery (2000) who compared the genetic diversity of two fragments of the growth hormone gene: GH-L1 and GH-L2, in composite and purebred Hereford herds, and although not significant, the observed heterozygosity was greater in the composite. Whereas, Agung *et al.,* (2015) compared 12 microsatellite markers to assess the genetic diversity among 11 populations of West Sumatran cattle, revealing a range of heterozygosity values in the Simmental crosses: 3 greater than, 4 similar and 2 less than that of the purebred Simmental and Ongole parents. However, Ebrahimzadeh *et al.,* (2013) investigated the polymorphism of the IGF-1 gene: growth and production rates for meat and milk, in Khuzestan hybrid cattle, identifying that gene diversity was relatively high in this population, compared to that of purebreds. Furthermore, Grossi *et al.,* (2017) genotyped populations of purebred Landrace, Large White and Duroc and one crossbred Large White x Landrace, using the Porcine 60 K Illumina BeadChip panel, and found that the crossbreds displayed the highest levels of observed and expected heterozygosity, compared to the purebreds, reflecting the effect of crossbreeding on increasing diversity. As there are no studies comparing purebred and crossbred animals for the DIO3 gene, if the principles outlined above were applied, this would support the crossbreeding of LW x LR dams with BL and GOS terminal sires to increase gene diversity for productivity traits.

The result for the GOS F_1 would most likely be explained by the numerical size of the breeding population, the largest of all traditional pig breeds, and the cyclic breeding system, historically implemented to limit and control inbreeding through the female lines. This was achieved by dividing the 15 female bloodlines into 4 colour categorised groups, the male offspring were named according to the colour group of their dam and the name given related to the colour group which he was to be mated (Gloucester Old Spot Pig Breeders Club (GOSPBC), 2012c).

It has been suggested that the large founder gene pool, controlled breeding programmes and increased population sizes are accountable for high levels of heterozygosity in commercial pig breeds such as the LW and LR (Druml *et al.,* 2012). This is supported by Ji *et al.,* (2011) whom revealed that domestic pigs and wild boars exhibited comparable levels of diversity for 13 out of 14 nuclear regions analysed. However, the lower heterozygosity result for the LW F_1 and LWLR sows, compared to the GOS F_1 and BL F_1, would presumably be due to the loss of genetic diversity and high levels of homozygosity, within these two commercial breeds, from intensive selection and artificial breeding strategies used to rapidly improve productivity traits (Zanella *et al.,* 2016). This is supported by Grossi *et al.,* (2017) whom reported that the commercial LW and LR demonstrated low individual genetic diversity, in comparison to the Duroc and F_1 LW x LR, as a result of high levels of recent inbreeding and a decline in effective population size. Also, the LW terminal sires used for this study were all from one synthetic line, with the same terminal origin, demonstrating the close relatedness of the boars, which may have limited the gene diversity of the crossbreds.

Similar to the LW F_1 and LWLR, the low result for the W F_1 could be attributed to the semi-commercialised history of the breed. The 'improved' W may have experienced genetic drift: fixation or extinction of alleles through generations, from a small breeding population, or inbreeding: increased homozygosity and reduced fitness levels, from genetic improvement of production traits (Freeland, 2005). Fabuel *et al.,* (2004) identified heterogeneity between the main varieties and preserved strains of the Iberian breed for 36 microsatellite markers; the subpopulations with low variability were considered to be as a result of maintaining closed herds, low effective population sizes and inbreeding. This could explain the low haplotype and gene diversity of the W crossbreds, as some bloodlines i.e. Tates Victor, may have lost gene diversity for this particular region of the DIO3 gene from line breeding.

3.7.3. Nucleotide Diversity

The GOS F_1 displayed the highest level of nucleotide diversity (0.028 ± SD 0.006) and number of polymorphic sites (35), whereas the other 3 crossbreds had similar levels of nucleotide diversity and

number of polymorphic sites: BL F_1 (0.015 ± SD 0.003) (27), LW F_1 (0.013 ± SD 0.006) (31) and W F_1 (0.009 ± SD 0.005) (25), and the LWLR sows had the lowest levels and sites (0.003 ± SD 0.002) (6).

The high nucleotide diversity of the GOS F_1 could be attributed to the large effective population size, which has stabilised following the population bottleneck; sustained reductions, during the 1940 – 1960s (Fernandez *et al.,* 2011). This is supported by the high haplotype diversity of the GOS F_1 (12), which demonstrates that there has been sufficient evolutionary time for new mutations to arise, increase in frequency and become established within the population (Frankham *et al.,* 2010). However, Kim *et al.,* (2017) identified the greatest level of nucleotide diversity in admixed taurine x zebu breeds, compared to indigenous African and commercial European breeds. This could be the effect of crossbreeding, with variation arising from germline point mutations: substitutions, insertions and deletions, or genetic recombination during meiosis (Clancy, 2008).

Similarly, the level of nucleotide diversity in the BL F_1 could also be explained by population bottleneck and expansion, but to a varying degree. Although haplotype diversity is high, the low nucleotide diversity of the BL F_1 would suggest little variation between haplotypes, indicative of a rapid demographic expansion, from a small effective population, following a bottleneck (de Jong *et al.,* 2011). This is consistent with the history of the breed, as a population bottleneck occurred during the 1950s (RBST, 2011b), with the population having now increased to a size greater than at any other time in the last 30 years (BLPS, 2014a). Although remaining the smallest census size, the results show recently diverged haplotypes of a low frequency, implying that within-breed genetic diversity is increasing. This is supported by Ferreri *et al.,* (2011), who identified high haplotype, but low nucleotide diversity in the mtDNA D-loop of Chinese Holstein cattle (native x introduced), indicative of a population bottleneck, followed by rapid population expansion. It is also stated that the haplotype diversity reflects the genetic variation of native Chinese cattle, which suggests that the haplotype and nucleotide diversity of the crossbreds could be explained by the genetic influence of the BL.

The lower number of haplotypes and nucleotide diversity of the LW F_1 and LWLR could be explained by positive selection. Modern breeds have been selected for particular alleles/genotypes which increase fitness, but the increase in diversity (gene frequency) is only temporary, as once the selected allele/genotype reaches fixation, variation is lost (Freeland, 2005). This is supported by Li *et al.,* (2014) who identified that the Large White had experienced strong positive selection for growth and reproduction traits.

The result for the W F_1 could be explained by selection, a population bottleneck and/or recent expansion. During semi-commercialisation, selective breeding would have narrowed genetic diversity within and between lineages, potentially resulting in the W breed being dominated by a few lines regarded as superior. The family groups which exist today may have descended from the original lines selected for commercial application, and recent expansion may not have allowed sufficient time for new mutations to occur, increase in frequency and disperse across the population (Frankham *et al.,* 2010).

3.7.4. Transitions and Transversions

All groups demonstrated greater transitions than transversions, which agrees with the modest transition bias, at a ratio of 2:1 in pig nuclear DNA. The GOS F_1 displayed 26 ts to 10 tv, followed by the LW F_1 with 25 ts to 7 tv, then the W F_1 with 22 ts to 4 tv, the BL F_1 with 15 ts to 12 tv and lastly the LWLR sows with 6 ts to 1 tv. This is supported by Ramos *et al.,* (2009), where the 2:1 ratio was observed in the nuclear DNA of commercial breeds; Duroc, Pietrain, Landrace and Large White, and Wild Boar. Similarly, Shen *et al.,* (2020) reported a ts/tv ratio of 2.36, in the genomic DNA, of the Chinese indigenous breed; the Yanbian, and 2.39 in the domestic West African breed; the N'Dama. Equally, Suárez-Vega *et al.,* (2017) identified a ts/tv ratio of 2.4, in the coding regions of the milk transcriptome of two sheep breeds; the ancient, dairy Spanish Churra and the domestic, dual-purpose Israelian Assaf.

3.7.5. Genetic Differentiation

The low to moderate genetic differentiation between the crossbred groups was as expected due to the confines of the nuclear DNA region studied. This could be due to limited divergence from the ancestral

sequence, and the slow mutation and evolution of nuclear, protein-coding genes. An additional explanation is that the 4 crossbred groups were only differentiated by the terminal sire; the maternal contribution was the same, LWLR sows and gilts, which were all genetically alike, produced from the same dam lines, from one breeding and genetics company (Buchanan, 2000).

The little to no genetic differentiation between the W and LW crossbreds was not unexpected, due to the results of the other gene measures, which imply that the parental allele frequencies for this DIO3 region are very similar (Nielsen and Slatkin, 2013). The explanation for which could be the historical modernisation and commercialisation of the W, LW and LR (BPA, 2012), indicating high levels of gene exchange between breeds from intensive selection and/or crossbreeding. This would also explain the little to no genetic differentiation between the W and LWLR sows.

However, the BL F_1 and LW F_1 also showed little genetic differentiation, but were thought not to be historically admixed (Porter 1987; Porter, 1993; Scali *et al.,* 2011), thus this was also considered to be similarities in parental allele frequencies and/or mutation, genetic drift or selection (Nielsen and Slatkin, 2013). Yet, the BL F_1 and LWLR sows showed moderate, significant differentiation, which could be attributed to genetic variation provided by the terminal sire. This may also explain the low, yet significant result between the LW F_1 and LWLR sows.

The F_{ST} results were numerically similar and significant between the GOS F_1 and the other three crossbreds, but not significant for the LWLR sows, demonstrating moderate genetic differentiation and biologically distinct populations. This could have been the result of the different allele frequencies in the two parental breeds, leading to slightly greater diversity in combinations of alleles when crossbreeding (Christensen *et al.,* 2015). This also seems a probable explanation for the low, yet significant result between the BL F_1 and the W F_1, and further supported by the historic notion that the purebreds are both of the same type and origin, yet were separated and developed as two entities (Porter, 1987; BLPS, 2014a). It is difficult to quantify whether the sows or terminal sires are providing the genetic variation, however it may be safe to assume that the crossing of dissimilar parental breeds tends to increase the

number of gene pairs that are heterozygous, due to differing gene frequencies (Gosey, 1991). In this study, only the sows have been studied: genetically and phenotypically similar, therefore the genetic variation between crossbreds has been attributed to the terminal sire breeds.

There were no studies directly comparing the genetic differentiation of crossbreds, to support the results of this chapter, however, there were some studies comparing purebred and crossbred populations. Radhika *et al.,* (2015) identified low F_{ST} values (0.02 ± 0.004) between native and crossbred goats, which was attributed to the close relatedness of the populations sampled. However, the crossbreds established their genetic identity, by differentiating into a separate group, thought to be the formation process of the composite population occurring over three decades. Additionally, Al-Atiyat (2016) identified that F_1 generation Damascus x Bedouin were more closely related to the Damascus than the Bedouin and the crossbred group were also differentiated from the two purebred groups.

Radhika *et al.,* (2015) study has supported the low to moderate genetic differentiation results of this study, as the four crossbred groups were closely related from the same maternal base being used. They also suggested that for populations to become a separate group, sufficient generation time was needed for evolutionary actions to occur, whereas this experiment only produced one generation of crosses. Also, Al-Atiyat's (2016) study demonstrated the sharing of similar alleles between crossbreds and one parental breed compared to the other, indicating that the minor genetic differentiation between the crossbreds in this study could be as a result of varying terminal sire breeds. Lastly, both studies differentiated the crossbreds into their own groups, which support the significant differences, representing separate biological populations, between the GOS F_1 and BL F_1, W F_1, and LW F_1; the BL F_1, and W F_1, and the LWLR sows; and the LW F_1 and LWLR sows.

3.7.6. Neutrality Tests

All 4 crossbred groups and the maternal sows exhibited negative results for Tajima's *D*, Fu and Li's *D* and *F* tests and Fay and Wu's *H* test, however Fu's *Fs* test was positive for the W F_1 and LW F_1, but negative for the GOS F_1, BL F_1 and LWLR sows. The negative values of the Tajima's *D* indicate an excess of low

frequency alleles, which can be caused by population growth, selective sweep or positive selection (Stajich and Hahn, 2004). The negative values of Fu and Li's *D* and *F* tests indicate an excess of low frequency mutations, and similar to Tajima's *D*, are caused by demographic and/or selective events (Biswas and Akey, 2006). The negative Fay and Wu's *H* test indicates an excess of high frequency derived mutations, as a result of population expansion, genetic hitchhiking or positive selection (Ferretti *et al.,* 2017). The positive values of the Fu's *Fs* test indicate relative excess of intermediate frequency alleles, as a result of population structure, bottlenecks or balancing selection (Bamshad *et al.,* 2002), whereas the negative values indicate an excess of recent mutations, because of population growth and/or selection (Alexandrino *et al.,* 2002).

The negative Tajima's *D* and Fu and Li's *D* and *F* for all the groups suggests an excess number of alleles/mutations as would be expected from population expansion for the traditional crosses and selective sweep, due to strong positive selection, for the commercial crosses and sows (Stajich and Hahn, 2004). However, the large significant Fay and Wu's *H* would be indicative of selective sweep for all 5 groups (Lohmueller et *al.,* 2011). For the traditional crosses, this could have been the effect of crossbreeding: sharing of the same alleles and homozygosity in the parental breeds, from intensive positive selection and low effective population sizes, may have increased the frequency of derived mutations in the crossbreds.

However, the greater positive Fu's *Fs* values for the W F_1 and LW F_1 implies population bottlenecks (Bamshad *et al.,* 2002), which could be the result of crossbreeding closely related individuals from limited gene pools. Yet, the results for the GOS F_1, BL F_1 and LWLR have been consistent throughout, with the negative Fu's *Fs* supporting the notion of population expansion for the traditional crosses and positive selection for the commercial sows (Alexandrino *et al.,* 2002).

The statistical tests of neutrality have produced conflicting results for the W F_1 and LW F_1, which was expected due to the short generation time analysed. Therefore, for the neutrality tests to

simultaneously detect which population demographics are affecting the DNA sequence data, further generations would have to be produced, to enable evolutionary progression to occur.

3.8. Comparison with Mitochondrial DNA

A comparison of mitochondrial and nuclear DNA as molecular markers was undertaken, on account of the differing modes of inheritance: maternal vs. biparental, to determine whether this affected the genetic diversity of the groups. As mitochondrial DNA evolves much faster than nuclear DNA, it would be thought that mitochondrial diversity would be higher than that of nuclear (Ji *et al.,* 2011). However, the mitochondrial and nuclear DNA results are comparable, in terms of the traditional purebreds and crosses showing greater levels of genetic diversity in contrast to their commercial counterparts, which was to be expected. In both instances, this could be heavily attributed to the narrow genetic base of commercial populations and the artificial selection for production traits within modern pig breeding (Herrero-Medrano *et al.,* 2014). However, Ji *et al.,* (2011) compared the genetic diversities of domestic pigs and wild boars, using the D-loop, 13 mtDNA coding genes and 14 nuclear markers, confirming that domestic pigs have a clearly lower level of mitochondrial genetic diversity, but the nuclear DNA revealed comparable levels between the two groups for 13 of the markers. Whereas, Wang *et al.,* (2011b), compared the genetic diversities of six Chinese indigenous breeds with the Landrace, Yorkshire and Duroc, using 26 microsatellite markers, showing the indigenous pigs to have higher genetic diversity than the commercial breeds.

Both mtDNA and nDNA studies showed the GOS purebreds and crosses demonstrating not necessarily the highest, but most consistent genetic variation for all parameters, credited to the breed's numerical size, stability and crossbreeding effect. Whereas, the W displayed great promise in the mitochondrial study: highest haplotype and gene diversity and second greatest F_{ST} with the LW, however, in the nuclear study the W F_1s consistently showed very low levels of genetic variation. This could be attributed to the purebred population retaining more of their original diversity and/or the high mutation rate of mitochondrial DNA, and that variation for the DIO3 region may have been narrowed in the

maternal and paternal breeds, used to produce the crosses, due to historic intensive selection. The intermediate throughout has been the BL, considered to be due to the historic maintenance of the breed, geographical isolation and rare presence in commercial production. The BL F_1s showed the highest haplotype and gene diversity, attributed to the crossbreeding of dams and sires with varying allelic combinations, thus increasing genetic variation.

3.9. Conclusion

As litter size continues to increase, it has been stated that management techniques, breeding and genetics are the combined strategies to address the long term issue of improving piglet survival. Traditional breeds are renowned for their survival attributes of: instinctiveness, hardiness, environmental tolerance and immune defence. Yet, there are presently very few studies demonstrating the genetic effects of crossbreeding traditional and commercial breeds to improve productivity. However, the analysis of genetic diversity revealed considerable variability for the nuclear DNA region of the DIO3 gene studied, within and between the traditional GOS, BL and W, the commercial LW crossbreds and maternal LWLR sows. The GOS F_1 and BL F_1 presented the highest levels of genetic diversity, followed by the LW F_1, W F_1 and LWLR sows. This was attributed to the crossbreeding effect: the genetic distances, allele and genotype frequencies of the parental breeds created new genetic combinations in the progeny. Whereas, low to moderate genetic differentiation was identified between all crossbred groups and maternal sows, considered to the result of: limited divergence from the ancestral sequence, slow mutation rates of nuclear DNA and the close genetic relatedness of the sows used. It was found that despite the differing modes of inheritance: mitochondrial vs. biparental, the traditional purebreds and crosses showed greater levels of genetic diversity for both mitochondrial and nuclear DNA in comparison to their commercial counterparts. This study has shown that crossbreeding traditional and commercial breeds can achieve greater genetic diversity in the resultant progeny, compared to the commercial F_1 hybrid, for the DIO3 gene. The variability between the crossbreds has been largely attributed to the genetic differences of the terminal sire breeds. This will enable the

utilisation of genetic variation, through selection, to improve productivity. This also supports the notion of combining the desirable characteristics of traditional boars (survival) and commercial dams (reproductive) to achieve higher overall performance in the crossbreds, compared to the parental breeds alone. However, further research is required to establish the relationship between the terminal sire effect of the DIO3 gene and piglet survivability, in terms of numbers born alive and pigs weaned.

