UNIVERSITY OF COPENHAGEN

Københavns Universitet

The ethical and welfare implications of large litter size in the domestic pig

challenges and solutions

Rutherford, Kenneth M.D. ; Baxter, Emma M. ; Ask, Birgitte ; Berg, Peer; D'Eath, Richard B. ; Jarvis, Susan; Jensen, Karsten Klint; Lawrence, Alistair B. ; Moustsen, Vivi A. ; Robson, Sheena K. ; Thorup, Flemming ; Turner, Simon P. ; Sandøe, Peter

Publication date:
2011

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Rutherford, K. M. D., Baxter, E. M., Ask, B., Berg, P., D'Eath, R. B., Jarvis, S., Jensen, K. K., Lawrence, A. B., Moustsen, V. A., Robson, S. K., Thorup, F., Turner, S. P., & Sandøe, P. (2011). *The ethical and welfare implications of large litter size in the domestic pig: challenges and solutions*. Danish Centre for Bioethics and Risk Assessment (CeBRA). Project report No. 17

Download date: 16. Oct. 2026

The Ethical and Welfare Implications of Large Litter Size in the Domestic Pig

Challenges and Solutions

Kenneth M.D. Rutherford, Emma M. Baxter, Birgitte Ask, Peer Berg, Richard B. D'Eath, Susan Jarvis, Karsten K. Jensen, Alistair B. Lawrence, Vivi A. Moustsen, Sheena K. Robson, Rainer Roehe, Flemming Thorup, Simon P. Turner & Peter Sandøe

Project report 17
DANISH CENTRE FOR BIOETHICS AND RISK ASSESSMENT
and SAC (Scottish Agricultural College)

The Ethical and Welfare Implications of Large Litter Size in the Domestic Pig:
Challenges and Solutions

Kenneth M.D. Rutherford [a)], Emma M. Baxter [a)], Birgitte Ask [b)], Peer Berg [c)] Richard B. D'Eath [a)], Susan Jarvis[a)], Karsten K. Jensen [d)], Alistair B. Lawrence [a)], Vivi A. Moustsen [b)], Sheena K. Robson [a)], Rainer Roehe [a)], Flemming Thorup [b)], Simon P. Turner [a)] & Peter Sandøe [d)]

[a)] *Animal and Veterinary Science Research Group, SAC, Edinburgh*
[b)] *Pig Research Centre, Copenhagen*
[c)] *Department of Genetics and Biotechnology, University of Aarhus*
[d)] *University of Copenhagen / Danish Centre for Bioethics and Risk Assessment*

© Danish Centre for Bioethics and Risk Assessment
and the authors 2011
Project report 17
Report editors: Geir Tveit & Peter Sandøe

This report is a joint publication with SAC (Scottish Agricultural College)

Danish Centre for Bioethics
and Risk Assessment
Rolighedsvej 25
DK - 1958 Frederiksberg C
bioethics@life.ku.dk
www.bioethics.dk
www.animalethics.net

SAC
West Mains Road
Edinburgh
EH9 3JG
UK
http://www.sac.ac.uk

Executive Summary ... **3**

Table 1: Summary of welfare impacts of large litter size on animal welfare outcomes for sows and piglets ... **5**

Table 2: Summary of possible mitigation strategies for welfare problems relating to large litter size ... **11**