Chapter 4. The Effect of Crossbreeding on Productivity Parameters: Growth and Back Fat

4.1. World Production of Pig Meat

Over the past few decades, the intensive pig producing sector has continually strived to improve production efficiency and enhance overall animal performance, with the primary intention of increasing productive output (Brooks and Varley, 2003; Food and Agriculture Organization (FAO), 2015). It has been identified that this has been in response to the increased universal demand for meat and animal based products (Thornton, 2010). The influential factors producing the changes are human-driven, for example rising population numbers: 7 to 9 billion by 2050, economic growth: twice the rate in developing countries, and urbanisation: employment and infrastructure (Kearney, 2010). Pork is the most widely consumed meat in the world (Rogers, 2012). In 2015, global consumption of pig meat was 117 567 million tonnes (mt), in comparison with poultry (112, 538 mt), beef and veal (67, 451 mt) and sheep meat (14, 256 mt). It was estimated that of this 117, 567 mt, 66% of pig meat was consumed in developing countries (Organisation for Economic Co-operation and Development (OECD), 2016). In 2015, it was forecasted that world production of pig meat would continue to grow by 1.9% to 119.4 mt (Gyton, 2015), yet it was estimated that 2016 experienced a 2% decrease to 109.3 mt (Agriculture and Horticulture Development Board (AHDB), 2016a). However, AHDB have recently announced that pork production and exports are due to reach record highs globally in 2017 (AHDB, 2016b).

The ability to fulfil this growing demand for pig meat has been attributable to rapid productivity growth and generation turnover in monogastrics, compared to ruminant species, which has occurred from science and technology advancements in feed and nutrition, reproduction and genetics and health and husbandry (Steinfield and Gerber, 2010). Since the 1950s, the commercial swine industry has focused on improving lean meat production efficiency and reducing carcass fat, in response to consumer demand for low cost, yet quality, leaner pork (van Barneveld, 2003; Olynk, 2012). Pig breeding and genetics companies have enhanced the lean tissue development and growth efficiency of finished pigs by 100%

(Merks *et al.,* 2012), which has dramatically reduced total carcass fat from 40% to 20%, with a 75% decrease in subcutaneous fat (Kouba and Sellier, 2011). The successes of improved carcass composition and maximised meat yield have been achieved by genetic improvement, through selection, within the breeding pyramid (Whittemore and Kyriazakis, 2006). However, this form of genetic progression has been concentrated in five prevailing international breeds: Large White, Landrace, Duroc, Pietrain and Hampshire (Chen *et al.,* 2007), which have been intensively selected for desirable performance characteristics, of economic importance: liveweight gain, feed conversion efficiency and carcass leanness (Kanis *et al.,* 2005).

4.2. Effects of the Terminal Sire

Several studies have reported that different breeds and lines of pigs possess genotypic variation (Ujan *et al.,* 2011) for different areas of production performance, carcass composition and meat quality (Miao *et al*., 2009). It has been proposed that the underlying cause of the evident distinctions between slaughter progeny result from the influential effects of the terminal sire breed genotype (Litten *et al.,* 2004; Bertol *et al.,* 2013). This has been supported by Fabrega *et al.,* (2003) and Magowan and McCann (2009) who have stated that the terminal sire breed is one of the central factors affecting the performance of slaughter generation pigs, from the identification of a definite paternal influence during the weaning to finishing period.

4.2.1. Feeding Parameters

It has been established that the terminal sire breed exhibits a significant effect on feeding parameters, with reports of considerable variances in daily feed intake (Magowan *et al.,* 2007), eating behaviours (number of visits, intake per meal, time spent per visit) and feed conversion ratio (Renaudeau *et al.,* 2006). This has been attributed to the intensive selection of terminal sire breeds for improved feed efficiency and carcass leanness, which has inadvertently reduced voluntary feed intake (Knap, 2009). Comparisons of the three leading terminal sire breeds show that although differences in feed conversion are not large (Mabry, 2012), behaviourally the Large White has the lowest feed intake and ingestion

time, the Duroc also consumes small amounts but more frequently, and the Pietrains have the highest feed intake, with the longest ingestion time (Fernandez *et al.,* 2011; Vidović *et al.,* 2011).

This establishes the genetic impact of breed on feed consumption and efficiency, and demonstrates how eating behaviour can influence production performance. This is supported by Augspurger *et al.,* (2002) who has shown that the feeding behaviour of the young growing pig of more frequent feeder visits, to consume small amounts, increases the rate and efficiency of converting feed into body weight gain and lean muscle. However, it has been identified that as slaughter age increases, feed efficiency declines (less frequent feed visits, but consumption of larger meals), reducing utilisation of feed into gain and limiting production efficiency (Latorre *et al.,* 2003).

4.2.2. Growth and Carcass Composition

Pig breeding and genetics companies are continually developing modern breeds and lines to produce high-yielding and faster growing progeny, in order to minimise production losses and reduce the time to reach market weight (FAO, 2007). The rate of growth is a performance characteristic of great economic importance in commercial pig production (Clutter, 2011), owing to the fact that if slaughter weight is achieved sooner, maintenance feeding and housing of animals is reduced. The effects of this are economically positive, from reduced expenditure and efficient use of productive capacity, allowing for a consistent flow of pigs though the system.

It has been identified that breeds and lines of terminal sire have a significant effect on progeny daily liveweight gains during the grow-finish phase (Latorre *et al.,* 2003; Magowan and McCann, 2009). This is supported by Schinckel *et al.,* (2012) who identified that body weight and average daily gain at days 84, 102, 120, 138 and 156 of age were significantly affected by sire line. Magowan and McCann (2009) also demonstrated variability in growth rate between the progeny of four terminal sire line breeds: Tempo, Pietrain (Austrian line), Pietrain (Belgian line) and Landrace. This strongly demonstrates that breeds and lines of terminal sire affect the lifetime growth performance of their progeny, which could benefit or impact production length to finished weight, dependent on genotype.

In addition, the growth rate and body conformation of terminal sire breeds and lines can influence the lean meat yield of the carcass produced by the slaughter generation (McCann and Beattie, 2004). It has been noted that improvements in carcass composition and yield have been attained from genetic selection for rapid growth and greater lean meat production (Whittemore and Kyriazakis, 2006), which has resulted in faster growing animals whom deposit more lean tissue than fat (Latorre *et al.,* 2008). Although, it has been determined that there is an unfavourable correlation between average daily gain and back fat (Hoque *et al.,* 2009), indicating that as age to slaughter increases, back fat depth escalates, whereas carcass leanness decreases (Latorre *et al.,* 2003; Conte *et al.,* 2011).

4.2.3. Terminal Sire Breed and Line Comparisons

There have been numerous breed and line comparison studies undertaken, investigating the influence of the four main commercially available terminal sires: Large White, Pietrain, Duroc and Hampshire, on the production performance and carcass composition of their crossbred slaughter progeny (McCann, *et al.,* 2008; Fernandez *et al.,* 2011).

Studies have shown that the traditionally used Large White have low daily feed intake (DFI), yet the best feed efficiency (Tang *et al.,* 2008), compared to the average DFI of the Duroc (Edwards *et al.,* 2006), and high DFI of the Pietrain and Hampshire (British Pig Executive (BPEX), 2009). However, the Large White and Pietrain are noted for moderate growth rates (Green *et al.,* 2003), whilst the Duroc and Hampshire exhibit rapid growth, resultant in reduced days to slaughter (Edwards *et al.,* 2006; BPEX, 2009). The Duroc and Hampshire are renowned for high lean meat yield and valuable meat quality traits: favourable pH values, desirable meat colour and reduced drip loss (Kusec *et al.,* 2004; BPEX, 2009). Whereas, the Pietrain is noted for the production of heavy carcasses with improved composition: a high yield of lean meat and significantly low fat content (Whittemore *et al.,* 2003; Saintilan *et al.,* 2011). Similarly, the Large White have the leanest carcasses (lean meat percentage and back fat), particularly to fulfil the conventional market standards (BPEX, 2009).

These breed and line comparisons strongly demonstrate the differences between terminal sires for productivity, carcass composition and meat quality traits. This variation in traits offers producers a selection of new genotypes, which could be used to improve herd productivity and product quality, and fulfil the changing market demands for commercial pork.

4.3. Breeding and Genetics Programmes

4.3.1. Terminal Sire Selection

However, it has been identified that many breeding programmes are presently interested in selecting terminal sires that are homozygous for the insulin-like growth factor 2 (IGF2) gene (Stinckens *et al.,* 2010). There are two major IGFs: IGF1 and IGF2. It has become apparent that they have central importance in the regulation of prenatal and postnatal growth and development in animals (Bondy and Zhou, 2005; Clark *et al.,* 2015). However, IGF2 is most abundantly expressed during embryonic and foetal development in the placental, uterine and foetal tissues (Ager *et al.,* 2008), whereas IGF1 has more significance in postnatal growth, development and maintenance, with expression gradually increasing from puberty to adulthood, in almost all tissues (Boysen *et al.,* 2011).

It has been shown that the IGF2 protein plays a fundamental role in skeletal muscle growth by altering carbohydrate and fat metabolism, promoting cell proliferation and regulating cell survival, growth and differentiation (Stinckens *et al.,* 2009). In pigs, a paternally expressed quantitative trait loci (QTL) was located in the telomeric end of the p arm of pig chromosome 2 (SSC2) (Amarger *et al.,* 2002), caused by a single nucleotide substitution (G-A) at position 3072 in intron 3 of the IGF2 gene (Jungerius *et al.,* 2004). The G to A transition produces a 3-fold overexpression of postnatal skeletal muscle IGF2 mRNA in progeny inheriting the mutation from their sires (Fontanesi *et al.,* 2011), resultant in larger muscle mass and reduced fat deposition (Thomsen *et al.,* 2004). It has been identified that the homozygous AA genotypes have higher lean growth and lower back fat thickness (Vykoukalova *et al.,* 2006), in comparison to the homozygous GG and heterozygous GA genotypes, which exhibit opposite and intermediary results (Fontanesi *et al.,* 2010).

The favourable A allele is shown to be present in high frequencies within the international, commercial breeds, which is considered to be attributable to the intensive selection for leanness and growth (Ruan *et al.,* 2013). On the other hand, Ojeda *et al.,* (2008) stated that the allele is generally scarce or of very low frequency within local breeds. This is supported by Klomtong *et al.,* (2015) who identified high frequencies of the G allele (or homozygous GG) in two types of Thai indigenous breeds and wild boar, but they were not fixed. Furthermore, Akopyan *et al.,* (2014) identified the frequencies of A allele in Russian local breeds to be from 0.000 to 0.528, compared to 0.767 to 1.000 in commercial Large White, Landrace and Duroc. Yet, Muñoz *et al.,* (2018) found the A allele at considerable frequencies in a few breeds: Italian Apulo-Calabrese (0.85), German Schwäbisch-Hällisches Schwein (0.50) and Slovenian Krškopolje (0.39), although this was explained by introgression of alleles from commercial breeds. However, the studies of the IGF2 gene have predominantly occurred within the conventional breeds stated above. Thus, the genetic selection of terminal sires for the homozygous genotype should be conducted to increase the carcass lean meat content and lower back fat thickness in the slaughter progeny. Further investigation is required to determine which indigenous boars possess the preferred allele, and whether the same approach can be applied to improve traditional breed carcass composition.

4.4. Commercial and Traditional Breeds

It is difficult to directly compare the current productivity parameters of modern and traditional UK slaughter progeny, owing to the fact that the scientific research on rare pig breeds is tremendously outdated and many smallholder producers do not maintain records on levels of production. Nevertheless, anecdotal evidence has arisen which suggests that traditional breeds reach a commercial slaughter weight at a considerably greater age (Salvatori *et al.,* 2008): because they are notable for slow growth, with a low average daily weight gain (Wood *et al.,* 2004). Additionally, it has been predisposed that in contrast to commercial breeds, traditional breeds have a high voluntary feed intake and poor feed conversion (Alfonso *et al.,* 2005; Bonneau and Lebret, 2010), which is consistent with low lean growth efficiency and increased fat deposition (Whittemore *et al.,* 2003).

However, it has been identified that traditional breeds possess superior meat quality traits: darker colour, higher moisture content, greater pH, tenderness and high intramuscular fat content (Honeyman *et al.,* 2006), which are perceived to greatly improve the eating quality of the meat and is thus regarded of higher-quality than that of the modern breeds (Bonneau and Lebret, 2010). It is well established that the Gloucester Old Spot produces meat of exceptional quality, owing to the back fat and intramuscular fat within the carcass, which enhances the succulence and flavour of the products (Gloucester Old Spot Pig Breeders Club (GOSPBC), 2012d). However, the Welsh and British Lop can produce high-yielding lean carcasses, but have sufficient intramuscular and back fat to retain the traditional pork flavour, from an improved ratio of fat: muscle (Rare Breed Survival Trust (RBST), 2011b; British Lop Pig Society (BLPS), 2014c). This demonstrates that traditional pig breeds have the potential to be utilised within modern pig production, to fulfil the commercial stipulation of leanness, yet offer opportunities for the improvement of eating quality.

The crossbreeding of commercial and traditional pigs could achieve an amalgamation of traits, of benefit to both groups, by overcoming the anecdotal negative productive capacity of traditional breeds and poor meat and eating quality of commercial breeds. An example of this approach has been applied in southern Germany, from the crossbreeding of Swabian-Hall purebred sows with Pietrain terminal sires. This ensures the survival of the pure traditional breed, and market competitiveness from improved carcass composition provided by the Pietrain (Weißmann, 2014). However, meat and eating quality traits are traditionally selected for in the terminal sire breeds and lines. Significant differences have been identified between sire breeds and lines for meat and eating quality traits, for example: pH, colour, cooking loss, intramuscular fat content and shear force (Bunter *et al.,* 2008). Yet, a comparison of six different commercial dam lines, for meat quality traits, identified no significant differences between groups, and only average results for pH, colour and intramuscular fat content (Mabry *et al.,* 1998). Therefore, this study performed the opposite dam and sire cross, to exploit the prolificacy traits of the modern dam and the meat quality traits of the traditional sire.

4.5. Chapter Objective

The objective of this chapter is to compare the performance and carcass quality traits of traditional crossbreds sired by three traditional British pig breeds, and commercial crossbreds sired by the Large White. This assessment will determine the productive capacity of the traditional crossbred progeny, and their suitability for inclusion within the commercial pig industry.

4.6. Materials and Methods

4.6.1. Sample Animals

Ethical approval was granted by Writtle College's Ethics Committee (Appendix 2). The pigs were reared at Sturgeons Farm of Writtle College in Essex, United Kingdom. A total of 167 slaughter progeny were bred from 18 commercial Large White x Landrace (LW x LR) sows. The sows were divided into 6 groups: A, C, D and E consisted of 14 second parity sows, Groups B and F consisted of 4 gilts (Appendix 3). Four gilts had to be used due to the limited availability of second parity sows and to ensure completion of data collection in the specified timeframe. However, the use of second parity sows was preferred, as the small size of gilts can be related to lower birth weights, milk output and weaning weights, compromising lifetime performance of the progeny. Older sows (parity three to six) were also discounted due to the reduction of fully working teats, with age, causing greater competition for milk and fighting within litters.

The 4 terminal sire breeds used were: Gloucester Old Spot (GOS), Welsh (W), British Lop (BL) and a Large White (LW) synthetic line. The rare breed semen was imported from a sole supplier, Deerpark Pedigree Pigs of Magherafelt, Northern Ireland, who during 2013-2014 kept 2 GOS (Forthill Rufus 367 and Forthill Rufus 456), 1 BL (Bezurrell Charles 10) and 1 Welsh (Tates Victor 24) stud boars. Due to the limited number of rare breed stud boars for commercial application, semen was sent based on boar availability and working condition: health status and physical soundness. The commercial breed semen was obtained from 4 Large White boars at one of the leading pig breeding and genetics companies. This

particular commercial line was selected as the boars were guaranteed A/A homozygotes for the IGF2 gene; however this was not tested for in this study.

Each traditional breed cross was conducted 4 times, as was the control commercial cross, in order to reduce variability and increase the significance of the results. In addition, it was decided with the Pig Unit Manager that it was only feasible to produce 16 litters: 4 of each breed, due to limited finishing pig space. The 16 litters were produced through the crossbreeding of: (LW x LR) x GOS, (LW x LR) x W, (LW x LR) x BL and (LW x LR) x LW. One gilt litter had to be removed from the study to eliminate the confounding factor of cross-fostering (Appendix 3).

4.6.2. Statistical Power

The means from a priori study, analysing the same productivity variables with GOS F_1 and LW F_1, were used to determine the sample size per group for this study. This statistical power analysis was conducted in G*Power 3.1.9.4., with the same input parameters of two tails, α: 0.05 and β: 0.8, and the effect size calculated from the means and standard deviations (0.5) of both groups. The output parameters provided the sample size and total power, displayed in Appendix 4. This justified the sample size of 24 individuals per group.

4.6.3. Rearing System

4.6.3.1. Birth to Weaning

Six piglets were randomly selected from each litter; this number was chosen as it was half of the average litter size (12), which allowed for sows with lower numbers born alive and pre-weaning mortality. One day post-farrowing, the weight and sex of each individual were recorded. Each piglet was ear tagged and assigned a number for ease of identification between litters and breeds (Blue – W F_1, Red – GOS F_1, Yellow – BL F_1 and White – LW x LR F_1). There were no differences in the housing: finger-bar farrowing crate, environmentally controlled rooms (16°c) and enclosed creep area with heat lamp (30°c), or management: twice daily feeding following the Stotfold lactation feed scale and routine litter tasks, such

as iron injecting, tail docking and teeth clipping, of the sows and piglets from birth to weaning. The piglets were offered 100 grams of creep feed: ForFarmers Easy Wean Pig Weaner, twice a day (8.30am and 4.30pm) from day 7 to weaning, to encourage early intake of solid feed and initiate gut development.