1. Introduction ... **19**

2. Litter size in domestic pigs ... **22**

2.1 Litter size in wild pigs and related species ... 22

2.2. History of litter size and piglet mortality in domestic pigs ... 23

2.3. What do we mean by large litter size in domesticated pigs? ... 27

3. Assessing animal welfare impacts relating to litter size ... **29**

3.1 The Decision situation ... 29

3.2 Philosophical accounts of welfare ... 30

3.2.1 Hedonism views ... 30

3.2.2 Preference-satisfaction views ... 31

3.2.3 Objective views ... 31

3.3 Animal welfare ... 32

3.4 Relevant alternatives and the non-identity problem ... 34

3.5 Welfare impacts of dying ... 37

3.6 Summary of welfare assessment criteria used in the report ... 38

4. Welfare impacts on the piglet ... **39**

4.1 Intra-uterine crowding and uterine hormone exposure ... 40

4.2 Still births, birth difficulties and asphyxia ... 40

4.3 Teat competition and establishment of the 'teat order' ... 43

4.4 Perinatal mortality and welfare implications ... 44

4.4.1 Overview of relationship between litter size and piglet mortality ... 44

4.4.2 Piglet birth weight and birth weight variation within a litter ... 44

4.4.3 Maternal behaviour ... 46

4.4.4 Comparative aspects of litter size and mortality species ... 46

4.4.5 Onset of sentience ... 48

4.4.6 Pain experiences in neonatal piglets ... 50

4.5 Long-term effects of birth weight ... 52

4.5.1 Stress physiology ... 52

4.5.2 Behaviour ... 54

4.5.3 Health implications ... 56

4.6 Sex ratio effects ... 58

4.7 Management responses to large litter sizes ... 59

4.7.1 Tooth reduction ... 59

4.7.2 Cross-fostering ... 60

4.7.3 Nurse sow systems ... 64

4.7.4 Weaning age 65
5. Welfare impacts of large litter size on the sow 69
5.1 Gestation 69
5.2 Parturition 71
5.3. Lactation and post-weaning 74
5.3.1 Sow health 74
5.3.2 Sow rest / irritation 76
5.3.3 Sow longevity / burn out 76
5.4 Welfare impact on foster or nurse sows 77
6. Mitigating the welfare impacts of large litter size 81
6.1 Genetic strategies 82
6.2 Strategies from early life to conception 91
6.2.1 Staff attitudes and behaviours towards pigs 91
6.2.2 Pre-conception nutrition and other factors 94
6.3 Strategies to support sows and fetal piglets during gestation 95
6.3.1 Minimising maternal stress 95
6.3.2 Nutrition to support fetal development 96
6.3.3 Maintaining maternal health through pregnancy 99
6.4 Peri-partum strategies 99
6.4.1 Farrowing environment 99
6.4.2 Farrowing supervision and piglet treatments 100
6.4.3 Sow treatments during lactation 101
***7.* Ethical perspectives 103**
7.1 Introduction 103
7.2 Overall assessment of welfare impacts 104
7.3 Perfectionist assessments 107
7.4 Other ethical concerns 108
7.5 Summary of ethical assessments 109
8. Conclusions 110
8.1 Welfare impacts of large litter size on piglets 110
8.2 Welfare impacts of large litter size on sow 112
8.3 Strategies to reduce the welfare impacts associated with large litters 112
8.4 Assessing the economic implications of litter size. 114
8.5 Balancing animal welfare against other societal concerns 115

Executive Summary

- **Driven by production efficiency, increasing litter size has long been a goal of pig producers, although this trend has accelerated in the past 15 years, particularly in Denmark and in other countries such as Holland, Germany and France.**

- **This report aims to review the pertinent scientific and practical evidence on sow and piglet welfare in relation to large litter size, and discusses the relevant ethical issues in order to inform a societal debate about the ethical acceptability of large litter size. In addition, possible approaches to mitigating health and welfare issues associated with large litter are identified**

    - Increasing litter size has economic and environmental benefits to the pig industry, but concern has been expressed that efforts to increase litter size, particularly those relating to genetic selection, may have gone too far.

    - In some cases large litter sizes may be a causal risk factor for decreased animal welfare in pig production; either through the biological consequences of large litter size or via possible effects of management measures taken to deal with large litters.

    - Identifying the challenges makes it possible to target solutions that mitigate the challenges that have the highest impact on animal welfare.

- **All the possible welfare consequences of large litter size are summarised in Table 1. Broadly, there are four main clusters of issues where major concerns about the impact of large litter size are seen.**

    - Firstly, increased litter size is associated with increased total piglet mortality.

    - Secondly, there are a number of additional welfare concerns relating to large litter size in piglets that survive the neonatal period.

    - Thirdly, for some piglets being born into a large litter may have other consequences for their postnatal experiences.

    - Finally, from the sow's perspective increasing litter size may also impair welfare

- **In addition to specific welfare issues, there are also other ethical concerns relating to the increased occurrence of large litters**

    - The overall ethical assessment of welfare implications is complicated by the fact that there are no widely accepted evaluation criteria concerning the evaluation of adding lives to the world.

- The range of welfare and ethical issues associated with litter size increase place the good image of Danish pig production at risk, both nationally and internationally.

- **Several possible approaches to mitigating health and welfare issues associated with large litter were identified and are summarised in Table 2.**

  - At a national level an important mitigation strategy is genetic selection encompassing traits that promote piglet survival, vitality and growth.

  - In Denmark, the breeding objective LP5 (**L**ive **P**igs day **5**) was introduced into the breeding and multiplier herds in 2004. Since then, survival rate until day 5 has increased by 6 percentage points in these herds, resulting in ≥ 20% less mortality. This response should also become apparent at the production level as dissemination of genes from the purebreds to the crossbred sows increases over the coming years.

  - Nutrition for gilts and sows, through rearing, gestation, lactation and subsequent reproductive cycles could also contribute to improving piglet outcomes.

  - At an individual farm level, management can be improved to promote piglet survival and subsequent life vigour. An important concept is that management at all stages of the reproductive cycle, not simply in the farrowing accommodation, can impact on piglet outcomes.

  - Understanding the attitudes and behaviours of stockhandlers that contribute to variable farm outcomes and designing intervention training could be an important source of progress.

- **A full economic analysis (including inclusion of 'ethical costs') is necessary to properly identify both economic costs and benefits of further increases in litter size as opposed to moving to a focus on keeping conceived piglets alive to weaning and beyond. This is beyond the scope of this report.**

Table 1: Summary of welfare impacts of large litter size on animal welfare outcomes for sows and piglets

Welfare Problem	Proximate Cause(s)	Relationship to Litter size (Speculative / Uncertain / Sound / Strong)	Welfare impact*	Individual Severity[$]	Certainty	Priority for Action[#]
MATERNAL SOWS						
Discomfort and reduced mobility during gestation [section 5.1]	Physical effect of carrying a large litter	Speculative	**MEDIUM**	**1**	**LOW**	**LOW/ MEDIUM**
Health problems during gestation [section 5.1]	Physiological effect of carrying a large litter	Speculative	**LOW**	**1**	**LOW**	**LOW**
Increased hunger during gestation [section 5.1]	Increased fetal demand for nutrients	Speculative. Probably only an issue during late gestation. Confounded with high general level of hunger in dry sows. But compromised nutritional balance or low energy may still be an issue.	**LOW**	**1**	**LOW**	**LOW**
Increased fear/anxiety during gestation [section 5.1]	Hormonal signals of large litter	Speculative. Although evidence of an effect in rodents: D'Amato et al., 2006.	**MEDIUM**	**2**	**LOW**	**LOW/ MEDIUM**
Pain / discomfort at farrowing [section 5.2]	Increased farrowing duration	Uncertain. Litter size positively associated with farrowing duration: Canario et al 2006ab. Presence of stillborn piglets associated with longer farrowings: VanDijk et al., 2005. But relationship between farrowing duration and experience of pain and discomfort is unknown.	**MEDIUM**	**3**	**MEDIUM**	**MEDIUM**
Pain / discomfort at farrowing [section 5.2]	Increased prevalence of stillborn/mummified piglets	Sound. Behavioural farrowing ease score found to be decreased when sows passed stillborn or mummified piglets: Mainau et al., 2010	**MEDIUM**	**3**	**MEDIUM**	**MEDIUM**
Dystocia [section 5.2]	Increased farrowing duration	Sound. Litter size positively associated with farrowing duration and stillbirth: Canario et al., 2006ab; VanDijk et al., 2005	**MEDIUM**	**3**	**MEDIUM**	**MEDIUM**
Infections of reproductive tract, sickness behaviour [section 5.2]	Tissue damage	Uncertain. Risk of infection exists for all farrowings. It may be increased with longer farrowings or the expulsion of stillborn piglets, particularly where this involves human intervention.	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**

Fear and neophobia [section 5.2]	Parturition pain	Uncertain. May be associated with pain, but extent to which larger litter impact upon overall pain associated with farrowing requires further exploration.	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Sow fatigue [section 5.2]	Increased farrowing duration	Uncertain. Uterine and maternal fatigue.	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Udder damage and infection [section 5.3.1]	Piglets fighting at the udder.	Sound. Teat competition in very early lactation can damage udder. Teat damage positively correlated to litter size: Norring et al., 2006	**MEDIUM**	**1**	**HIGH**	**MEDIUM/ HIGH**
Energetically costly lactation [section 5.3.1]		Uncertain. Body condition and weight loss related to weaned litter size: Grandison et al., 2005. Nutrient mobilisation related to litter size: Kim and Easter, 2001	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Impaired rest during lactation [section 5.3.2]		Speculative. Suggested as a possibility by De Passillé and Robert, 1989; Arey and Sancha, 1996.	**MEDIUM**	**1**	**LOW**	**LOW/ MEDIUM**
Reduced sow longevity [section 5.3.3]	Injury (shoulder ulcers), infertility, lameness, agalactia	Speculative. Thought that higher litter size may result in sow "burn out" at 4th parity. Injury, lameness, agalactia all cause pain, sometimes chronic and although reduced longevity would end this, the reasons have high welfare concerns.	**MEDIUM**	**3**	**MEDIUM**	**MEDIUM**
OFFSPRING PIGS						
Still births [section 4.2]	Intrauterine crowding / difficult birth	Strong. Litter size negatively associated with still births: Svendsen et al., 1991; Roehe and Kalm, 2002; VanDijk et al., 2005; Canario et al., 2006a,b; Rosendo et al., 2007; Kapell et al., 2009. However, low welfare impact because literature suggests that piglets are unlikely to be sentient before first postpartum breath (Mellor and Diesch 2006; Mellor, 2010). However, studies have not been conducted in piglets.	**LOW**	**0**	**MEDIUM**	**LOW**
Intra-partum asphyxia / hypoxia [section 4.2]		Sound. Same as above as intra-partum asphyxia main cause of type 2 stillbirths (type 1 = mummies). May not involve suffering at time of occurrence: Mellor and Stafford, 2004. But is associated with negative outcomes later: e.g. reduced postnatal vigour and delayed landmark behaviours (Zaleski and Hacker, 1993) and physiological compromise, e.g. MAS (see Alonso-Spilsbury et al., 2005 for review).	**MEDIUM**	**1**	**MEDIUM**	**MEDIUM**
Neonatal mortality [section 4.4]	All causes	Strong. Litter size unfavourably associated with mortality: Stewart and Diekman, 1989; VanDerLende and deJager, 1991; Blasco et al., 1995; Johnson et al., 1999; Sorensen et al., 2000; Lund et al., 2002	**HIGH**	**4**	**HIGH**	**HIGH**
Neonatal mortality [section 4.4]	Chilling	Strong. Increased litter size associated with lower birth weights, low birth weight piglets have poorer thermoregulatory capacity: Herpin et al., 2002 and increased risk of chilling, which increases mortality (Malmkvist et al., 2006)	**MEDIUM**	**4**	**HIGH**	**MEDIUM /HIGH**