4.6.3.2. Weaning to Slaughter

The piglets were weaned at 4 weeks (28 ±4 days) in mixed-sex, weight categorised (small, medium and large), evenly numbered groups of between 16-18 individuals per pen. The traditional breed litters were amalgamated at weaning, but were penned separately from the commercial litters, for ease of management and direct comparison. The weaner house consisted of 3 environmentally controlled rooms, containing 6 pens measuring 3.5m x 4.6m, with fully slated flooring. All piglets were fed *ad libitum* following the standard farm feed regime: 1.5kg per pig of ForFarmers Easy Wean Pig Weaner for 4 days post-weaning, 7.0kg per pig of ForFarmers Pre-Grow Plus until 6 weeks of age (42 ± 4 days) and Duffields Grower 2 until 12 weeks of age (84 ± 4 days), to fulfil age-specific dietary requirements. Feed was provided in two four-space feeders, and water was available through two bite-type drinkers per pen.

The pigs were transferred to finisher building 1 or 2 at 12 weeks (84 ± 4 days), and were kept in the same weaning groups, to alleviate fighting from mixing and stress from a novel environment. Finisher house 1 consisted of 8 naturally ventilated pens, each measuring 4.3 x 4.4m, with a capacity of 18 growing pigs per pen. Each pen was comprised of a raised covered 'kennel type' lying area, bedded with straw three times weekly, and a solid concrete floor exercise/mucking area. The front of each pen could be opened for the mechanical removal of excreta, which was undertaken three times a week. Finisher house 2 consisted of 10 pens, each measuring 4.6 x 4.75m, with a capacity of 19 finisher pigs per pen. The layout and management of this accommodation was the same as finisher house 1.

Groups B to F were fed Duffields Finisher 1 *ad libitum* from weeks 12-15, and then a maintenance ration per head (0.5 kilos for every month of age) from weeks 15-18, half-divided to be fed in the morning

(8.00am) and afternoon (4.00pm), in a long trough. From week 18-slaughter the morning ration of feed was Duffields lactation diet, whereas the afternoon ration was Duffields Finisher 1. This feed composition was selected as slaughter results from Batch 1 indicated *ad libitum* feeding was correlated with excessive back fat, therefore the incorporation of sow feed was used to reduce the digestible energy of the finisher diet. Batch 1 was removed from this study to account for the confounding factor of different diet compositions (Appendix 3). Water was available through two bite-type drinkers per pen.

The pigs remained in this accommodation until slaughter, which ranged between 18-24 weeks, dependent upon the carcass weight stipulated by the abattoir/butcher, an average of 65kg deadweight for commercial breeds and 60kg deadweight for the traditional breeds. The commercial crossbreds were slaughtered and purchased by a large abattoir/processor. The traditional crossbreds were slaughtered at a local abattoir, and purchased by two specialist family owned butchers and retailers.

4.6.4. Performance Testing and Carcass Quality Traits

4.6.4.1. Liveweight Gain

All trial pigs were weighed individually, using calibrated pig weighing scales, at birth, weaning and the day prior to slaughter for the direct comparison of weight influence on growth. The average daily gain (ADG, g/day) was calculated per individual trial pig, from weaning to slaughter, using the formula:

$$\frac{(weight\ 1 - weight\ 2)}{production\ length}$$

4.6.4.2. Abattoir Measurements

Post slaughter, the dressed carcasses were individually weighed, using calibrated scales, to record the hot weights. The hot carcass is reduced in weight by 2%, if weighed within 45 minutes of slaughter, to allow for moisture loss and for the calculation of the carcass cold weight. At the time of weighing, the lean meat percentage of the carcass was assessed and graded using the cold carcass weight and P2 fat depth. The carcass P2 fat depth was measured using an optical probe.

4.6.5. Statistical Analysis

The number of piglets for statistical analysis was: 18 GOS F_1, 12 BL F_1, 24 W F_1 and 24 LW F_1. The productivity data was formatted in Microsoft Office Excel 2007, and then imported into IBM SPSS Statistics version 24. The seven variables analysed were: birth weight, weaning weight, slaughter weight, carcass weight, back fat, ADG (weaning – slaughter) and production length. An independent samples pairwise t-test was selected to determine if a difference existed between the means of two independent groups, on a continuous dependant variable, using each grouping variable independently: batch, parity, season and abattoir. The data was checked to meet the assumptions of the independent samples t-test. There were no outliers for six of the variables, as assessed by inspection of the boxplots. There were five outliers for weaning weight for the GOS F_1. The independent t-test was run with and without the outliers included in the analysis, and on comparison, both produced a statistically significant result for weaning weight. All variables were normally distributed, as assessed by Shapiro-Wilk's test, apart from weaning weight for the W F_1, slaughter weight for the GOS F_1 and back fat for the W F_1 and LW F_1. The independent t-test is reported to be robust to deviations from normality; therefore the test proceeded with not normally distributed data for some groups and variables (Lund Research Ltd, 2018a).

A multivariate analysis of covariance (MANCOVA) was selected to incorporate three covariates: batch, parity and season, and multiple dependent variables, to detect differences between the four groups. The covariates are linearly related to the dependent variables and their inclusion into the analysis can increase the ability to detect differences between groups of an independent variable. A MANCOVA is used to determine statistical significance between the adjusted means of three or more independent groups, having controlled for the covariate/s (Lund Research 2018b).

The data was checked to meet the assumptions of the MANCOVA. There were linear relationships between each pair of dependent variables, and between the three covariates and each of the dependent variables, for each group, as assessed by visual inspection of scatterplots. There was homogeneity of regression slopes, as assessed by the interaction term between breed and batch, breed

and parity and breed and season. There was homogeneity of variance and covariances, as assessed by Box's M test. There were no univariate outliers in the data, as assessed by standardised residuals greater than ± 3 standard deviations. There were no multivariate outliers in the data, as assessed by Mahalanobis distance. All variables were normally distributed, as assessed by Shapiro-Wilk's test, apart from weaning weight for the GOS F_1 and LW F_1, back fat for the W F_1 and LW F_1, production length for the W F_1 and LW F_1 and slaughter weight for the GOS F_1 and LW F_1. The MANCOVA is reported to be robust to deviations from normality; therefore the test proceeded with not normally distributed data for some groups and variables (Lund Research Ltd, 2018b).

4.7. Results

There were some significant differences for the productivity variables analysed between the traditional: GOS F_1, BL F_1 and W F_1, and the commercial LW F_1.

The independent samples t-tests were statistically significant ($p < 0.05$) for all dependant variables with each grouping variable: batch, parity and season, between all groups (Appendix 5). Therefore, these three variables were incorporated within the MANCOVA as covariates. Abattoir was not significant with any dependant variables apart from back fat; therefore it was not incorporated within the MANCOVA.

Table 10 presents the unadjusted means and standard deviations, and the adjusted means: adjusted for the covariates and standard errors, for the dependent variables and for the different groups of the independent variable.

Using the multivariate test statistic Pillai's trace, there was a significant effect of breed on the combined dependent variables: birth, weaning, slaughter and carcass weights, back fat, ADG (weaning to slaughter) and production length, after controlling for batch, parity and season (F (21, 201) = 6.087, $p <$ 0.001), Pillai's Trace = 1.166, partial $\eta_2 = 0.389$ (Appendix 6).

The covariate batch, was significantly related to birth weight, F (1, 71) = 9.97, $p < 0.01$, weaning weight, F (1, 71) = 6.58, $p < 0.05$, and production length, F (1, 71) = 9.94, $p < 0.05$. The covariate parity, was

significantly related to weaning weight, F (1, 71) = 6.35, $p < 0.05$, slaughter weight, F (1, 71) = 5.40, $p < 0.05$, carcass weight, F (1, 71) = 9.70, $p < 0.01$, back fat, F (1, 71) = 10.21, $p < 0.01$ and production length, F (1, 71), 26.82, $p < 0.001$. The covariate season, was significantly related to weaning weight, F (1, 71) = 3.98, $p < 0.05$, slaughter weight, F (1, 71) = 3.96, $p < 0.05$, carcass weight, F (1, 71) = 8.54, $p < 0.01$, back fat, F (1, 71) = 12.23, $p < 0.001$ and production length, F (1, 71) = 33.83, $p < 0.001$ (Appendix 6).

Post hoc univariate one-way ANCOVA's were performed, with a Bonferroni adjustment, to test the effect of breed, whilst controlling for the three covariates. There were significant differences in adjusted means for birth weight, F (3, 71) = 6.76, $p < 0.001$, partial $\eta_2 = 0.222$, weaning weight, F (3, 71) = 3.73, $p < 0.05$, partial $\eta_2 = 0.136$, back fat, F (3, 71) = 43.69, $p < 0.001$, partial $\eta_2 = 0.649$ and production length, F (3, 71) = 4.81, $p < 0.05$, partial $\eta_2 = 0.093$. The significant one-way ANCOVA's were followed up with pairwise comparisons, with a Bonferroni adjustment (Table 11). The Bonferroni adjustment was applied to control the overall Type I error rate: likelihood of discovering false positives, during multiple comparison testing. There were significant differences between the: GOS F_1, and BL F_1 ($p < 0.001$), and W F_1 ($p < 0.01$) for birth weight; W F_1, and GOS F_1 ($p < 0.05$), and LW F_1 ($p < 0.05$) for weaning weight; GOS F_1, and BL F_1 ($p < 0.05$), and W F_1 ($p < 0.001$), and LW F_1 ($p < 0.001$), BL F_1, and W F_1 ($p < 0.01$), and LW F_1 ($p < 0.001$), and W F_1 and LW F_1 ($p < 0.01$) for back fat; BL F_1, and W F_1 ($p < 0.05$), and LW F_1 ($p < 0.01$) for production length.

Table 10. Means, adjusted means, standard deviations and standard errors for the productivity variables measured per group (GOS F_1: n=18, BL F_1: n=12, W F_1: n=24, LW F_1: n=24).

	Dependent Variables													
	Birth Weight (kg)		Weaning Weight (kg)		Slaughter Weight (kg)		Carcass Weight (kg)		Back Fat (mm)		Production Length (days)		ADG (g)	
Group	*M* (*SD*)	M_{adj} (*SE*)	*M* (*SD*)	M_{adj} (*SE*)	*M* (*SD*)	M_{adj} (*SE*)	*M* (*SD*)	M_{adj} (*SE*)	*M* (*SD*)	M_{adj} (*SE*)	*M* (*SD*)	M_{adj} (*SE*)	*M* (*SD*)	M_{adj} (*SE*)
GOS F_1	1.64 (0.430)	1.85 (0.098)	7.79 (1.377)	8.00 (0.434)	81.78 (3.282)	83.54 (1.768)	66.27 (4.562)	68.76 (1.619)	13.94 (2.388)	15.15 (0.429)	157.17 (14.464)	162.43 (1.909)	0.567 (0.072)	0.555 (0.016)
BL F_1	1.28 (0.302)	1.28 (0.105)	7.49 (0.742)	7.26 (0.469)	85.42 (1.929)	86.38 (1.911)	69.99 (2.022)	70.65 (1.750)	13.42 (1.084)	13.40 (0.463)	167.58 (6.882)	166.43 (2.064)	0.556 (0.022)	0.571 (0.017)
W F_1	1.53 (0.370)	1.29 (0.950)	6.10 (1.663)	6.07 (0.422)	86.25 (6.102)	83.69 (1.722)	69.69 (6.355)	67.13 (1.577)	12.12 (1.849)	11.25 (0.418)	158.71 (5.116)	157.73 (1.859)	0.608 (0.049)	0.593 (0.015)
LW F_1	1.45 (0.452)	1.52 (0.081)	7.96 (2.151)	7.96 (0.360)	86.25 (9.857)	87.01 (1.468)	67.79 (8.391)	68.14 (1.345)	9.29 (1.546)	9.27 (0.356)	160.52 (5.116)	158.15 (1.585)	0.587 (0.071)	0.605 (0.013)

ADG = average daily gain (weaning to slaughter), M = Means, SD = standard deviation, M_{adj} = adjusted means, SE = standard error, GOS = Gloucester Old Spot, BL = British Lop, W = Welsh, LW = Large White.

Table 11. Pairwise comparisons for adjusted means, with standard errors, for the productivity variables between groups (GOS F_1: n=18, BL F_1: n=12, W F_1: n=24, LW F_1: n=24). The asterix denotes the post-hoc statistical differences between groups.

Differences in adjusted means							
Groups	**Dependent Variables**						
	Birth Weight (kg)	Weaning Weight (kg)	Slaughter Weight (kg)	Carcass Weight (kg)	Back fat (mm)	Production Length (days)	ADG (g)
GOS F_1 vs. BL F_1	0.575 (***)	0.733	-2.833	-1.892	1.750 (*)	-4.000	-0.017
	(0.144)	(0.641)	(2.614)	(2.394)	(0.634)	(2.823)	(0.023)
GOS F_1 vs. W F_1	0.560 (**)	1.923 (*)	-0.147	1.630	3.897 (***)	4.699	-0.038
	(0.150)	(0.666)	(2.713)	(2.485)	(0.658)	(2.930)	(0.024)
GOS F_1 vs. LW F_1	0.333	0.038	-3.468	0.619	5.885 (***)	4.276	-0.050
	(0.126)	(0.563)	(2.293)	(2.100)	(0.556)	(2.476)	(0.020)
BL F_1 vs. W F_1	-0.015	1.190	2.686	3.521	2.147 (**)	8.699 (*)	-0.021
	(0.150)	(0.666)	(2.713)	(2.485)	(0.658)	(2.930)	(0.024)
BL F_1 vs. LW F_1	-0.242	-0.695	-0.635	2.511	4.135 (***)	8.276 (**)	-0.033
	(0.126)	(0.563)	(2.293)	(2.100)	(0.556)	(2.476)	(0.020)
W F_1 vs. LW F_1	-0.227	-1.885 (*)	-3.321	-1.010	1.987 (**)	-0.423	-0.012
	(0.139)	(0.616)	(2.512)	(2.301)	(0.609)	(2.712)	(0.022)

ADG = average daily gain (weaning to slaughter), GOS = Gloucester Old Spot, BL = British Lop, W = Welsh, LW = Large White. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

4.8. Discussion

Of all the productivity variables investigated, there were significant differences between the traditional crossbreds: GOS, BL and W, and the commercial LW crossbreds, for birth weight, weaning weight, carcass back fat depth and production length.

4.8.1. Confounding Factors

There were several management requirements overlaid on the experiment, due to the small and commercial nature of the unit. In order to equalise litter sizes and ensure future functionality of teats (Richardson, 2013), one gilt litter of 4 trial BL F_1 was cross-fostered with 6 non-trial LW F_1. This litter was removed from the study due to the gilt effect and the combining of trial and non-trial piglets, which eliminated the confounding factor of cross-fostering.

As the commercial LW F_1 were fed *ad libitum*, the same was applied to the traditional F_1. However, Batch 1 of 6 trial GOS F_1 and 6 trial BL F_1 presented carcasses with extremely high levels of penalisable back fat (average: 18.5mm). Therefore, in discussion with the unit manager, it was agreed to alter the feeding regime and diet composition to reduce carcass back fat. Therefore, these 12 pigs had to be removed from the trial to standardise practices and eliminate the confounding factor of diet.

The unit had a contract to supply a large abattoir/processor with commercial LW F_1 pigs at a stipulated weight. The traditional crossbreds were not accepted by this abattoir/processor; therefore they were supplied to a local abattoir and purchased by two specialist butchers/retailers. Abattoir was included as a grouping variable in the independent sample t-test, and was only significant for the dependent variable back fat. However, the dressing, weighing, grading and recording of carcasses are regulated by The Beef and Pig Carcase Classification (England) Regulations 2010, and standardised measures taken. The difference in abattoir could not cause back fat to be statistically significant, it could only be the breed effect; therefore abattoir was not included in the MANCOVA and eliminated as a confounding factor.

The experimental design was originally 4 batches of 4 litters: 1 (LW x LR) x GOS, 1 (LW x LR) x BL, 1 (LW x LR) x W and 1 (LW x LR) x LW, produced across a 65 week period. Unfortunately due to breed changes, working availability of the traditional boars and limited finishing space, the batches became uneven in terms of sires/breeds, seasonal changes and environmental conditions.

Instead of the original 4 batches, 6 batches of uneven litters and breeds were produced. This meant that each breed of pigs was not subjected to the same environmental conditions throughout the trial. Environmental conditions encompass a wide range of needs, for example: temperature and ventilation, feeding and watering, stocking density, hygiene, health and welfare (Close, 2000). There are several studies depicting the influences of housing conditions, feeding regime and management practices on the growth performance and carcass characteristics of growing-finishing pigs (Lebret, 2008; Lebret *et al.,* 2011; Douglas *et al.,* 2015). However, this is also influenced by genotype, and its interactive effect with the environment (G x E) (Grohmann, 2012). For this study, the environmental conditions were the same throughout, for example feed regimes, stocking density, housing; the only factor that could not be fully controlled was temperature/season. However, due to the G x E interaction, with different breeds, terminal sires and lines showing variation in growth performance and carcass characteristics, when under the same and differing environmental conditions (Grohmann, 2012), batch was included as a confounding factor.

For growing and finishing pigs, changes in temperature directly affects feed intake, with a subsidiary affect on growth rate and feed conversion efficiency. In the winter months, excessive quantities of feed can be consumed to accommodate for heat loss and regulation of body temperature, whereas in the summer months, feed consumption can be decreased to reduce heat production associated with digestion and nutrient absorption (Coffey *et al.,* 2017). For breeding sows and gilts, the above can also have the same effect on feed consumption during pregnancy, directly impacting litter size and postnatal piglet survival (Knecht *et al.,* 2015). Increased temperature can also affect rearing ability, as during lactation feed intake can be reduced, leading to decreased milk production and thus lower gains in

piglet body weight (Bergsma and Hermesch, 2012). However, the farrowing house and weaner shed were both environmentally controlled rooms, with forced ventilation and heating, to provide a consistent temperature and minimise seasonal fluctuations. In addition, the feed ration for the gilts and sows was adjusted throughout the year, to maintain ideal body condition and stabilise piglet birth weight. Although, the finishing sheds were naturally ventilated barns, therefore, the colder months for batches 2 and 7, vs. the warmer months for batches 3, 4, 5 and 6 could have impacted feed intake, growth rates, production length and carcass weights (Renaudeau *et al.,* 2014; Rauw *et al.,* 2017). However, temperature fluctuations throughout the year were managed by altering straw/bedding levels, adjusting ventilation and evaporative cooling. Although these management techniques were applied, season will still have an effect on reproduction and performance, therefore it was included as a confounding factor.

The original experimental design was to use 16 second parity LW x LR sows to produce the crossbred litters. Unfortunately, due to the small scale of the unit, there was limited availability of second parity sows in the timescale to complete the data collection, therefore 4 gilts had to be used (1 gilt was discounted from analysis to eliminate the confounding factor of cross-fostering). It is generally accepted that parity has an effect on the postnatal growth performance of the progeny, due to the physiological and milking ability differences between low and high parity dams (Zotti *et al.,* 2017). It has been shown that gilts can have a smaller number of piglets born alive, lower litter weights and decreased piglet gains, compared to second parity and above sows (Hinkle, 2012). This continues throughout development, with lower weaning weights and average daily gains, longer production lengths and fatter, lighter carcasses for gilt progeny (Yoder *et al.,* 2014). The use of gilts could have impacted the growth and carcass performance of 1 GOS F_1 and 2 W F_1 litters; therefore it was included as a confounding factor.

4.8.2. Birth Weight

The GOS F_1 demonstrated the heaviest adjusted mean individual piglet birth weight (1.85kg ± SE 0.098), followed by the LW F_1 (1.52kg ± SE 0.081), W F_1 (1.29kg ± SE 0.950) and the BL F_1 (1.28kg ± SE 0.105). When controlling for batch, significant breed differences were found between the GOS and W ($p < 0.01$), and the GOS and BL ($p < 0.001$) for birth weight. This could be explained by the lower average litter size per sow for the GOS group (n=8), in comparison to the LW (n=15), W (n=12) and BL (n=16). It has been shown that the birth weight of piglets from smaller litters (n<11) is greater than that of piglets from larger litters (n>15) (Bergstrom *et al.,* 2009). The lower litter size could be attributed to individual reproductive performance of the dam and/or poor semen quality.

The GOS F_1 and LW F_1 birth weights were in accordance with the industry standard of 1.4kg and above. The BL F_1 birth weights were below the industry standard, which could be attributed to the high number born alive per litter. The W F_1 birth weights were also below industry standard, which could be the result of the confounding factors described, as the unadjusted mean individual piglet birth weight for the W F_1 was 1.53kg (± SD 0.370). It has been demonstrated that piglets with a birth weight of 1.4kg and heavier are more productive and profitable, from decreased pre-weaning and post-weaning mortality, and increased market weight and carcass value, compared to piglets below 1.4kg (Mabry, 2015). Numerous studies have stated that piglet birth weight is determined by a combination of maternal factors: condition, genotype, health status, intrauterine environment, nutrition and parity (Solanes *et al.,* 2004; Canario *et al.,* 2010; Rekiel *et al.,* 2015). The uterine capacity of modern sows remains relatively unchanged, yet the component traits of ovulation rate and embryonic survival have positively responded to intensive selection for increased litter size (Foxcroft, 2008). This has resulted in greater pre-weaning mortality and inconsistency in weaning weights from increased numbers of low birth weight piglets per litter and within-litter heterogeneity in birth weight (Milligan *et al.,* 2002; Kapell *et al.,* 2009).

In this study, 3 gilts had to be used due to the limited availability of second parity sows and to ensure completion of data collection in the specified timeframe. It is noted that parity influences birth weight, and generally gilts in first parity have lower birth weight piglets than second parity and above sows (Václavková *et al.,* 2012), attributed to the body size, condition and age of the gilt at first service (Tummaruk *et al.,* 2001). Yet, the covariate parity was not significantly related to birth weight. In addition, for individual piglet birth weight, the 3 gilt litters averaged (unadjusted) at: 1.44kg (GOS F_1), 1.50kg (W F_1) and 1.89kg (W F_1), which are all in line with the industry standard. This could be explained by the gestational feeding regime implemented at the farm and/or the phenotype of the gilt, marketed as a smaller, mature size. Alternatively, Assan *et al.,* (2014) demonstrated that terminal sire line has a significant effect on average litter weight at birth, and that differences occur between breeds/lines. However, it was stated that the dam line could be more important than the sire in affecting birth weights, due to the influence of the intrauterine environment and nutrition on foetal growth. This is supported by Chimonyo *et al.,* (2006) whom stated that the maternal genetic effects on individual birth weight are caused by the genetically controlled components of uterine capacity and nutrition. The direct additive genetic effect is due to the genetic potential of the embryo or foetus for growth during gestation. Although reproductive traits, including individual birth weight, have low-moderate heritabilities, the genetic variability for selection is generally high (Paixão *et al.,* 2019). The purebred LW and LR are improved by selection due to the presence of additive genetic variation and the individual superiority of sires/dams, and crossed to produce the LW x LR to utilise the heterosis for lowly heritable traits, such as reproduction (Whittemore, 1998).

The covariate batch was significantly related to birth weight, which could imply that the variation between groups is the result of this factor, rather than breed. It has been shown that several environmental factors influence piglet birth weight, for example feeding regimes during gestation, housing and overall farm hygiene (Opschoor *et al.,* 2011). Batch 5 was comprised of 6 litters: 1 x GOS F_1, 2 x GOS F_1, 1 x W F_1 and 1 x LW F_1, the collective mean individual piglet birth weight was 1.06kg for an average of 11 piglets born alive per litter. In comparison to all the other batches, these figures were

extremely low, which would infer that the significance found is related to the environmental conditions experienced by this batch. However, breed explained a larger proportion of the variance not attributable to other variables than batch (Appendix 6).

4.8.3. Weaning Weight

The weaning weight of a pig is considered as an important determinant of its post-weaning and lifetime growth performance (Lawlor *et al.,* 2002; Dunshea *et al.,* 2003). The W F_1 demonstrated the lightest adjusted mean individual pig weaning weight (6.07kg ± SE 0.422), followed by the BL F_1 (7.26kg ± SE 0.469), LW F_1 (7.96kg ± SE 0.360) and GOS F_1 (8.00kg ± SE 0.434). The weaning weights for the GOS F_1, LW F_1 and BL F_1 were in accordance with the industry standard for average weaned weight per pig of 7.30kg (AHDB, 2017b). The low adjusted mean individual weaning weight for the W F_1 could be explained by the milking ability of the dam (Lawlor *et al.,* 2002; Schinckel *et al.,* 2004), the genetic effects of the terminal sire line/breed (Assan *et al.,* 2014), the season of birth (Paredes *et al.,* 2012) and/or the variation in batches.

4.8.3.1. Milking Ability of the Dam

The covariate parity was significantly related to weaning weight, which was not unexpected, as gilts and second parity sows were used to produce the crossbreds. It has been said that the milking ability of the dam significantly influences piglet growth from birth to weaning (Schinckel *et al.,* 2004). In order to fulfil the nutritional requirements of large, fast-growing litters, the modern dam has been genetically selected for increased milk production (Kim *et al.,* 2013b). The capacity for greater milk production can only be reached if the dam's nutritional requirements (energy and amino acids) and feed intake (amount and type) are correctly managed, because of the high metabolic demand placed on the body during lactation (Neill and Williams, 2010). In addition to nutrition, the milk yield of a dam will vary depending on a combination of factors: parity, litter size, breed, genetics and body condition (Whittemore, 1998). Several studies have stated that gilts fail to produce sufficient milk, due to their nutritional requirements not being met, from low feed intake and physiological growth (Dove, 2009; Piao *et al.,* 2010). Miller *et*

al., (2008) are in support of this, as they demonstrated that gilt progeny had slower pre-weaning growth and lighter weaning weights, compared to parity 2-7 sows, due to lower milking capacity. The low mean individual weaning weight for the W F_1 could be explained by the use of 2 gilts and 2 second parity sows to produce the 4 W F_1 litters. The average (unadjusted) weaning weight of one gilt litter was 5.0kg (n=9), whereas the other was 7.7kg (n=10). The lower weaning weights of the gilt litter may have affected the average of all 4 litters combined, thus causing the covariate parity to be significant.

4.8.3.2. Season and Batch

The covariates season and batch were also significantly related to weaning weight. Paredes *et al.,* (2012) stated that season of birth is a significant determinant of body weight gain during the nursery phase. In addition, Sabbioni *et al.,* (2010) identified that piglets born in the Autumn and Winter had higher daily weight gains compared to those born in the Spring and Summer. This is supported by Williams *et al.,* (2013), who found that piglets exposed to high temperatures were 0.5kg lighter at weaning, when compared to those unexposed. This would concur with the farrowing months and light weaning weights of this study, as the 2 gilt litters used to produce the W F_1 farrowed late July and early August and weaned late August. However, the farrowing house had environmentally controlled rooms, with forced ventilation and heating, to provide a consistent temperature, therefore seasonal fluctuations should have been minimal. Yet, heat stress can impact sow feed intake during lactation, thus reducing milk production and litter weight gain (Schinckel *et al.,* 2019). The combination of season and parity: reduced milk production, could be the cause of the lighter weaning weights of the W F_1. The significance of the covariate batch could be attributed to the unevenness of batches in terms of parity, with the gilt litters in Batches 2 and 6, and the sow litters in Batches 3, 4 and 5.

4.8.3.3. Genetic Effects of the Terminal Sire Breed and Lines

When controlling for batch, parity and season, significant breed differences were found between the GOS F_1 and W F_1 ($p < 0.05$) and LW F_1 and W F_1 ($p < 0.05$). In addition, breed explained a larger proportion of the variance not attributable to other variables than batch, parity and season (Appendix

6). It has been demonstrated that breed/line of terminal sire can significantly influence piglet weight at weaning (Gopinathan and Usha, 2010; Assan *et al.,* 2014). There could have been a greater additive genetic effect in the LW F_1, attributed to the selective breeding for specific traits in the purebred terminal sire and dam populations (Whittemore, 1998), but a reduced non-additive effect due to the sharing of parental breeds in the three-way cross (Boddicker, 2015). However, the traditional F_1s would show 100% heterosis (non-additive effect) due to the unrelatedness of the parental breeds in the three-way cross (Boddicker, 2015), but could have a reduced additive genetic effect due to the level of heterozygosity/homozygosity in the purebred populations (Frankham *et al.,* 2010).

The heavy mean individual pig weaning weight of the LW F_1 could be explained by expression of the paternally inherited IGF2 mutation for increased muscle mass. It has been stated that progeny sired by IGF2 homozygous boars have heavier weaning weights, compared to progeny sired by other terminal breeds/lines (Rattlerow Farms Ltd, 2013). Whereas, Xue and Xu (2008) compared the genetic effects of the IGF2 gene on weaning weight and found no significant differences among commercial and traditional pig breeds. Tortereau *et al.,* (2011) also stated that the IGF2-in3-G3072A allele is very rare or even non-existent in traditional breeds and wild boars. However, there are numerous studies reporting the beneficial effects of the mutation on growth performance and carcass composition in Large White pigs (Kolarikova *et al.,* 2003; Vykoukalova *et al.,* 2006; Fontanesi *et al.,* 2010). Yet, the weaning weights for the GOS F_1 and BL F_1 were close to that of the LW F_1, suggesting that the traditional terminal sires may have possessed the IGF2 mutation, or that the effect of the IGF2 mutation on weaning weight is not significant between IGF2 mutants and non-mutants.

4.8.4. Slaughter Weight and Carcass Weight

The LW F_1 had the heaviest adjusted mean individual slaughter weight (87.01kg ± SE 1.468) followed by the BL F_1 (86.38kg ± SE 1.911), W F_1 (83.69 ± SE 1.722) and the GOS F_1 (83.54kg ± SE 1.768). The BL F_1 had the heaviest adjusted mean individual carcass weight (70.65kg ± SE 1.750) followed by the GOS F_1 (68.76kg ± SE 1.619), LW F_1 (68.14kg ± SE 1.345) and the W F_1 (67.13kg ± SE 1.577). Whilst the

unadjusted and adjusted means remained similar for the GOS F_1, BL F_1 and LW F_1, the difference between the unadjusted slaughter weight, 86.25kg (± SD 6.102), and carcass weight, 69.69kg (± SD 6.355), for the W F_1, and the adjusted were quite notable, demonstrating the effect of the covariates on this cross. When controlling for batch, parity and season, there were no significant breed differences for slaughter or carcass weight.

The target for all trial pigs was to reach a liveweight of 80-85kg, to achieve the carcass weights stipulated by the abattoir/butcher of 65kg average deadweight for commercial LW F_1 and 60kg average deadweight for the GOS F_1, BL F_1 and W F_1. As discussed earlier, temperature can have a significant effect on growth rates, feed efficiency, production length and finishing weights (Renaudeau *et al.,* 2014; Rauw *et al.,* 2017). During the grow-finish stages, pigs exposed to cold temperatures will consume excessive quantities of feed to compensate for heat loss and maintain body temperature, whereas the opposite will occur during heat stress (Coffey *et al.,* 2017). Cruzen *et al.,* (2015) established that pigs subjected to heat stress during finishing had lighter slaughter weights and thus decreased carcass weights, compared to those unexposed. The significance of the covariate season could be as a result of the batches being finished across different times of the year, but also by seasonal demand, with some pigs having to be sold lighter or retained to heavier weights, thus creating wide ranges and impacting the means.

Weaning weight has been shown to have a profound effect on growth performance and thus slaughter weight, with piglets weaned heavier growing faster and having greater slaughter and carcass weights than piglets weaned lighter (Collins *et al.,* 2017). It would be assumed that the 2 W gilt litters, with low weaning weights, would result in lighter slaughter and carcass weights, however the unadjusted mean slaughter weight for that batch was 90.16kg (± SD 5.557) and carcass weight was 73.5kg (± SD 5.380): greater than the trial targets. This could be attributed to the potential of piglets compensating for light weaning weights, during postnatal growth (Douglas *et al.,* 2013). This is supported by Calderón Díaz *et al.,* (2016) who showed that pigs, born to gilts, were able to 'catch up', to pigs born to multiparous sows,

during the finishing period and have similar slaughter and carcass weights. In addition, the unadjusted mean slaughter weight and carcass weight for the 3 gilt litters were greater than that of the second parity litters. This could explain the significance of the covariate parity, but not as would have been expected as an effect of using gilts.

4.8.5. Back Fat

The LW F_1 displayed the lowest adjusted mean individual carcass back fat depth (9.27mm ± SE 0.356), followed by the W F_1 (11.25mm ± SE 0.418), BL F_1 (13.40mm ± SE 0.463) and the GOS F_1 (15.15mm ± SE 0.429).

The carcass back fat depth for the LW F_1 was in accordance with the UK industry average for P2 back fat depth of between 9-12mm (AHDB, 2016c). This result could be explained by one of the main industry objectives to increase the lean to fat ratio in the pig carcass, through genetic selection for decreased back fat thickness in commercial breeds (Monziols *et al.,* 2005; Permentier *et al.,* 2013). The Large White breed is renowned for carcass characteristics of high lean meat percentage and low fat content (Latorre *et al.,* 2009). In addition, the low adjusted mean individual carcass back fat depth of the LW F_1 could also be explained by expression of the paternally inherited IGF2 mutation for reduced back fat deposition (Fontanesi *et al.,* 2011). Fontanesi *et al.,* (2010) demonstrated that homozygous AA progeny have greater lean cuts and lower back fat thickness, in comparison to the homozygous GG and heterozygous GA progeny, which exhibit opposite and intermediary results.

When controlling for batch, parity and season, there were significant breed differences between the GOS F_1 and, BL F_1 ($p < 0.05$), W F_1 ($p < 0.001$), LW F_1 ($p < 0.001$), the BL F_1 and, W F_1 ($p < 0.01$), LW F_1 ($p < 0.001$), and the W F_1 and LW F_1 ($p < 0.01$). In addition, breed explained a larger proportion of the variance not attributable to other variables than batch, parity and season. It has been identified that the breed/line of terminal sire has a profound effect on back fat thickness (Fabrega *et al.,* 2003; Latorre *et al.,* 2003), which could explain the differences in results between LW F_1 and the GOS F_1, BL F_1 and W F_1. It has been noted that there are breed differences in fat characteristics: distribution and mobilisation,

which can influence carcass composition (Jones *et al.,* 1980; Kolstad, 2001). Traditional breeds are often stated to have greater subcutaneous fat deposition and low lean meat percentage, compared to commercial breeds (Chimonyo and Dzama, 2007; Damon *et al.,* 2012). However, the W is stated to produce lean, well-conformed carcasses, with sufficient back fat (RBST, 2015c). The adjusted mean individual carcass back fat depth for the W F_1 (11.25mm ± SE 0.418) was within the industry average of 9-12mm, however the unadjusted mean (12.12mm ± SD 1.849) was only marginally above and was within the accepted upper P2 range of 12-14mm. Due to consumer demand for leaner meat, producers face price penalties per kg of deadweight for over fat pigs: P2 measurements of > 14mm (Brooks and Varley, 2003). On the other hand, the BL is also stated to be a leaner breed than most of the other rare pig breeds, and less prone to becoming over fat (RBST, 2011b), yet the adjusted mean individual carcass back fat depth was 13.40mm (± SE 0.463). However, the result for the GOS F_1 (15.15mm ± SE 0.429) was in accordance with previous studies, as this breed is known for greater back fat depths of 12-16mm (Wood *et al.,* 1979; Warriss *et al.,* 1990).