		Lower challenge to welfare than hunger/pain: Mellor and Stafford, 2004				
Neonatal mortality [section 4.4]	Starvation	Strong. More competition for teats. Lower birth weight piglets or heterogeneity, leads to unfair competition (English and Smith, 1975; Fraser et al., 1995; Andersen et al., 2011). Welfare impact can be ameliorated through management.	**HIGH**	**4**	**HIGH**	**HIGH**
Neonatal mortality [section 4.4]	Injury (crushing/savaging)	Uncertain. More piglets, more disturbances and a more restless mother (see Andersen et al 2005 for discussion). Low birth weight associated with increased likelihood of crushing: Pedersen et al., 2011. Large litter size associated with more crushing: Andersen et al., 2011. Crushing is part of a hypothermia and starvation complex, with chilled hungry piglets more likely to be in risky areas at the udder and more lethargic so less likely to escape rolling sow (Edwards, 2002). Possible increased risk of savaging related injury is highly speculative.	**HIGH**	**4**	**HIGH**	**HIGH**
Neonatal mortality [section 4.4.2]	Low birth weight	Strong. Litter size negatively associated with birth weight: Thompson and Fraser. 1986; VanDerLende and deJager. 1991; Kerr and Cameron 1995; Roehe. 1999; Bilkei and Biro, 1999; Sorensen et al., 2000; Tuchscherer et al., 2000; Roehe and Kalm. 2000; Quiniou et al., 2002; Wolf et al., 2008. Birth weight negatively associated with neonatal mortality: Gardner et al., 1989; VanDerLende and deJager 1991; Fix et al., 2010; Pedersen et al., 2011. Not a problem for all piglets in any given litter. Causal impact on mortality not fully established.	**MEDIUM**	**4**	**MEDIUM**	**MEDIUM**
Neonatal mortality [section 4.4.2]	High within litter variation in birth weight	Strong. Litter size positively associated with birth weight variation: Wolf et al., 2008; Quesnel et al., 2008; Roehe, 1999; Milligan et al., 2002; Quiniou et al., 2002. Not a problem for all piglets in any given litter.	**MEDIUM**	**4**	**MEDIUM**	**MEDIUM**
Neonatal mortality [section 4.4]	Disease	Sound. Associated with poor colostrum intake, thus insufficient absorption of immunoglobulins and maternal lymphocytes for immunity (Le Dividich et al., 2005; Salmon, 2000).	**MEDIUM**	**4**	**MEDIUM**	**MEDIUM**
Neonatal pain [section 4.4]	Injury (crushing/savaging)	Speculative. Litter size may be associated with increased risk of chilling and starvation: Andersen et al., 2011 (lowering capacity of piglets to avoid injury) and with impaired maternal behaviour (making injuries more likely). Apart from instantaneous deaths, it can be assumed being partially crushed or bitten is painful and distressing.	**HIGH**	**3**	**MEDIUM**	**HIGH**
Neonatal pain [section 4.3]	Increased teat competition	Sound. Large litter size is associated with more fighting and more chance of facial injury from needle teeth (Fraser, 1975; Hutter et al., 1993).	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Neonatal pain / infection	Tooth reduction	Strong. Litter size associated with greater competition at teats and more facial damage (Fraser, 1975; Hutter et al., 1993).	**MEDIUM**	**2**	**HIGH**	**MEDIUM/ HIGH**

[section 4.7.1]		Tooth reduction is stressful (Marchant-Forde et al., 2009), can cause pain (Hay et al., 2004), can be associated with accidently injuries (Burger, 1983; Bruckner, 1986; Hutter et al., 1993) and increases risk of infection (Lewis et al., 2005). However, when average litter size is very large tooth reduction may actually be less prevalent as other management responses are required.				
Neonatal morbidity [section 4.5.3]	Disease	Sound. Associated with poor colostrum intake, thus insufficient absorption of immunoglobulins and maternal lymphocytes for immunity (Le Dividich et al., 2005; Salmon, 2000).	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Neonatal morbidity [section 4.5.3]	Injury	Uncertain. Facial lacerations, knee abrasions (Norring et al., 2006), teeth reduction (see above): all provide entry points for infection	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Neonatal hunger [section 4.3]	Teat competition	Sound. Large litter associated with increased teat competition (Fraser, 1975; Hutter et al., 1993; Milligan et al., 2001a) and greater likelihood of some individuals not being to access a teat.	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Splayleg [section 4.5.3]	Intrauterine environment	Strong. Prevalence of splayleg piglets associated with increased litter size, lowered birth weight, reduced gestation length: Holl and Johnson 2005; Sellier and Ollivier 1982; Vogt et al., 1984;; VanDerHeyde et al., 1989; Sellier et al., 1999. Potential for large welfare impact on affected individuals. Associated with increased mortality and likely welfare problems for those that survive (e.g. reduced colostrum intake: Devillers et al 2007).	**MEDIUM**	**3**	**HIGH**	**MEDIUM/ HIGH**
Reduced play behaviour [section 4.5.2]	Low birth weight	Sound. Reduced play behaviour seen in low birth weight piglets: Litten et al., 2003	**LOW**	**1**	**LOW**	**LOW**
Increased emotionality [section 4.5.2]	Low birth weight / social interactions in large litter	Sound. Evidence of an effect in rodents: LaBarba and White, 1971; Ryan and Wehmer, 1975; Hinz et al., 1983; Janczak et al., 2000. But studies showing the opposite also exist. No specific studies on pigs, although effect on stress reactivity (see below) suggests that a behavioural impact might also be seen.	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Increased stress reactivity [section 4.5.2]	Low birth weight	Strong. Litter size negatively associated with birth weight (see above). Low birth weight negatively associated with increased stress reactivity: Klemcke et al., 1993; Poore and Fowden, 2003; Kranendonk et al., 2006.	**MEDIUM**	**2**	**HIGH**	**MEDIUM /HIGH**
Altered social behaviour (aggression) [section 4.5.2]	Intrauterine crowding, social interactions in large litter	Uncertain. Found by D'Eath and Lawrence 2004, but failed to replicate this result in larger datasets (Personal communication: D'Eath, SAC).	**LOW**	**1**	**LOW**	**LOW**
Altered organ development [section 4.5.3]	Intrauterine crowding / Low birth weight	Strong. Low birth weight associated with compromised growth of the gastrointestinal tract, liver, kidneys, thymus, ovaries, muscles and skeleton: Handel and Stickland, 1987; Xu et al.,	**LOW**	**1**	**LOW**	**LOW**

		1994; Bauer et al., 2002; Da Silva-Buttkus et al., 2003, Mollard et al., 2004; Cromi et al., 2009.				
Impaired gut function [section 4.5.3]	Intrauterine crowding / Low birth weight	Sound. Low birth weight associated with an immature gastrointestinal tract: Wang et al., 2005; Morise et al 2008 (review).	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Cognitive dysfunction [section 4.5.3]	Hypoxia, Cerebral injury	Sound. Hypoxia during birth process is associated with later cognitive dysfunction: Vannucci and Perlman 1997	**LOW**	**1**	**MEDIUM**	**LOW**
Impaired immune function [section 4.5.3]	Intrauterine crowding / Low birth weight	Sound. Associated with neonatal disease and poor colostrum intake: Tuchscherer et al., 2010; D'Inca et al., 2011. Direct effect of litter size seen in other species: Prager et al., 2010.	**HIGH**	**2**	**LOW**	**MEDIUM**
Cross-fostering and use of rescue decks [section 4.7.2]	Transient hunger	Sound. Positive for welfare when necessary as aids survival (Cecchinato et al., 2008) but may have negatives (Price et al., 1994, Straw et al., 1998), particularly when >2-3 days after birth.	**LOW**	**1**	**LOW**	**LOW**
Distress [section 4.7.2/3]	Maternal separation etc during Cross-fostering / Nurse sow system	Uncertain. Early weaning stress for 4-7d piglets removed: Weary et al., 2008	**MEDIUM**	**1**	**LOW**	**LOW/ MEDIUM**
Rejection by sow [section 4.7.2/3]	Cross-fostering / Nurse sow system	Uncertain. Largely occurs when moving older piglets.	**MEDIUM**	**1**	**LOW**	**LOW/ MEDIUM**
Tail-biting [section 4.7.2]	Cross-fostering	Uncertain. Cross-fostering associated at farm level with tail biting occurrence: Moinard et al., 2003	**HIGH**	**3**	**LOW**	**MEDIUM**
NURSE SOWS						
Early removal of native piglets [section 5.4]		Speculative. Evidence in other mammalian species of confusion and apprehension at not being able to locate offspring which maybe exacerbated by confinement (Newberry and Swanson, 2008).	**MEDIUM**	**2**	**LOW**	**LOW/ MEDIUM**
Acceptance of new litter [section 5.4]		Uncertain. Discomfort due to udder pressure may occur when piglets are not a given immediately. Disturbance from foster litter and fighting at the udder	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Prolonged lactation [section 5.4]		Uncertain. Parent-offspring conflict and potential catabolic state (Elsley, 1971; Valros et al., 2003)	**MEDIUM**	**2**	**MEDIUM**	**MEDIUM**
Prolonged environmental restriction [section 5.4]		Uncertain. A longer period in a farrowing crate may be stressful for sows, and may exacerbate shoulder sores as they are associated with depleted body condition (Ritter et al., 1999)	**HIGH**	**3**	**MEDIUM**	**HIGH**
Longevity [section 5.4]		Uncertain. Associated with longer return to oestrus.	**MEDIUM**	**1**	**MEDIUM**	**MEDIUM**

* Welfare impact is an estimate of the overall effect on the individual (severity x duration) combined with the proportion of individuals affected.
$ See Appendix one for descriptions of individual severity scores.
# See Appendix two for how combinations of impact and uncertainty dictate suggested priority for action.

Table 2: Summary of possible mitigation strategies for welfare problems relating to large litter size

Welfare Problem (proximate cause)	Piglet solution	Sow solution	Biological effect (Low / Med / High)	Feasibility[#] (Low / Med / High)	Potential (Poor / Good / Excellent)
Genetic					
Stillbirth		Breeding for maternal genetic effects of perinatal survival	**LOW** Heritability: low, but substantial variation among animals	**MEDIUM**	**GOOD**
Stillbirth	Breeding for direct genetic effects of perinatal survival		**LOW** Heritability: very low for sire contribution	**MEDIUM** Difficult to differentiate maternal from direct effect	**GOOD**
Neonatal mortality to day 5		Breeding for maternal genetic effects of survival after birth to day 5.	**LOW** Heritability: low, but sufficient variation among animals	**MEDIUM**	**GOOD**
Neonatal mortality to day 5		Breeding for litter size at 5 days	**LOW/MEDIUM** Heritability low, but trait measured on continuous scale. Positive genetic correlations with survival rate at birth and from birth until 5 days (Su et al., 2007: Selection For Litter Size At Day 5 To Improve Litter Size At Weaning And Piglet Survival Rate)	**HIGH**	**GOOD**
Neonatal mortality to day 5	Breeding for direct genetic effects of survival after birth to day 5		**LOW** Heritability: very low for sire contribution	**MEDIUM** Difficult to differentiate maternal from direct effect since all animals to some	**GOOD**