The covariate, season, was significantly related to back fat. This is supported by Trezona *et al.,* (2004) who identified a significant effect of season on carcass quality. Finishing pigs are very sensitive to changes in ambient temperature, which is reflected in changes of appetite and feed intake (Linden, 2014). It has been shown that fluctuations in P2 back fat throughout the year correspond with seasonal temperature changes: leaner pigs in the summer and fatter pigs in the winter (Trezona *et al.,* 2004). The propensity to deposit fat rather than protein can be as a result of excessive and irregular intake of feed (Linden, 2014). The BL F_1, W F_1 and LW F_1 conform to this seasonal pattern, however the GOS F_1 are inverted, which could be attributed to the Spring finished gilt litter and Summer finished sow litters. The covariate, parity, was also significantly related to back fat. As previously mentioned, weaning weight is an important determinant of lifetime growth performance and carcass quality (Lawlor *et al.,* 2002; Dunshea *et al.,* 2003). It would have been expected that the low weaning weights of the W F_1 would have lead to slower growth performance, lighter carcasses and greater P2 back fat thickness (Collins *et al.,* 2017). However, the W F_1 disputed this, with back fat depths within the average and upper industry

standards, due accelerated growth and the deposition of protein rather than fat, to compensate for their lower weaning weight (Whittemore, 1998). In addition, the unadjusted mean back fat for the 3 gilt litters was less than that of the second parity litters. This could explain the significance of the covariate parity, but not as would have been expected as an effect of using gilts. Lastly, the covariate batch was also significantly related to back fat. Although a target slaughter and carcass weight was set, due to supply and demand, some pigs had to be sold at lighter/heavier weights, with shorter/longer production lengths. This would have caused some variation across batches, owing to those kept to an older age and heavier weight, because as slaughter age and weight increases, the ratio of fat to lean deposition rises (Latorre *et al.,* 2003; Conte *et al.,* 2011).

In contrast to the results of this study, it has been reported that the crossbreeding of traditional and commercial pig breeds can improve carcass characteristics of leanness and fat content (Lan *et al.,* 1993). This is supported by Jiang *et al.,* (2011) who identified that crossbreeding the indigenous Dahe with the modern Duroc, resulted in Dawu crossbreds with lower fat deposition and higher lean meat percentage, compared with the purebred Dahe. This could be explained by the methodology of the crossbreeding: the other studies crossed traditional dams and modern sires, with the progeny expressing the commercial phenotype. This study crossed modern dams and traditional sires, with the progeny appearing to express the traditional phenotype. Thus, the results suggest that the differences between breeds for carcass back fat can be largely attributed to the terminal sire effect.

4.8.6. Production Length and ADG – Weaning to Slaughter

The pig industry use average daily gain as a tool to monitor the growth rates of slaughter pigs. The general industry principle is: the higher the average daily gain, the shorter the production length (days to slaughter) and vice versa (English *et al.,* 1998). The LW F_1 displayed the highest adjusted mean individual ADG (605g/day ± SE 0.013), followed by the W F_1 (593 g/day ± SE 0.015), BL F_1 (571g/day ± SE 0.017) and the GOS F_1 (555g/day ± SE 0.016). The W F_1 had the shortest adjusted mean individual production length (157 days ± SE 1.859), followed by the LW F_1 (158 days ± SE 1.585), GOS F_1 (162 days ±

SE 1.909) and the BL F_1 (166 days ± SE 2.064). There were significant breed differences between the BL F_1 and W F_1 ($p < 0.05$) and BL F_1 and LW F_1 ($p < 0.01$) for production length, attributed to the large contrasting time frames to finish. ADG was not significant for any of the covariates, which could be explained by the relatively similar rates of growth from weaning to slaughter.

The ADG and production length for the LW F_1 was to be expected, as they were unable to express their genetic growth potential, due to the restricted feeding imposed during the finishing stage (Dzama, 2002). This is supported by Lovatto *et al.,* (2007) who demonstrated that feed restriction in (LW x LR) x Pietrain growing pigs resulted in a decrease in growth rate: reduced daily liveweight gain, as metabolisable energy was used for maintenance. Anecdotal evidence suggests that traditional breeds have low ADG (Wood *et al.,* 2004) and poor feed efficiency (Alfonso *et al.,* 2005), which results in long production lengths from slow growth (Salvatori *et al.,* 2008). Yet, the W F_1 had comparable results to the commercial LW F_1 for production length and ADG - weaning to slaughter. However, it was considered that *ad libitum* feeding would have shown different results, with the LW F_1 having outperformed the traditional crossbreds, due to the genetic relationship between growth rate and feed efficiency (Hermesch *et al.,* 2002).

It has been identified that breed/line of terminal sire has a significant effect on progeny daily liveweight gains and feed efficiency during the grow-finish phase (Latorre *et al.,* 2003; Magowan and McCann, 2009; Schinckel *et al.,* 2012). The second highest ADG (593g/day ± SE 0.015) and shortest production length (157 days ± SE 1.859) of the W F_1 could be explained by the semi-commercialised nature of the breed. In support of this, it is stated that the W are fast growing, with good liveweight gain and feed conversion ratio (PWPS, 2014b). These results were not expected for the W F_1, as lighter weaned piglets tend to grow slower, with time to slaughter longer, than their heavier weaned counterparts (Collins *et al.,* 2017). However, there is the capacity for lighter weaned piglets to exhibit compensatory growth during the grow-finish stage (Perez-Palencia and Levesque, 2019). In addition, the unadjusted mean production length for the 3 gilt litters was less than that of the second parity litters. This could explain

the significance of the covariate parity, but not as would have been expected as an effect of using gilts. Therefore, the compensatory growth would likely be attributed to the breed effect, thus demonstrating the viability of using traditional terminal sires in an intensive system.

The covariates season and batch were also significantly related to production length. As already mentioned, temperature can have a significant effect on growth rates, feed efficiency and production length (Renaudeau *et al.,* 2014; Rauw *et al.,* 2017). Of the 13 litters analysed for this study, 23% grew and finished in the Winter months, contrast to 77% during the Summer months. Douglas *et al.,* (2014b) found that pigs born during the Summer and finished during the Winter were more likely to have greater growth rates. This is due to lower consumption of feed, to compensate for the temperature increases, during the Summer months (Coffey *et al.,* 2017). This could explain the low ADG and long production lengths of the GOS F_1 and BL F_1, as two of the three GOS litters and both of the BL litters grew and finished during the Spring and Summer months. Alternatively, the significance of batch could be explained by seasonal demand, as some pigs had to be sold lighter/retained to heavier weights, with production lengths varying slightly across batches.

4.9. Conclusion

The results of this chapter have provided the commercial and traditional pig sectors new, valuable data on the productive capacity of traditional crossbreds. The anecdotal evidence: slow growth, low ADG and long production length has been refuted, as the results demonstrated the opposite effect.

There were several management requirements overlaid on the experiment, due to the small and commercial nature of the unit, which resulted in the confounding factors of batch, parity and season being included in the statistical analysis. The unadjusted means showed the W F_1 outperforming the GOS F_1 and BL F_1, from having the lowest weaning weights, to the heaviest slaughter and carcass weights, lowest back fat and greatest ADG. However, the adjusted means for the W F_1 birth weight, slaughter weight and carcass weight were much lower, demonstrating the effect of the confounding factors on this cross. Although there were differences between the unadjusted and adjusted means for

some productivity variables, the W F_1 results were largely comparable to those of the LW F_1, which was to be expected from the semi-commercialised nature of the breed.

In comparison with the LW F_1, the GOS F_1 and BL F_1 both also performed well from birth to slaughter, however their carcass back fats were penalisable: over the industry accepted P2 range. As commercial breeds are generally fed *ad libitum*, due to the positive correlation with growth rate and feed efficiency, this study may not have validly represented the LW F_1. However, to ensure consistency of direct comparison, the same feeding conditions had to be applied to the LW F_1.

Using traditional breeds for commercial pork production is one of the two main conservation strategies for their survival: by improving their economic use/value and maintaining a purebred population for crossbreeding. Overall, this study revealed that traditional crossbreds can perform comparably to the commercial slaughter pig. Although, further research needs to be conducted into the methods of retaining, yet minimising carcass back fat in traditional breeds, whether that is through genetics, nutrition or management. The W was revealed to be the most likely candidate to be incorporated within commercial production. The popularity of the GOS continues to grow, with numerous outlets producing and selling the breed's reputable high quality meat. However, more consideration needs to be given to the BL, which has shown similarities to the W, for commercial application, and could be used for future diversification.

Chapter 5. Summation of Findings and Recommendations

5.1. General Summation

This study has established that the crossbreeding of traditional and commercial pig breeds is a viable strategy for the conservation of unique farm animal genetic resources, but also to genetically improve the future productivity of both groups. Firstly, the assessment of genetic potential of traditional purebred populations: Gloucester Old Spot (GOS), British Lop (BL) and W (Welsh), revealed that they possess much greater levels of genetic diversity, than commercial hybrid Large White x Landrace (LW x LR). Secondly, it was demonstrated that the variability exhibited by traditional breeds could be used to improve future productivity, by increasing nuclear DNA diversity, through crossbreeding with modern breeds. Lastly, the productivity assessment discovered that the traditional crossbreds performance for most of the variables measured was comparable to that of the commercial crossbreds, showing their potential for future application within the pig industry.

5.2. An Assessment of Genetic Diversity Using Mitochondrial DNA

This chapter identified that on an individual breed basis, the three traditional British pig breeds possessed more genetic diversity, at the mitochondrial DNA (mtDNA) D-loop fragment, than the commercial LW x LR. The greatest overall level of mtDNA genetic diversity was observed in the GOS, followed by the W and BL, whereas the LW x LR displayed the lowest levels across all gene measures. This is in agreement with Groeneveld *et al.,* (2010) who identified that local livestock populations tend to have greater molecular diversity than highly productive breeds. The BL showed the highest level of genetic differentiation to the LW x LR, followed by the W and GOS. The results for the BL and W are somewhat in accordance with previous studies. Wilkinson *et al.,* (2011) demonstrated a clear lack of admixture between the BL and LW, depicting the two breeds as distinct genetic units, however, the BL showed high affinity to the British LR, implying introgression. This interpretation is similar to another study by Wilkinson *et al.,* (2012) who revealed low F_{ST} between the W and LR, but moderate F_{ST} between

the W and LW. This could be explained by the commercial sample population being hybrid crosses, and/or the genetic contribution of the LR may not have been of British origin.

This chapter supports the FAO's recommendation to conserve the genetic diversity of traditional breeds as an adaptive insurance against future challenges: climate change, emerging diseases, resource availability and market demands, to improve animal production and support global food security (FAO, 2007; FAO, 2015b). The results have revealed the conservation value and crossbreeding viability of traditional British pig breeds. This would not only increase commercial within-breed diversity, but also facilitate genetic improvement, ensure sustainable utilisation and improve the productive capacity of both groups. In addition, this assessment could provide the commercial industry with the ability not only to select by productivity, but also genetic distinctiveness: to increase genetic variability by crossing distantly related modern and traditional breeds. Finally, this chapter has demonstrated that the BL and W have the greatest potential for future commercial application, by maintaining purebred populations, for crossbreeding with the LW x LR.

5.2.1. Further Research

This study only sampled 3 native pig breeds, one from each category of the Rare Breed Survival Trust (RBST) Watchlist. An increase in sample size, to include all 11 native pig breeds, would reveal unknown genetic diversity and identify phylogenetic relationships among breeds, which could facilitate decisions on conservation priorities and selection for future utilisation. It would also determine whether number of breeding females' correlates with within-breed genetic diversity, which could change the way in which the conservation status of a breed is assessed in the UK. Lastly, this study broadly represented each breed: not all bloodlines were included due to the limitations of herd numbers, diversity within herds, location and owner willingness to participate. The molecular analysis of each female and male bloodline would create a genetic profile of the breed as a whole: to identify those of high risk and close relatedness, and develop breeding strategies to increase diversity within and between lines.

5.3. Assessing the Impact of Crossbreeding on Nuclear DNA Diversity

This chapter discovered wide variation between the traditional crossbreds, commercial crossbreds and maternal LWLR sows for a nuclear DNA region of the DIO3 gene. The GOS F_1 and BL F_1 presented the greatest levels of diversity, for all gene measures, followed by the LW F_1 and W F_1 and LWLR sows. This was attributed to the crossbreeding effect of the modern hybrid dam with different terminal sires, from differences in allele and genotype frequencies and genetic distances between the parental breeds. The low results of the W and LW crossbreds and LWLR would indicate sharing of alleles and homozygosity for this region in one or both parents. This is supported by Sørensen *et al.,* (2008) who stated that crossbreeding individuals from different lines, breeds or populations can generate offspring with increased heterozygosity, caused by different alleles or allele frequencies in the parental populations, which creates new genetic combinations. However, only low to moderate genetic differentiation was identified between all crossbred groups and maternal sows, considered to the result of: limited divergence from the ancestral sequence, slow mutation rates of nuclear DNA and the close genetic relatedness of the sows used.

This chapter has demonstrated that crossbreeding traditional and commercial breeds can achieve an increase in nuclear genetic diversity of the resultant progeny. In addition, the comparison of both mitochondrial and nuclear DNA results revealed that the traditional purebreds and crosses showed greater levels of genetic diversity for both regions studied. In terms of productivity, it is a general rule that heterozygous animals generally have better performance than their homozygous counterparts (Sørenson *et al.,* 2008). Therefore, breeding and genetic programmes would have to select for increased genetic distance between parental breeds and divergent genotypes: utilising genetic variation to improve productivity by maximising heterozygosity. This supports the notion of combining the desirable characteristics of traditional survivability and commercial reproductivity to achieve greater crossbred performance. To finalise, the results of this chapter have shown that traditional breeds possess the

variability, which could have the selection potential, to improve the future productivity of commercial breeds.

5.3.1. Further Research

The statistical tests of neutrality, of this chapter, produced conflicting results for two of the four crossbred groups. To achieve consistency, an increase in the number of F_1 generations produced, over a longer time scale, would create more genetic changes at the molecular level. Further research needs to be conducted to fully establish the role and effects of the DIO3 gene on porcine embryonic, foetal and postnatal growth, development and survival. Progression could include the detection of single nucleotide polymorphisms (SNP), and identification of those which are positively associated with productivity traits, using survivability data: numbers born alive and numbers of pigs weaned. It would be of benefit to identify any SNP genotype and expression differences between traditional and commercial terminal breeds, and the effects on progeny survivability. The results of these further studies could then be compared with other survivability genes, to determine whether the DIO3 gene is a candidate for future selection to improve piglet survivability to weaning.

5.4. The Effect of Crossbreeding on Productivity Parameters: Growth and Back Fat

This chapter revealed that, under the experimental conditions, the traditional and commercial crossbreds performed comparably for most of the productivity variables measured, however there were highly significant differences between breeds for birth weight, weaning weight, carcass back fat depth and production length. There were several management requirements overlaid on the experiment, due to the small and commercial nature of the unit, which resulted in the confounding factors of batch, parity and season being accounted for in the statistical analysis. The unadjusted means showed the W F_1 outperforming the GOS F_1 and BL F_1, from having the lowest weaning weights, to the heaviest slaughter and carcass weights, lowest back fat and greatest ADG. However, the adjusted means for the W F_1 birth weight, slaughter weight and carcass weight were much lower, demonstrating the effect of the confounding factors on this cross. Although the GOS F_1 and BL F_1 performed well, their back fat results

were not in agreement with Jiang *et al.,* (2011) and Weißmann (2014) who stated that crossbreeding indigenous dams with modern sires resulted in crossbreds with lower fat deposition and higher lean meat percentage. However, this study crossed modern dams and traditional sires, with the progeny appearing to express the traditional phenotype. When controlling for the confounding factors, the results suggested that the differences in growth (weaning to finishing) and carcass performance, between the four groups, could largely be attributed to the effect of the terminal sire breed.

This chapter provides novel and current data on the growth and carcass composition capabilities of traditional crossbred progeny, and how this compares to the commercial finishing pig. The results can be used to disprove some of the negative anecdotal evidence about the productive capacity of traditional breeds. It has also been demonstrated that traditional breed sires show potential for future commercial application; achieving similar productivity rates, being reared in an intensive system and ability to influence back fat deposition. However, the traditional breed variation for carcass composition (subcutaneous fat) may be of future benefit to improve commercial breed meat-eating quality. Although there were differences between the unadjusted and adjusted means for some productivity variables, due to the comparability with the LW, it was deemed that the W would be most suited for commercial production.

5.4.1. Further Research

Due to the management requirements overlaid on this experiment, the batches became uneven in terms of sires/breeds, seasonal changes and environmental conditions, which could have caused the production differences between the crossbreds. Therefore, if this experiment was repeated, it would be ensured that all productional elements would be standardised. For example, 4 batches of 4 litters: 1 (LW x LR) x GOS, 1 (LW x LR) x BL, 1 (LW x LR) x W and 1 (LW x LR) x LW, 4 batches per season, the same sow parity and the same slaughter weight. It was hypothesised that the crossbreeding traditional and commercial breeds would significantly reduce back fat deposition in the progeny; however this was not the case for two of the crossbred groups. Further research needs to be conducted to determine which

feed ingredients, dietary compositions and feed regimes, will promote optimum lean growth, increase feed efficiency, yet decrease back fat. Due to the restrictive feeding applied to all trial pigs, this study may not have validly represented the LW F_1. A comparison of all crosses on a commercial *ad libitum* diet could be performed: it would be expected that the traditional crosses would not perform well on this formulation and regime, as depicted in this study. Therefore, to ensure a new feed formulation and regime for the traditional crossbreds was viable, in comparison to current commercial diets, feed intake versus weight gain would have to be measured, to determine the production and cost differences. The LW terminal sires used in this study possessed the IGF2 mutation for increased muscle mass and reduced back fat. A genetic analysis of traditional breed boars could identify possession of the mutation, whether selection for traditional mutants can be applied to improve carcass composition, or if traditionals lack the mutation, how their crossbreds perform compared to the commercial mutants. Lastly, it would be of benefit to traditional breeds to determine whether their 'superior meat quality traits' could be conferred through crossbreeding. If laboratory measures and taste panel assessments were to show that traditional crossbred meat-eating quality excelled that of the commercial crossbred, this would create an economic value and ensure the future sustainability of purebred traditional populations.