				extent are nursed by biological mother	
Mortality from day 6 to weaning		Breeding for maternal genetic effects of survival from day 6 to weaning	**LOW** Heritability: low, lower variation among animals than the previous mortality traits	**LOW to MEDIUM**	**GOOD**
Mortality from day 6 to weaning	Breeding for direct genetic effects of survival from day 6 to weaning		**LOW** Heritability: very low, lower variation among animals than the previous mortality traits	**LOW** Selection for direct survival from day 5 to weaning	**POOR**
Mortality from birth until weaning		Breeding for maternal ability to nurse piglets (behaviour, milk yield, milk quality, etc)	**LOW** Heritability:?	**?**	**?**
Piglet mortality (variable piglet birth weight)		Breeding for litter homogeneity (canalised selection for birth weight within litter) Selection for an optimum birth weight based on lowest stillbirth.	**LOW** Heritability: low. Undesirable correlation to mean birth weight. Low birth weight: favourable genetic correlation with survival during the suckling period, but unfavourable genetic correlation with stillborn.	**LOW** Difficult both statistically and practically with regards to necessary recordings; Mulder et al. 2007, 2008). Difficult to measure birth weights on all born animals in the breeding system.	**POOR**
Piglet mortality (cooling)	Breeding for improved thermogenesis		**?** Heritability:? Genetic research necessary	**LOW** Difficult to measure.	**POOR**
Piglet mortality (low vitality)	Breeding for improved piglet vitality		**LOW** Heritability: low	**LOW** Difficult to measure	**POOR**
Piglet mortality		Breeding for improved	**LOW**	**LOW**	**POOR**

(low vitality)		placental efficiency (less asphyxia, less growth retardation, better thermoregulations)	Heritability: low Mesa et al., 2005; 2006, Van rens et al., 2005	Difficult to measure.	
Piglet mortality (crushing)	Breeding for improved vitality (see above – more vigorous piglets will respond to sow cues and move out the way)		**LOW** Heritability: very low (Hellbrügge et al., 2008:)	**LOW** Difficult to measure	**POOR**
Piglet mortality (crushing)		Breeding for maternal behaviour	**MEDIUM** Heritability: medium Baxter et al. 2011 showed sows with genetic potential for survival were more careful	**LOW** Scoring maternal behaviour is difficult. Information is generated late in life	**GOOD**
Piglet mortality		Breeding for teat number	**MEDIUM** Heritability: moderate (e.g. Pumfrey et al., 1980: inheritance of teat number and its relationship to maternal traits in swine).	**HIGH** Scoring for teat number is easy	**POOR**
Piglet mortality		Breeding for placental efficiency	**LOW** Heritability: low	**LOW** Measuring placental efficiency could be done at a litter level with higher feasibility. More accurate measurements are time consuming	**POOR**
Piglet mortality (intrauterine crowding)		Breeding for uterine capacity	**LOW** Heritability: low Vallet and Freking 2006: Sows selected for uterine capacity. No diff between these and controls in fetal, placental or fetal organ weights. Liver grew disproportionately slower in unselected (i.e. more crowded) line during early pregnancy.	**LOW** (Phenotyping is difficult)	**POOR**
Piglet mortality	Direct genetic effects of	Maternal genetic effects of	**LOW/MEDIUM**	**MEDIUM**	**POOR**

(starvation)	birth weight or aggression/competition? Associated with birth weight and vitality – so breeding for optimum birth weight may contribute to this outcome.	birth weight. Breeding for greater lipid content in milk? Or more milk?	Direct heritability of birth weight: Low (indoor), moderate (outdoor) Maternal heritability of birth weight: moderate Undesirable correlation to still born (limited net result of attempt to reduce mortality through selection on birth weight; Damgaard et al., 2003).		
Increased stress reactivity (low birth weight)	Breed for reduced stress responsiveness.		**MEDIUM** Heritability: medium to high (e.g. Kadarmideen & Janss 2007) Relationship between specific measures (e.g. cortisol response) and affective states of animals is unclear and selection for some traits could be counterproductive in producing animals that are less able to respond to stressors in an adaptive way.	**MEDIUM**	**POOR**
Increased disease susceptibility	Breed for increased disease resistance, better immune function.		**MEDIUM** Resistance against specific pathogens possible but long term effect unknown. Selection for general disease resistance has low heritability.	**MEDIUM** Depends on whether it is a disease which is very common or not, and depending on whether it is bacteria or virus, which will simply mutate so that increased genetic resistance against one strain will not work against the new strain(s).	**POOR / GOOD**
Early life and rearing					
Stillbirth		Reduce fear in gilts and sows.	**MEDIUM** Hemsworth et al., 1999	**HIGH**	**GOOD**