6.0. References

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Appendix 1 – Background information of the pig keepers, premises and sample population for the 4 breed groups.

Producer	Location	Purpose	Breed	Line/s	Samples
Gloucester Old Spots					
1	Essex	Breeding stock, showing	Gloucester Old Spot	Sows: Dolly, Princess, Princess Joans Boars: Rufus	2 boars 8 sows
2	Suffolk	Breeding stock, meat production, showing	Gloucester Old Spot	Sows: Princess Boars: Unknown	2 boars 3 sows
3	Oxford	Research	Gloucester Old Spot	Sows: Princess, Josephine Boar: Patrick	2 boars 4 sows
4	East Sussex	Breeding stock, college farm	Gloucester Old Spot	Unknown	1 sow
5	Northern Ireland	Pig breeding and genetic company	Gloucester Old Spot	Rufus	2 boars
British Lop					
6	Essex	Conservation, breeding stock, meat production, showing	British Lop	Boars: Charles Sows and gilts: Unknown	2 boars 3 sows 2 gilts
7	Buckinghamshire	Meat production, conservation, farm events	British Lop	Boars: Ben, Charles Sows: Actress, Gracious, Pride, Thatcher, Queen, Mary	2 boars 10 sows
4	East Sussex	Breeding stock, college farm	British Lop	Boars: General Sows and gilts:	2 boars 1 sow 2 gilts

				Actress	
5	Northern Ireland	Pig breeding and genetic company	British Lop	Charles	1 boar
Welsh					
8	Shropshire	Meat production, research	Welsh	Unknown	25 various
Large White x Landrace					
9	Yorkshire	Pig breeding and genetic company	Large White x Landrace	Commercial	18 sows 2 boars
10	Yorkshire	Pig breeding and genetic company	Large White x Landrace	Commercial	3 sows 2 gilts

Appendix 2 – Ethics Approval

dissertationforms@writtle.ac.uk

Tue 6/18, 2:59 PM

COLLINGBOURNE, STEPHANIE (98270498)
Dear Stephanie Collingbourne,

The Ethics Committee has reviewed your dissertation proposal form set and approved it.

Approval Comments:
APPROVED (Ref: 98270498-AW1)

Please do not reply to this message as the account is not monitored.

Appendix 3 - Record of the crosses completed, identifying the sows and boars used, and the progeny outcome.

Sows	Inseminated	Terminal sire breed	Farrowing date	Total Born Alive	Weaning date	Total at Weaning
Second parity sows: Group A/Batch 1						
97-Removed	18.03.13	GOS 456	11.07.13	13	08.08.13	13
101-Removed	05.03.13	BL	27.06.13	17	27.07.13	14
85-Removed	25.03.13	BK	19.07.13	9	08.08.13	1
Gilts: Group B/Batch 2						
136-Removed	30.07.13	BL	23.11.13	4	19.12.13	10
138	30.07.13	GOS 367	23.11.13	11	19.12.13	11
Second parity sows: Group C/Batch 3						
99	30.09.13	LW 1	23.01.14	20	20.02.14	8
108	01.10.13	LW 2	27.01.14	14	20.02.14	12
Second parity sows: Group D/Batch 4						
125	22.10.13	BL	12.02.14	14	13.03.14	14
128	22.10.13	LW 3	13.02.14	13	13.03.14	12
102-Removed	22.10.13	W	14.02.14	8	13.03.14	2
126	23.10.13	BL	15.02.14	18	13.03.14	13
127	23.10.13	GOS 456	15.02.14	7	13.03.14	7
112	22.10.13	W	16.02.14	11	13.03.14	8
129	24.10.13	GOS 456	15.02.14	5	13.03.14	5
Second parity sows: Group E/Batch 5						
130	11.11.13	LW 4	06.03.14	13	03.04.14	9
131	12.11.13	W	07.03.14	13	03.04.14	12
Gilts: Group F/Batch 6						
160	08.04.14	W	31.07.14	11	28.08.14	10
161	08.04.14	W	02.08.14	14	28.08.14	9

Appendix 4 – Statistical Power

	Dependent Variables						
	Birth Weight	Weaning Weight	Slaughter Weight	Carcass Weight	Back Fat	Production Length	ADG (Weaning to Slaughter)
Statistical power	*	*	*	*	*	*	*
Sample size	12	4	6	6	2	6	6
Effect size	1.2	3	2	2	8	2	2

*denotes statistical power of >80%.

Appendix 5 – Independent Samples T-Tests

Group Statistics

	Abattoir	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	1	24	1.454	.4520	.0923
	2	54	1.507	.3947	.0537
Weaning Weight	1	24	7.958	2.1510	.4391
	2	54	6.978	1.5974	.2174
Slaughter Weight	1	24	86.25	9.857	2.012
	2	54	84.57	4.947	.673
Carcass Weight	1	24	67.7875	8.39080	1.71276
	2	54	68.6163	5.27816	.71827
Backfat	1	24	9.29	1.546	.316
	2	54	13.02	2.060	.280
Production Length	1	24	160.54	5.116	1.044
	2	54	160.17	10.415	1.417
ADG W to S	1	24	.5871	.07099	.01449
	2	54	.5831	.05778	.00786

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	.650	.423	-.526	76	.601	-.0532	.1013	-.2550	.1485

	Equal variances not assumed			-.499	39.272	.621	-.0532	.1068	-.2691	.1627
Weaning Weight	Equal variances assumed	4.801	.032	2.242	76	.028	.9806	.4375	.1093	1.8518
	Equal variances not assumed			2.001	34.750	.053	.9806	.4899	-.0143	1.9754
Slaughter Weight	Equal variances assumed	21.306	.000	1.002	76	.319	1.676	1.672	-1.655	5.007
	Equal variances not assumed			.790	28.285	.436	1.676	2.122	-2.668	6.020
Carcass Weight	Equal variances assumed	10.652	.002	-.529	76	.598	-.82880	1.56577	-3.94730	2.28971
	Equal variances not assumed			-.446	31.380	.658	-.82880	1.85727	-4.61488	2.95728
Backfat	Equal variances assumed	1.571	.214	-7.915	76	.000	-3.727	.471	-4.665	-2.789
	Equal variances not assumed			-8.829	57.974	.000	-3.727	.422	-4.572	-2.882
Production Length	Equal variances assumed	6.283	.014	.167	76	.868	.375	2.243	-4.092	4.842
	Equal variances not assumed			.213	75.138	.832	.375	1.761	-3.132	3.882
ADG W to S	Equal variances assumed	1.809	.183	.258	76	.797	.00394	.01523	-.02640	.03427
	Equal variances not assumed			.239	37.144	.813	.00394	.01649	-.02946	.03733

Group Statistics

	Parity	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	1	18	1.494	.3280	.0773
	2	60	1.490	.4352	.0562
Weaning Weight	1	18	5.950	1.3700	.3229
	2	60	7.678	1.7677	.2282
Slaughter Weight	1	18	86.83	7.164	1.689
	2	60	84.57	6.683	.863
Carcass Weight	1	18	69.9000	7.29730	1.71999
	2	60	67.8997	6.03184	.77871
Backfat	1	18	12.50	1.978	.466
	2	60	11.68	2.715	.351
Production Length	1	18	155.44	8.699	2.050
	2	60	161.73	8.752	1.130
ADG W to S	1	18	.6261	.04913	.01158
	2	60	.5718	.05984	.00773

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	3.907	.052	.040	76	.968	.0044	.1112	-.2170	.2258
	Equal variances not assumed			.047	36.739	.963	.0044	.0956	-.1893	.1981

Weaning Weight	Equal variances assumed	.841	.362	-3.812	76	.000	-1.7283	.4533	-2.6312	-.8254
	Equal variances not assumed			-4.371	35.661	.000	-1.7283	.3954	-2.5305	-.9262
Slaughter Weight	Equal variances assumed	.681	.412	1.242	76	.218	2.267	1.826	-1.369	5.903
	Equal variances not assumed			1.195	26.513	.243	2.267	1.896	-1.627	6.161
Carcass Weight	Equal variances assumed	1.590	.211	1.175	76	.244	2.00033	1.70299	-1.39146	5.39212
	Equal variances not assumed			1.059	24.388	.300	2.00033	1.88805	-1.89314	5.89381
Backfat	Equal variances assumed	4.237	.043	1.183	76	.240	.817	.690	-.558	2.192
	Equal variances not assumed			1.400	38.145	.170	.817	.583	-.364	1.997
Production Length	Equal variances assumed	.176	.676	-2.677	76	.009	-6.289	2.349	-10.967	-1.611
	Equal variances not assumed			-2.686	28.146	.012	-6.289	2.341	-11.083	-1.494
ADG W to S	Equal variances assumed	1.193	.278	3.505	76	.001	.05428	.01548	.02344	.08512
	Equal variances not assumed			3.899	33.587	.000	.05428	.01392	.02598	.08258

Group Statistics

	Season	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	1	60	1.490	.4352	.0562
	2	12	1.633	.2741	.0791
Weaning Weight	1	60	7.678	1.7677	.2282
	2	12	5.458	1.2154	.3509
Slaughter Weight	1	60	84.57	6.683	.863
	2	12	90.17	5.557	1.604
Carcass Weight	1	60	67.8997	6.03184	.77871
	2	12	73.5333	5.38066	1.55326
Backfat	1	60	11.68	2.715	.351
	2	12	13.00	1.758	.508
Production Length	1	60	161.73	8.752	1.130
	2	12	161.00	1.044	.302
ADG W to S	1	60	.5718	.05984	.00773
	2	12	.6292	.04316	.01246

1 = January-March
2 = July-September

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	4.884	.030	-1.095	70	.277	-.1433	.1309	-.4045	.1178

	Equal variances not assumed			-1.477	23.758	.153	-.1433	.0971	-.3437	.0571
Weaning Weight	Equal variances assumed	1.717	.194	4.147	70	.000	2.2200	.5353	1.1523	3.2877
	Equal variances not assumed			5.304	21.557	.000	2.2200	.4185	1.3510	3.0890
Slaughter Weight	Equal variances assumed	.189	.665	-2.717	70	.008	-5.600	2.061	-9.711	-1.489
	Equal variances not assumed			-3.075	18.003	.007	-5.600	1.821	-9.427	-1.773
Carcass Weight	Equal variances assumed	.744	.391	-3.002	70	.004	-5.63367	1.87657	-9.37637	-1.89096
	Equal variances not assumed			-3.242	17.024	.005	-5.63367	1.73753	-9.29914	-1.96819
Backfat	Equal variances assumed	5.116	.027	-1.609	70	.112	-1.317	.819	-2.949	.316
	Equal variances not assumed			-2.135	23.022	.044	-1.317	.617	-2.593	-.041
Production Length	Equal variances assumed	14.624	.000	.288	70	.774	.733	2.544	-4.341	5.808
	Equal variances not assumed			.627	65.909	.533	.733	1.169	-1.602	3.068
ADG W to S	Equal variances assumed	1.270	.264	-3.151	70	.002	-.05733	.01820	-.09363	-.02104
	Equal variances not assumed			-3.911	20.519	.001	-.05733	.01466	-.08786	-.02680

Group Statistics

	Season	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	1	60	1.490	.4352	.0562
	3	6	1.217	.2483	.1014
Weaning Weight	1	60	7.678	1.7677	.2282
	3	6	6.933	1.1793	.4814
Slaughter Weight	1	60	84.57	6.683	.863
	3	6	80.17	5.154	2.104
Carcass Weight	1	60	67.8997	6.03184	.77871
	3	6	62.6333	4.72342	1.92833
Backfat	1	60	11.68	2.715	.351
	3	6	11.50	2.168	.885
Production Length	1	60	161.73	8.752	1.130
	3	6	144.33	5.715	2.333
ADG W to S	1	60	.5718	.05984	.00773
	3	6	.6200	.06356	.02595

3 = October-December

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	2.624	.110	1.507	64	.137	.2733	.1814	-.0890	.6356

	Equal variances not assumed			2.358	8.475	.044	.2733	.1159	.0086	.5380
Weaning Weight	Equal variances assumed	.652	.422	1.006	64	.318	.7450	.7403	-.7339	2.2239
	Equal variances not assumed			1.398	7.467	.202	.7450	.5328	-.4990	1.9890
Slaughter Weight	Equal variances assumed	.610	.438	1.563	64	.123	4.400	2.816	-1.225	10.025
	Equal variances not assumed			1.935	6.806	.095	4.400	2.274	-1.009	9.809
Carcass Weight	Equal variances assumed	.479	.491	2.071	64	.042	5.26633	2.54336	.18539	10.34728
	Equal variances not assumed			2.532	6.749	.040	5.26633	2.07962	.31141	10.22125
Backfat	Equal variances assumed	1.153	.287	.160	64	.873	.183	1.146	-2.106	2.473
	Equal variances not assumed			.193	6.678	.853	.183	.952	-2.090	2.457
Production Length	Equal variances assumed	1.819	.182	4.751	64	.000	17.400	3.663	10.083	24.717
	Equal variances not assumed			6.712	7.585	.000	17.400	2.593	11.364	23.436
ADG W to S	Equal variances assumed	.117	.734	-1.870	64	.066	-.04817	.02575	-.09961	.00328
	Equal variances not assumed			-1.779	5.922	.126	-.04817	.02707	-.11463	.01829

Group Statistics

	Season	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	2	12	1.633	.2741	.0791
	3	6	1.217	.2483	.1014
Weaning Weight	2	12	5.458	1.2154	.3509
	3	6	6.933	1.1793	.4814
Slaughter Weight	2	12	90.17	5.557	1.604
	3	6	80.17	5.154	2.104
Carcass Weight	2	12	73.5333	5.38066	1.55326
	3	6	62.6333	4.72342	1.92833
Backfat	2	12	13.00	1.758	.508
	3	6	11.50	2.168	.885
Production Length	2	12	161.00	1.044	.302
	3	6	144.33	5.715	2.333
ADG W to S	2	12	.6292	.04316	.01246
	3	6	.6200	.06356	.02595

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	.000	1.000	3.129	16	.006	.4167	.1332	.1344	.6990
	Equal variances not assumed			3.240	11.080	.008	.4167	.1286	.1338	.6995

Weaning Weight	Equal variances assumed	.049	.827	-2.450	16	.026	-1.4750	.6021	-2.7514	-.1986
	Equal variances not assumed			-2.476	10.389	.032	-1.4750	.5957	-2.7956	-.1544
Slaughter Weight	Equal variances assumed	.263	.615	3.680	16	.002	10.000	2.717	4.240	15.760
	Equal variances not assumed			3.779	10.837	.003	10.000	2.646	4.166	15.834
Carcass Weight	Equal variances assumed	.001	.971	4.205	16	.001	10.90000	2.59212	5.40496	16.39504
	Equal variances not assumed			4.402	11.410	.001	10.90000	2.47610	5.47393	16.32607
Backfat	Equal variances assumed	.365	.554	1.583	16	.133	1.500	.948	-.509	3.509
	Equal variances not assumed			1.470	8.415	.178	1.500	1.020	-.833	3.833
Production Length	Equal variances assumed	7.358	.015	10.069	16	.000	16.667	1.655	13.158	20.175
	Equal variances not assumed			7.084	5.168	.001	16.667	2.353	10.677	22.656
ADG W to S	Equal variances assumed	.189	.669	.364	16	.721	.00917	.02522	-.04429	.06262
	Equal variances not assumed			.318	7.393	.759	.00917	.02878	-.05817	.07651

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	1	6	1.217	.2483	.1014
	2	12	1.458	.3704	.1069
Weaning Weight	1	6	6.933	1.1793	.4814
	2	12	6.417	1.7299	.4994
Slaughter Weight	1	6	80.17	5.154	2.104
	2	12	86.00	12.270	3.542
Carcass Weight	1	6	62.6333	4.72342	1.92833
	2	12	67.7667	9.82551	2.83638
Backfat	1	6	11.50	2.168	.885
	2	12	8.92	1.676	.484
Production Length	1	6	144.33	5.715	2.333
	2	12	163.58	4.602	1.328
ADG W to S	1	6	.6200	.06356	.02595
	2	12	.5792	.09150	.02641

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	.347	.564	-1.434	16	.171	-.2417	.1685	-.5989	.1156
	Equal variances not assumed			-1.640	14.279	.123	-.2417	.1473	-.5571	.0738

Weaning Weight	Equal variances assumed	1.003	.332	.655	16	.522	.5167	.7893	-1.1565	2.1899
	Equal variances not assumed			.745	14.118	.469	.5167	.6936	-.9699	2.0032
Slaughter Weight	Equal variances assumed	4.940	.041	-1.103	16	.286	-5.833	5.287	-17.041	5.374
	Equal variances not assumed			-1.416	15.804	.176	-5.833	4.120	-14.576	2.909
Carcass Weight	Equal variances assumed	3.169	.094	-1.199	16	.248	-5.13333	4.28205	-14.21087	3.94420
	Equal variances not assumed			-1.497	15.999	.154	-5.13333	3.42980	-12.40421	2.13754
Backfat	Equal variances assumed	.585	.456	2.802	16	.013	2.583	.922	.629	4.538
	Equal variances not assumed			2.561	8.108	.033	2.583	1.009	.263	4.904
Production Length	Equal variances assumed	.045	.834	-7.736	16	.000	-19.250	2.488	-24.525	-13.975
	Equal variances not assumed			-7.170	8.367	.000	-19.250	2.685	-25.395	-13.105
ADG W to S	Equal variances assumed	2.007	.176	.975	16	.344	.04083	.04189	-.04796	.12963
	Equal variances not assumed			1.103	13.931	.289	.04083	.03703	-.03862	.12029

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	1	6	1.217	.2483	.1014
	3	36	1.381	.4509	.0752
Weaning Weight	1	6	6.933	1.1793	.4814
	3	36	8.225	1.2909	.2152
Slaughter Weight	1	6	80.17	5.154	2.104
	3	36	84.69	3.970	.662
Carcass Weight	1	6	62.6333	4.72342	1.92833
	3	36	68.9883	3.75135	.62523
Backfat	1	6	11.50	2.168	.885
	3	36	13.22	2.140	.357
Production Length	1	6	144.33	5.715	2.333
	3	36	163.86	9.660	1.610
ADG W to S	1	6	.6200	.06356	.02595
	3	36	.5586	.04859	.00810

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	4.436	.042	-.863	40	.393	-.1639	.1900	-.5479	.2201
	Equal variances not assumed			-1.299	11.509	.219	-.1639	.1262	-.4402	.1124

Weaning Weight	Equal variances assumed	.004	.953	-2.293	40	.027	-1.2917	.5633	-2.4302	-.1531
	Equal variances not assumed			-2.449	7.156	.043	-1.2917	.5273	-2.5331	-.0502
Slaughter Weight	Equal variances assumed	.053	.819	-2.482	40	.017	-4.528	1.824	-8.214	-.841
	Equal variances not assumed			-2.053	6.029	.086	-4.528	2.206	-9.919	.863
Carcass Weight	Equal variances assumed	.227	.636	-3.708	40	.001	-6.35500	1.71364	-9.81840	-2.89160
	Equal variances not assumed			-3.135	6.097	.020	-6.35500	2.02715	-11.29622	-1.41378
Backfat	Equal variances assumed	.011	.919	-1.822	40	.076	-1.722	.945	-3.632	.188
	Equal variances not assumed			-1.805	6.730	.116	-1.722	.954	-3.997	.553
Production Length	Equal variances assumed	2.036	.161	-4.783	40	.000	-19.528	4.083	-27.780	-11.275
	Equal variances not assumed			-6.888	10.553	.000	-19.528	2.835	-25.800	-13.256
ADG W to S	Equal variances assumed	.044	.836	2.746	40	.009	.06139	.02236	.01620	.10658
	Equal variances not assumed			2.258	6.013	.065	.06139	.02718	-.00509	.12787

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	1	6	1.217	.2483	.1014
	4	12	1.850	.2236	.0645
Weaning Weight	1	6	6.933	1.1793	.4814
	4	12	7.300	2.3653	.6828
Slaughter Weight	1	6	80.17	5.154	2.104
	4	12	82.75	5.739	1.657
Carcass Weight	1	6	62.6333	4.72342	1.92833
	4	12	64.7667	6.26278	1.80791
Backfat	1	6	11.50	2.168	.885
	4	12	9.83	1.528	.441
Production Length	1	6	144.33	5.715	2.333
	4	12	153.50	.522	.151
ADG W to S	1	6	.6200	.06356	.02595
	4	12	.6042	.03942	.01138

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	.531	.477	-5.469	16	.000	-.6333	.1158	-.8788	-.3878
	Equal variances not assumed			-5.270	9.189	.000	-.6333	.1202	-.9044	-.3623

Weaning Weight	Equal variances assumed	5.675	.030	-.354	16	.728	-.3667	1.0345	-2.5597	1.8264
	Equal variances not assumed			-.439	15.972	.667	-.3667	.8355	-2.1380	1.4047
Slaughter Weight	Equal variances assumed	.848	.371	-.929	16	.367	-2.583	2.781	-8.479	3.313
	Equal variances not assumed			-.965	11.169	.355	-2.583	2.678	-8.467	3.300
Carcass Weight	Equal variances assumed	.698	.416	-.732	16	.475	-2.13333	2.91280	-8.30818	4.04152
	Equal variances not assumed			-.807	13.065	.434	-2.13333	2.64329	-7.84093	3.57427
Backfat	Equal variances assumed	.928	.350	1.902	16	.075	1.667	.876	-.191	3.525
	Equal variances not assumed			1.685	7.578	.132	1.667	.989	-.636	3.969
Production Length	Equal variances assumed	10.125	.006	-5.686	16	.000	-9.167	1.612	-12.584	-5.749
	Equal variances not assumed			-3.920	5.042	.011	-9.167	2.338	-15.162	-3.171
ADG W to S	Equal variances assumed	.205	.657	.656	16	.521	.01583	.02414	-.03534	.06701
	Equal variances not assumed			.559	6.990	.594	.01583	.02833	-.05118	.08285

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	1	6	1.217	.2483	.1014
	5	12	1.633	.2741	.0791
Weaning Weight	1	6	6.933	1.1793	.4814
	5	12	5.458	1.2154	.3509
Slaughter Weight	1	6	80.17	5.154	2.104
	5	12	90.17	5.557	1.604
Carcass Weight	1	6	62.6333	4.72342	1.92833
	5	12	73.5333	5.38066	1.55326
Backfat	1	6	11.50	2.168	.885
	5	12	13.00	1.758	.508
Production Length	1	6	144.33	5.715	2.333
	5	12	161.00	1.044	.302
ADG W to S	1	6	.6200	.06356	.02595
	5	12	.6292	.04316	.01246

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	.000	1.000	-3.129	16	.006	-.4167	.1332	-.6990	-.1344
	Equal variances not assumed			-3.240	11.080	.008	-.4167	.1286	-.6995	-.1338

Weaning Weight	Equal variances assumed	.049	.827	2.450	16	.026	1.4750	.6021	.1986	2.7514
	Equal variances not assumed			2.476	10.389	.032	1.4750	.5957	.1544	2.7956
Slaughter Weight	Equal variances assumed	.263	.615	-3.680	16	.002	-10.000	2.717	-15.760	-4.240
	Equal variances not assumed			-3.779	10.837	.003	-10.000	2.646	-15.834	-4.166
Carcass Weight	Equal variances assumed	.001	.971	-4.205	16	.001	-10.90000	2.59212	-16.39504	-5.40496
	Equal variances not assumed			-4.402	11.410	.001	-10.90000	2.47610	-16.32607	-5.47393
Backfat	Equal variances assumed	.365	.554	-1.583	16	.133	-1.500	.948	-3.509	.509
	Equal variances not assumed			-1.470	8.415	.178	-1.500	1.020	-3.833	.833
Production Length	Equal variances assumed	7.358	.015	-10.069	16	.000	-16.667	1.655	-20.175	-13.158
	Equal variances not assumed			-7.084	5.168	.001	-16.667	2.353	-22.656	-10.677
ADG W to S	Equal variances assumed	.189	.669	-.364	16	.721	-.00917	.02522	-.06262	.04429
	Equal variances not assumed			-.318	7.393	.759	-.00917	.02878	-.07651	.05817

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	2	12	1.458	.3704	.1069
	3	36	1.381	.4509	.0752
Weaning Weight	2	12	6.417	1.7299	.4994
	3	36	8.225	1.2909	.2152
Slaughter Weight	2	12	86.00	12.270	3.542
	3	36	84.69	3.970	.662
Carcass Weight	2	12	67.7667	9.82551	2.83638
	3	36	68.9883	3.75135	.62523
Backfat	2	12	8.92	1.676	.484
	3	36	13.22	2.140	.357
Production Length	2	12	163.58	4.602	1.328
	3	36	163.86	9.660	1.610
ADG W to S	2	12	.5792	.09150	.02641
	3	36	.5586	.04859	.00810

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	2.937	.093	.539	46	.593	.0778	.1443	-.2128	.3683

	Equal variances not assumed			.595	22.803	.558	.0778	.1307	-.1927	.3483
Weaning Weight	Equal variances assumed	2.227	.142	-3.852	46	.000	-1.8083	.4695	-2.7533	-.8634
	Equal variances not assumed			-3.326	15.297	.005	-1.8083	.5437	-2.9653	-.6513
Slaughter Weight	Equal variances assumed	26.724	.000	.565	46	.575	1.306	2.309	-3.343	5.954
	Equal variances not assumed			.362	11.777	.724	1.306	3.603	-6.562	9.173
Carcass Weight	Equal variances assumed	18.995	.000	-.630	46	.532	-1.22167	1.93773	-5.12212	2.67879
	Equal variances not assumed			-.421	12.086	.681	-1.22167	2.90447	-7.54498	5.10164
Backfat	Equal variances assumed	1.407	.242	-6.337	46	.000	-4.306	.679	-5.673	-2.938
	Equal variances not assumed			-7.162	23.966	.000	-4.306	.601	-5.546	-3.065
Production Length	Equal variances assumed	3.649	.062	-.096	46	.924	-.278	2.907	-6.130	5.574
	Equal variances not assumed			-.133	39.958	.895	-.278	2.087	-4.497	3.941
ADG W to S	Equal variances assumed	9.516	.003	1.001	46	.322	.02056	.02054	-.02080	.06191
	Equal variances not assumed			.744	13.129	.470	.02056	.02763	-.03907	.08018

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	2	12	1.458	.3704	.1069
	4	12	1.850	.2236	.0645
Weaning Weight	2	12	6.417	1.7299	.4994
	4	12	7.300	2.3653	.6828
Slaughter Weight	2	12	86.00	12.270	3.542
	4	12	82.75	5.739	1.657
Carcass Weight	2	12	67.7667	9.82551	2.83638
	4	12	64.7667	6.26278	1.80791
Backfat	2	12	8.92	1.676	.484
	4	12	9.83	1.528	.441
Production Length	2	12	163.58	4.602	1.328
	4	12	153.50	.522	.151
ADG W to S	2	12	.5792	.09150	.02641
	4	12	.6042	.03942	.01138

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	1.683	.208	-3.136	22	.005	-.3917	.1249	-.6507	-.1326

	Equal variances not assumed			-3.136	18.078	.006	-.3917	.1249	-.6540	-.1293
Weaning Weight	Equal variances assumed	2.655	.117	-1.044	22	.308	-.8833	.8459	-2.6377	.8710
	Equal variances not assumed			-1.044	20.150	.309	-.8833	.8459	-2.6471	.8804
Slaughter Weight	Equal variances assumed	5.858	.024	.831	22	.415	3.250	3.910	-4.859	11.359
	Equal variances not assumed			.831	15.593	.418	3.250	3.910	-5.057	11.557
Carcass Weight	Equal variances assumed	2.311	.143	.892	22	.382	3.00000	3.36357	-3.97561	9.97561
	Equal variances not assumed			.892	18.672	.384	3.00000	3.36357	-4.04841	10.04841
Backfat	Equal variances assumed	.020	.890	-1.400	22	.175	-.917	.655	-2.274	.441
	Equal variances not assumed			-1.400	21.812	.176	-.917	.655	-2.275	.442
Production Length	Equal variances assumed	67.819	.000	7.542	22	.000	10.083	1.337	7.311	12.856
	Equal variances not assumed			7.542	11.283	.000	10.083	1.337	7.150	13.017
ADG W to S	Equal variances assumed	7.288	.013	-.869	22	.394	-.02500	.02876	-.08464	.03464
	Equal variances not assumed			-.869	14.947	.398	-.02500	.02876	-.08632	.03632

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	2	12	1.458	.3704	.1069
	5	12	1.633	.2741	.0791
Weaning Weight	2	12	6.417	1.7299	.4994
	5	12	5.458	1.2154	.3509
Slaughter Weight	2	12	86.00	12.270	3.542
	5	12	90.17	5.557	1.604
Carcass Weight	2	12	67.7667	9.82551	2.83638
	5	12	73.5333	5.38066	1.55326
Backfat	2	12	8.92	1.676	.484
	5	12	13.00	1.758	.508
Production Length	2	12	163.58	4.602	1.328
	5	12	161.00	1.044	.302
ADG W to S	2	12	.5792	.09150	.02641
	5	12	.6292	.04316	.01246

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	.519	.479	-1.316	22	.202	-.1750	.1330	-.4509	.1009

	Equal variances not assumed			-1.316	20.270	.203	-.1750	.1330	-.4522	.1022
Weaning Weight	Equal variances assumed	1.920	.180	1.570	22	.131	.9583	.6103	-.3074	2.2240
	Equal variances not assumed			1.570	19.732	.132	.9583	.6103	-.3158	2.2325
Slaughter Weight	Equal variances assumed	6.797	.016	-1.072	22	.296	-4.167	3.888	-12.230	3.897
	Equal variances not assumed			-1.072	15.330	.300	-4.167	3.888	-12.439	4.105
Carcass Weight	Equal variances assumed	4.715	.041	-1.783	22	.088	-5.76667	3.23383	-12.47323	.93989
	Equal variances not assumed			-1.783	17.053	.092	-5.76667	3.23383	-12.58784	1.05450
Backfat	Equal variances assumed	.037	.849	-5.823	22	.000	-4.083	.701	-5.538	-2.629
	Equal variances not assumed			-5.823	21.950	.000	-4.083	.701	-5.538	-2.629
Production Length	Equal variances assumed	50.523	.000	1.897	22	.071	2.583	1.362	-.242	5.408
	Equal variances not assumed			1.897	12.130	.082	2.583	1.362	-.381	5.548
ADG W to S	Equal variances assumed	6.643	.017	-1.712	22	.101	-.05000	.02920	-.11057	.01057
	Equal variances not assumed			-1.712	15.664	.107	-.05000	.02920	-.11202	.01202

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	3	36	1.381	.4509	.0752
	4	12	1.850	.2236	.0645
Weaning Weight	3	36	8.225	1.2909	.2152
	4	12	7.300	2.3653	.6828
Slaughter Weight	3	36	84.69	3.970	.662
	4	12	82.75	5.739	1.657
Carcass Weight	3	36	68.9883	3.75135	.62523
	4	12	64.7667	6.26278	1.80791
Backfat	3	36	13.22	2.140	.357
	4	12	9.83	1.528	.441
Production Length	3	36	163.86	9.660	1.610
	4	12	153.50	.522	.151
ADG W to S	3	36	.5586	.04859	.00810
	4	12	.6042	.03942	.01138

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	12.274	.001	-3.450	46	.001	-.4694	.1361	-.7434	-.1955

	Equal variances not assumed			-4.739	38.690	.000	-.4694	.0991	-.6699	-.2690
Weaning Weight	Equal variances assumed	13.704	.001	1.719	46	.092	.9250	.5381	-.1581	2.0081
	Equal variances not assumed			1.292	13.252	.218	.9250	.7159	-.6186	2.4686
Slaughter Weight	Equal variances assumed	3.848	.056	1.309	46	.197	1.944	1.486	-1.046	4.935
	Equal variances not assumed			1.090	14.672	.293	1.944	1.784	-1.865	5.754
Carcass Weight	Equal variances assumed	4.792	.034	2.826	46	.007	4.22167	1.49394	1.21452	7.22881
	Equal variances not assumed			2.207	13.727	.045	4.22167	1.91297	.11109	8.33225
Backfat	Equal variances assumed	1.860	.179	5.057	46	.000	3.389	.670	2.040	4.738
	Equal variances not assumed			5.976	26.526	.000	3.389	.567	2.224	4.553
Production Length	Equal variances assumed	16.306	.000	3.687	46	.001	10.361	2.810	4.705	16.018
	Equal variances not assumed			6.407	35.608	.000	10.361	1.617	7.080	13.642
ADG W to S	Equal variances assumed	.156	.695	-2.935	46	.005	-.04556	.01552	-.07680	-.01432
	Equal variances not assumed			-3.262	23.102	.003	-.04556	.01397	-.07444	-.01667

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	3	36	1.381	.4509	.0752
	5	12	1.633	.2741	.0791
Weaning Weight	3	36	8.225	1.2909	.2152
	5	12	5.458	1.2154	.3509
Slaughter Weight	3	36	84.69	3.970	.662
	5	12	90.17	5.557	1.604
Carcass Weight	3	36	68.9883	3.75135	.62523
	5	12	73.5333	5.38066	1.55326
Backfat	3	36	13.22	2.140	.357
	5	12	13.00	1.758	.508
Production Length	3	36	163.86	9.660	1.610
	5	12	161.00	1.044	.302
ADG W to S	3	36	.5586	.04859	.00810
	5	12	.6292	.04316	.01246

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	7.707	.008	-1.825	46	.075	-.2528	.1385	-.5316	.0260

	Equal variances not assumed			-2.316	31.687	.027	-.2528	.1091	-.4752	-.0304
Weaning Weight	Equal variances assumed	.033	.857	6.519	46	.000	2.7667	.4244	1.9123	3.6210
	Equal variances not assumed			6.722	19.942	.000	2.7667	.4116	1.9080	3.6253
Slaughter Weight	Equal variances assumed	1.592	.213	-3.729	46	.001	-5.472	1.467	-8.426	-2.519
	Equal variances not assumed			-3.154	14.926	.007	-5.472	1.735	-9.172	-1.772
Carcass Weight	Equal variances assumed	.362	.550	-3.247	46	.002	-4.54500	1.39963	-7.36231	-1.72769
	Equal variances not assumed			-2.714	14.732	.016	-4.54500	1.67438	-8.11951	-.97049
Backfat	Equal variances assumed	.947	.336	.324	46	.747	.222	.685	-1.156	1.601
	Equal variances not assumed			.358	22.796	.723	.222	.620	-1.062	1.506
Production Length	Equal variances assumed	14.059	.000	1.017	46	.315	2.861	2.814	-2.803	8.525
	Equal variances not assumed			1.747	37.352	.089	2.861	1.638	-.457	6.179
ADG W to S	Equal variances assumed	.186	.668	-4.470	46	.000	-.07056	.01578	-.10232	-.03879
	Equal variances not assumed			-4.748	21.075	.000	-.07056	.01486	-.10145	-.03966