Piglet mortality (poor maternal behaviour)	Avoid prenatal stress	**HIGH** Low maternal stress improves gilt maternal behaviour: Jarvis et al., 2006b, Rutherford et al., 2009	**MEDIUM**	**EXCELLENT**
Piglet mortality (variable piglet birth weight)	Reduced vitamin A in diet	**MEDIUM** Lower within litter birth weight variation: Antipatis et al., 2008	**?**	**GOOD**
Piglet mortality (stillbirth and impacts on live-born)	Optimise gilt nutrition: over-fat or emaciated gilts more prone to dystocia and lameness so less likely to respond to piglet cues	**HIGH**	**HIGH**	**EXCELLENT**
Prenatal	**Gestation**			
Piglet mortality	Supplementing gestation diet with Salmon oil	**MEDIUM** Reduced piglet mortality: Rooke et al., 2001	**MEDIUM** Large amounts of farmed salmon means this is feasible and cheaper than fish meal in sow diets, at least in the UK.	
Piglet mortality (poor maternal behaviour)	Reduce fear during gestation	**MEDIUM** Fear/anxiety associated with poor maternal behaviour: Janczak et al, 2003; Lensink et al., 2009; Marchant-Forde, 2002	**HIGH** Can be readily achieved with improved stockhandling (Andersen et al., 2006 – positive handling in late pregnancy improved maternal behaviour)	**EXCELLENT**
Piglet mortality	Improving sow health status	**MEDIUM** Exercising stall housed gilts improved piglet mortality: Schenck et al., 2008	**MEDIUM** The specific examples of exercising sows would be time consuming to implement and is only relevant for sow stalls, however broader issues relating to sow health (such as minimising	**GOOD**

				lameness) could contribute to improved piglet outcomes and would be feasible to implement.	
Piglet mortality		Reduce gestation stress	**MEDIUM** Gestation stress increased piglet mortality: Tuchscherer et al., 2002, Kanitz et al., 2003, Otten et al., 2001	**MEDIUM** Better mixing practice and housing can minimise but not eliminate stress.	**GOOD**
Piglet mortality		Long photoperiod	**LOW** Niekamp et al., 2006 (also lowered litter size)	**LOW**	**POOR**
Piglet mortality		Increased dietary fibre	**HIGH** Andersen et al., 2007	**HIGH**	**EXCELLENT**
Piglet mortality		L-carnitine dietary supplement	**MEDIUM** Musser et al., 1999, Eder et al., 2001	**?**	**?**
Piglet mortality		Conjugated Linoleic Acid (CLA) dietary supplement	**MEDIUM** Corino et al., 2009	**?**	**?**
Piglet mortality		Medium chain triglyceride dietary supplement	**MEDIUM** Jean and Chang 1999	**?**	**?**
Piglet mortality		Increased dietary energy level	**MEDIUM** Long et al., 2010	**?**	**?**
Post weaning stress and poor health		Flavour addition to sow diet	**MEDIUM** Oostindjer et al., 2010	**MEDIUM**	**GOOD**
	Birth / Early neonatal	**Peri-parturient**			
Pain (extended farrowing duration)		Pain relief (post parturition)	**MEDIUM** Improves maternal behaviour: Haussmann et al., 1999. Beneficial effect on low birth weight piglets: Manteca, 2009. Reduce piglet mortality (Hirsch et al., 2003)	**MEDIUM**	**GOOD**
Piglet mortality	Improved stockperson		**MEDIUM**	**HIGH**	**EXCELLENT**

	training		Hemsworth et al., 1994	Hemsworth et al., 1994	
Piglet mortality (asphyxia)	Oxygen treatment of piglets		**HIGH** Herpin et al., 2001	**LOW**	**POOR**
Piglet mortality (low Immunoglobulin uptake)		Sow diet supplemented with CLA (gestation and lactation)	**MEDIUM** Corino et al., 2009	**?**	
Piglet mortality (poor maternal behaviour)		Mild sedation with Azaperone	**MEDIUM** Miquet and Viana, 2010	**LOW**	**POOR**
Piglet mortality (poor maternal behaviour)		Consistency between gestation and farrowing environment	**LOW** Beattie et al., 1995, Weng et al., 2009	**LOW**	**POOR**
Piglet mortality	Farrowing Supervision. Ensure high colostrum intake		**HIGH** Friendship et al., 1986, Holyoake et al., 1995; White et al., 1996; Andersen et al., 2007	**MEDIUM**	**EXCELLENT**
Low vitality (hypoxia)	2-IminoBiotin injection		**MEDIUM** VanDijk et al., 2008, Peeters-Scholte et al., 2002ab	**LOW**	**POOR**
	Pre-weaning	**Lactation**			
Environmental restriction (use of nurse sows)		Lactation in open pen. Ease acceptance of new piglets	**MEDIUM** Greater ability for gradual separation from litter and increased lactational feed and water intake	**LOW**	**GOOD**
Sow irritation (high piglet numbers)	Increased space. Enrichment. Well designed creep area. Appropriate tooth reduction protocol.		**MEDIUM**	**HIGH**	**GOOD**
Prenatal mortality		Optimum lactation nutrition	**MEDIUM** Vinsky et al., 2006	**HIGH**	**GOOD**
	Post weaning	**Weaning to Oestrus**			

Increased stress reactivity (low birth weight)	Minimise stressor exposure.		**MEDIUM**	**HIGH**	**MEDIUM**
Altered immune function	Maintain high health status. Wean later?		**HIGH**	**MEDIUM**	**MEDIUM**
Altered social behaviour	Maintain stable groups, minimise mixing		**HIGH**	**MEDIUM**	**MEDIUM**
Piglet mortality		Dextrose / lactose supplements to sow diet	**HIGH** VanDenBrand et al., 2006, 2009	**MEDIUM**	**MEDIUM**

Estimates of feasibility should be considered as being relative within a category rather than absolute. For instance, for genetic selection purposes it should include more factors than selection for a certain trait. Also: registration possibilities (both operationally and traitwise, i.e. subjective versus objective measure), informative value of recordings (categorical, continuous scale; genetic relationship between animals with registrations and breeding stock), appropriate statistical models (for routine evalutions; for dealing with e.g. low information, so also information availability, i.e. prevalence).