Group Statistics

	Batch	N	Mean	Std. Deviation	Std. Error Mean
Birth Weight	4	12	1.850	.2236	.0645
	5	12	1.633	.2741	.0791
Weaning Weight	4	12	7.300	2.3653	.6828
	5	12	5.458	1.2154	.3509
Slaughter Weight	4	12	82.75	5.739	1.657
	5	12	90.17	5.557	1.604
Carcass Weight	4	12	64.7667	6.26278	1.80791
	5	12	73.5333	5.38066	1.55326
Backfat	4	12	9.83	1.528	.441
	5	12	13.00	1.758	.508
Production Length	4	12	153.50	.522	.151
	5	12	161.00	1.044	.302
ADG W to S	4	12	.6042	.03942	.01138
	5	12	.6292	.04316	.01246

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Birth Weight	Equal variances assumed	.514	.481	2.122	22	.045	.2167	.1021	.0049	.4285

	Equal variances not assumed			2.122	21.146	.046	.2167	.1021	.0044	.4290
Weaning Weight	Equal variances assumed	9.589	.005	2.399	22	.025	1.8417	.7677	.2496	3.4337
	Equal variances not assumed			2.399	16.430	.029	1.8417	.7677	.2177	3.4656
Slaughter Weight	Equal variances assumed	.186	.671	-3.216	22	.004	-7.417	2.306	-12.199	-2.634
	Equal variances not assumed			-3.216	21.977	.004	-7.417	2.306	-12.199	-2.634
Carcass Weight	Equal variances assumed	.765	.391	-3.678	22	.001	-8.76667	2.38352	-13.70978	-3.82355
	Equal variances not assumed			-3.678	21.512	.001	-8.76667	2.38352	-13.71630	-3.81704
Backfat	Equal variances assumed	.120	.732	-4.710	22	.000	-3.167	.672	-4.561	-1.772
	Equal variances not assumed			-4.710	21.579	.000	-3.167	.672	-4.563	-1.771
Production Length	Equal variances assumed	1238489897526886.500	.000	-22.249	22	.000	-7.500	.337	-8.199	-6.801
	Equal variances not assumed			-22.249	16.176	.000	-7.500	.337	-8.214	-6.786
ADG W to S	Equal variances assumed	.004	.953	-1.482	22	.153	-.02500	.01687	-.05999	.00999
	Equal variances not assumed			-1.482	21.821	.153	-.02500	.01687	-.06001	.01001

Appendix 6 – Multivariate Analysis of Covariance (MANCOVA)

Descriptive Statistics

	Breed	Mean	Std. Deviation	N
Birth Weight	1	1.639	.4300	18
	2	1.275	.3019	12
	3	1.525	.3698	24
	4	1.454	.4520	24
	Total	1.491	.4109	78
Weaning Weight	1	7.794	1.3773	18
	2	7.492	.7416	12
	3	6.108	1.6631	24
	4	7.958	2.1510	24
	Total	7.279	1.8292	78
Slaughter Weight	1	81.78	3.282	18
	2	85.42	1.929	12
	3	86.25	6.102	24
	4	86.25	9.857	24
	Total	85.09	6.817	78
Carcass Weight	1	66.2744	4.56232	18
	2	69.9867	2.02165	12
	3	69.6875	6.35516	24
	4	67.7875	8.39080	24
	Total	68.3613	6.35249	78
Backfat	1	13.94	2.388	18
	2	13.42	1.084	12

	3	12.12	1.849	24
	4	9.29	1.546	24
	Total	11.87	2.575	78
Production Length	1	157.17	14.464	18
	2	167.58	6.882	12
	3	158.71	5.894	24
	4	160.54	5.116	24
	Total	160.28	9.084	78
ADG W to S	1	.5672	.07234	18
	2	.5575	.02221	12
	3	.6079	.04908	24
	4	.5871	.07099	24
	Total	.5844	.06170	78

Multivariate Tests[a]

Effect		Value	F	Hypothesis df	Error df	Sig.	Partial Eta Squared
Intercept	Pillai's Trace	.775	32.003[b]	7.000	65.000	.000	.775
	Wilks' Lambda	.225	32.003[b]	7.000	65.000	.000	.775
	Hotelling's Trace	3.446	32.003[b]	7.000	65.000	.000	.775
	Roy's Largest Root	3.446	32.003[b]	7.000	65.000	.000	.775
Season	Pillai's Trace	.557	11.668[b]	7.000	65.000	.000	.557
	Wilks' Lambda	.443	11.668[b]	7.000	65.000	.000	.557
	Hotelling's Trace	1.257	11.668[b]	7.000	65.000	.000	.557
	Roy's Largest Root	1.257	11.668[b]	7.000	65.000	.000	.557
Parity	Pillai's Trace	.525	10.266[b]	7.000	65.000	.000	.525
	Wilks' Lambda	.475	10.266[b]	7.000	65.000	.000	.525

	Hotelling's Trace	1.106	10.266[b]	7.000	65.000	.000	.525
	Roy's Largest Root	1.106	10.266[b]	7.000	65.000	.000	.525
Batch	Pillai's Trace	.275	3.520[b]	7.000	65.000	.003	.275
	Wilks' Lambda	.725	3.520[b]	7.000	65.000	.003	.275
	Hotelling's Trace	.379	3.520[b]	7.000	65.000	.003	.275
	Roy's Largest Root	.379	3.520[b]	7.000	65.000	.003	.275
Breed	Pillai's Trace	1.166	6.087	21.000	201.000	.000	.389
	Wilks' Lambda	.140	8.750	21.000	187.195	.000	.480
	Hotelling's Trace	4.126	12.510	21.000	191.000	.000	.579
	Roy's Largest Root	3.642	34.856[c]	7.000	67.000	.000	.785

a. Design: Intercept + Season + Parity + Batch + Breed

b. Exact statistic

c. The statistic is an upper bound on F that yields a lower bound on the significance level.

Tests of Between-Subjects Effects

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Corrected Model	Birth Weight	4.144[a]	6	.691	5.535	.000	.319
	Weaning Weight	82.354[b]	6	13.726	5.560	.000	.320
	Slaughter Weight	667.192[c]	6	111.199	2.712	.020	.186
	Carcass Weight	664.838[d]	6	110.806	3.221	.007	.214
	Backfat	339.455[e]	6	56.576	23.455	.000	.665
	Production Length	2958.833[f]	6	493.139	10.313	.000	.466
	ADG W to S	.068[g]	6	.011	3.577	.004	.232
Intercept	Birth Weight	.004	1	.004	.035	.852	.000
	Weaning Weight	5.031	1	5.031	2.038	.158	.028
	Slaughter Weight	1011.682	1	1011.682	24.674	.000	.258
	Carcass Weight	1007.521	1	1007.521	29.288	.000	.292

	Backfat	52.266	1	52.266	21.668	.000	.234
	Production Length	5155.326	1	5155.326	107.815	.000	.603
	ADG W to S	.004	1	.004	1.264	.265	.017
Season	Birth Weight	.001	1	.001	.009	.925	.000
	Weaning Weight	9.820	1	9.820	3.978	.050	.053
	Slaughter Weight	162.541	1	162.541	3.964	.050	.053
	Carcass Weight	293.747	1	293.747	8.539	.005	.107
	Backfat	29.493	1	29.493	12.227	.001	.147
	Production Length	1617.373	1	1617.373	33.825	.000	.323
	ADG W to S	.008	1	.008	2.498	.118	.034
Parity	Birth Weight	.017	1	.017	.140	.709	.002
	Weaning Weight	15.684	1	15.684	6.353	.014	.082
	Slaughter Weight	221.284	1	221.284	5.397	.023	.071
	Carcass Weight	333.578	1	333.578	9.697	.003	.120
	Backfat	24.630	1	24.630	10.211	.002	.126
	Production Length	1282.202	1	1282.202	26.815	.000	.274
	ADG W to S	.002	1	.002	.738	.393	.010
Batch	Birth Weight	1.244	1	1.244	9.968	.002	.123
	Weaning Weight	16.248	1	16.248	6.582	.012	.085
	Slaughter Weight	12.321	1	12.321	.300	.585	.004
	Carcass Weight	30.344	1	30.344	.882	.351	.012
	Backfat	.029	1	.029	.012	.913	.000
	Production Length	475.080	1	475.080	9.936	.002	.123
	ADG W to S	.005	1	.005	1.480	.228	.020
Breed	Birth Weight	2.529	3	.843	6.755	.000	.222
	Weaning Weight	27.609	3	9.203	3.728	.015	.136

	Slaughter Weight	132.679	3	44.226	1.079	.364	.044
	Carcass Weight	80.195	3	26.732	.777	.511	.032
	Backfat	316.179	3	105.393	43.692	.000	.649
	Production Length	690.063	3	230.021	4.811	.004	.169
	ADG W to S	.023	3	.008	2.435	.072	.093
Error	Birth Weight	8.860	71	.125			
	Weaning Weight	175.273	71	2.469			
	Slaughter Weight	2911.179	71	41.003			
	Carcass Weight	2442.429	71	34.400			
	Backfat	171.263	71	2.412			
	Production Length	3394.962	71	47.816			
	ADG W to S	.225	71	.003			
Total	Birth Weight	186.410	78				
	Weaning Weight	4390.920	78				
	Slaughter Weight	568319.000	78				
	Carcass Weight	367621.927	78				
	Backfat	11504.000	78				
	Production Length	2010200.000	78				
	ADG W to S	26.928	78				
Corrected Total	Birth Weight	13.004	77				
	Weaning Weight	257.627	77				
	Slaughter Weight	3578.372	77				
	Carcass Weight	3107.266	77				
	Backfat	510.718	77				
	Production Length	6353.795	77				
	ADG W to S	.293	77				

a. R Squared = .319 (Adjusted R Squared = .261)

b. R Squared = .320 (Adjusted R Squared = .262)

c. R Squared = .186 (Adjusted R Squared = .118)

d. R Squared = .214 (Adjusted R Squared = .148)

e. R Squared = .665 (Adjusted R Squared = .636)

f. R Squared = .466 (Adjusted R Squared = .421)

g. R Squared = .232 (Adjusted R Squared = .167)

Estimates

Dependent Variable	Breed	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
Birth Weight	1	1.854[a]	.098	1.660	2.049
	2	1.279[a]	.105	1.069	1.489
	3	1.294[a]	.095	1.105	1.484
	4	1.521[a]	.081	1.360	1.683
Weaning Weight	1	7.996[a]	.434	7.131	8.861
	2	7.263[a]	.469	6.328	8.197
	3	6.073[a]	.422	5.230	6.915
	4	7.957[a]	.360	7.239	8.676
Slaughter Weight	1	83.541[a]	1.768	80.016	87.067
	2	86.375[a]	1.911	82.564	90.185
	3	83.689[a]	1.722	80.256	87.122
	4	87.009[a]	1.468	84.082	89.937
Carcass Weight	1	68.762[a]	1.619	65.533	71.991
	2	70.654[a]	1.750	67.164	74.144
	3	67.133[a]	1.577	63.988	70.277
	4	68.143[a]	1.345	65.461	70.824

Backfat	1	15.151[a]	.429	14.296	16.006
	2	13.401[a]	.463	12.477	14.325
	3	11.253[a]	.418	10.421	12.086
	4	9.266[a]	.356	8.556	9.976
Production Length	1	162.428[a]	1.909	158.621	166.235
	2	166.428[a]	2.064	162.313	170.543
	3	157.729[a]	1.859	154.022	161.437
	4	158.152[a]	1.585	154.991	161.314
ADG W to S	1	.555[a]	.016	.524	.586
	2	.571[a]	.017	.538	.605
	3	.593[a]	.015	.563	.623
	4	.605[a]	.013	.579	.631

a. Covariates appearing in the model are evaluated at the following values: Season = 1.31, Parity = 1.77, Batch = 3.15.

Pairwise Comparisons

						95% Confidence Interval for Difference[b]	
Dependent Variable	(I) Breed	(J) Breed	Mean Difference (I-J)	Std. Error	Sig.[b]	Lower Bound	Upper Bound
Birth Weight	1	2	.575*	.144	.001	.184	.966
		3	.560*	.150	.002	.153	.966
		4	.333	.126	.063	-.011	.676
	2	1	-.575*	.144	.001	-.966	-.184
		3	-.015	.150	1.000	-.422	.391
		4	-.242	.126	.357	-.586	.101
	3	1	-.560*	.150	.002	-.966	-.153
		2	.015	.150	1.000	-.391	.422
		4	-.227	.139	.635	-.603	.149
	4	1	-.333	.126	.063	-.676	.011

		2	.242	.126	.357	-.101	.586
		3	.227	.139	.635	-.149	.603
Weaning Weight	1	2	.733	.641	1.000	-1.008	2.474
		3	1.923*	.666	.031	.116	3.730
		4	.038	.563	1.000	-1.488	1.565
	2	1	-.733	.641	1.000	-2.474	1.008
		3	1.190	.666	.469	-.617	2.996
		4	-.695	.563	1.000	-2.222	.832
	3	1	-1.923*	.666	.031	-3.730	-.116
		2	-1.190	.666	.469	-2.996	.617
		4	-1.885*	.616	.019	-3.557	-.212
	4	1	-.038	.563	1.000	-1.565	1.488
		2	.695	.563	1.000	-.832	2.222
		3	1.885*	.616	.019	.212	3.557
Slaughter Weight	1	2	-2.833	2.614	1.000	-9.929	4.262
		3	-.147	2.713	1.000	-7.511	7.216
		4	-3.468	2.293	.809	-9.691	2.755
	2	1	2.833	2.614	1.000	-4.262	9.929
		3	2.686	2.713	1.000	-4.677	10.049
		4	-.635	2.293	1.000	-6.858	5.588
	3	1	.147	2.713	1.000	-7.216	7.511
		2	-2.686	2.713	1.000	-10.049	4.677
		4	-3.321	2.512	1.000	-10.137	3.496
	4	1	3.468	2.293	.809	-2.755	9.691
		2	.635	2.293	1.000	-5.588	6.858
		3	3.321	2.512	1.000	-3.496	10.137

Carcass Weight	1	2	-1.892	2.394	1.000	-8.391	4.607
		3	1.630	2.485	1.000	-5.115	8.374
		4	.619	2.100	1.000	-5.081	6.319
	2	1	1.892	2.394	1.000	-4.607	8.391
		3	3.521	2.485	.965	-3.223	10.266
		4	2.511	2.100	1.000	-3.189	8.211
	3	1	-1.630	2.485	1.000	-8.374	5.115
		2	-3.521	2.485	.965	-10.266	3.223
		4	-1.010	2.301	1.000	-7.254	5.234
	4	1	-.619	2.100	1.000	-6.319	5.081
		2	-2.511	2.100	1.000	-8.211	3.189
		3	1.010	2.301	1.000	-5.234	7.254
Backfat	1	2	1.750*	.634	.044	.029	3.471
		3	3.897*	.658	.000	2.112	5.683
		4	5.885*	.556	.000	4.375	7.394
	2	1	-1.750*	.634	.044	-3.471	-.029
		3	2.147*	.658	.010	.362	3.933
		4	4.135*	.556	.000	2.625	5.644
	3	1	-3.897*	.658	.000	-5.683	-2.112
		2	-2.147*	.658	.010	-3.933	-.362
		4	1.987*	.609	.010	.334	3.641
	4	1	-5.885*	.556	.000	-7.394	-4.375
		2	-4.135*	.556	.000	-5.644	-2.625
		3	-1.987*	.609	.010	-3.641	-.334
Production Length	1	2	-4.000	2.823	.965	-11.662	3.662
		3	4.699	2.930	.679	-3.253	12.650

		4	4.276	2.476	.531	-2.445	10.996
	2	1	4.000	2.823	.965	-3.662	11.662
		3	8.699*	2.930	.024	.747	16.650
		4	8.276*	2.476	.008	1.555	14.996
	3	1	-4.699	2.930	.679	-12.650	3.253
		2	-8.699*	2.930	.024	-16.650	-.747
		4	-.423	2.712	1.000	-7.785	6.939
	4	1	-4.276	2.476	.531	-10.996	2.445
		2	-8.276*	2.476	.008	-14.996	-1.555
		3	.423	2.712	1.000	-6.939	7.785
ADG W to S	1	2	-.017	.023	1.000	-.079	.046
		3	-.038	.024	.689	-.103	.027
		4	-.050	.020	.092	-.105	.005
	2	1	.017	.023	1.000	-.046	.079
		3	-.021	.024	1.000	-.086	.043
		4	-.033	.020	.608	-.088	.021
	3	1	.038	.024	.689	-.027	.103
		2	.021	.024	1.000	-.043	.086
		4	-.012	.022	1.000	-.072	.048
	4	1	.050	.020	.092	-.005	.105
		2	.033	.020	.608	-.021	.088
		3	.012	.022	1.000	-.048	.072

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Univariate Tests

Dependent Variable		Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Birth Weight	Contrast	2.529	3	.843	6.755	.000	.222
	Error	8.860	71	.125			
Weaning Weight	Contrast	27.609	3	9.203	3.728	.015	.136
	Error	175.273	71	2.469			
Slaughter Weight	Contrast	132.679	3	44.226	1.079	.364	.044
	Error	2911.179	71	41.003			
Carcass Weight	Contrast	80.195	3	26.732	.777	.511	.032
	Error	2442.429	71	34.400			
Backfat	Contrast	316.179	3	105.393	43.692	.000	.649
	Error	171.263	71	2.412			
Production Length	Contrast	690.063	3	230.021	4.811	.004	.169
	Error	3394.962	71	47.816			
ADG W to S	Contrast	.023	3	.008	2.435	.072	.093
	Error	.225	71	.003			

The F tests the effect of Breed. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.