1. Introduction

SUMMARY:

Driven by production efficiency, increasing litter size has long been a goal of pig producers, although this trend has accelerated in the past 15 years, particularly in Denmark and in other countries such as Holland, Germany and France.

This report aims to review the pertinent scientific and practical evidence on sow and piglet welfare in relation to large litter size, and discusses the relevant ethical issues in order to inform a societal debate about the ethical acceptability of large litter size. In addition, possible approaches to mitigating health and welfare issues associated with large litter are identified

Human beings began the process of domesticating wild boar about 10,000 years ago (Larson et al., 2011). Since then domesticated pig breeds have been selected for a number of different traits including litter size. As a consequence, litter size in domestic pigs has increased in comparison to that of the wild boar ancestor. Whilst this change has been going on slowly throughout domestication it has become more rapid recently due to modern animal breeding techniques. Animal breeders believe that further selection on litter size is possible and that litter sizes will continue to increase for the foreseeable future.

The pig industry is subject to numerous drivers, but ultimately its aim is to produce a quality product at low cost and in a socially acceptable way (Webb, 1998; Spötter and Distl, 2006). The drive for increased litter size through genetic selection and management techniques has been driven by a desire to improve production efficiency by increasing the number of slaughter animals produced from the relatively high fixed costs associated with intensive pig farming. Increasing litter size therefore improves the efficiency of pork production, maximising financial gains and also reduces the environmental impact of pork production, all of which explains the continued interest in increasing litter size.

Like other areas where artificial selection has been applied to farm animals, such as milk yield in dairy cattle (Oltenacu and Broom, 2010) or growth rate in broilers (Bessei, 2006), concern has been expressed that increasing litter size may be detrimental to animal welfare (Prunier et al., 2010). Welfare issues relating to litter size are potentially more complex than some other examples of intensive selection for production traits. Firstly, (until recently) changes in litter size have occurred slowly and have overall been less pronounced. Secondly, the consequences of selection for litter size are variable and impact in different ways on different individuals and at different times. Unlike specific areas of welfare concern, such as housing conditions or husbandry interventions, the issue of breeding for increased

litter size is a harder concept to consider from a welfare perspective. Here we consider the evidence for different possible welfare challenges relating to large litter size and possible mitigation strategies to meet the challenges. Many of the individual issues we consider have been discussed previously; however, this discussion has not been in the context of the larger causal variable of litter size.

Potential welfare issues, for either sow or piglets, relating to large litter size may derive from either biological consequences (aspects of large litter size that are bad for welfare *per se*) or management responses (where poor management or failure to intervene could exacerbate a welfare issue). Biological consequences can be further divided into outcomes that are causally related to a crowded gestation environment and outcomes that are related to experiencing postnatal life in a large litter. These two do not perfectly co-vary since, either through early piglet mortality or active management responses, such as cross fostering to even up litter size, litter size experienced during neonatal life will be less variable than litter size experienced during fetal life.

The welfare impacts of litter size in pigs have not, until now, been the focus of much attention. For instance, the SVC report into the welfare of pigs did not mention it as a specific issue (SVC, 1997). Similarly, in the UK the Farm Animal Welfare Council (FAWC) "Report on the welfare implications of animal breeding and breeding technologies in commercial agriculture" (2004) does not specifically raise the issue of litter size in pigs. However, even around this time there were concerns being expressed in society about the issue of selection for ever larger litter sizes. For instance, in 2003 it was reported in the UK press that a sow at a farm belonging to a UK breeding company had given birth to 27 piglets ("And this little piggy gave birth to 27 piglets", The Telegraph June 10th 2003). In its headline the Daily Mail asked the question: "Scientific triumph – or yet another grotesque milestone in mankind's abuse of animals?" and a spokesperson for the Royal Society for the Prevention of Cruelty to Animals (RSPCA) was quoted as saying "The sow is likely to suffer discomfort through the pregnancy because she is carrying so many piglets". A representative of the animal welfare advocacy charity Compassion in World Farming (CIWF) said "It typifies what is wrong with modern factory farming. The industry should try to reduce litter size, not increase it".

More recently, in Denmark, the issue of large litter size drew media attention in 2010 when the Danish Animal Protection Society highlighted the issue of high levels of piglet mortality. By their calculations the relatively high level of piglet mortality in Denmark equated to nine million dead piglets per year and they challenged the practice of breeding for higher litter size on welfare and ethical grounds and also questioned whether the negative outcomes effectively rendered the practice illegal.

In relation to breeding and animal welfare, EU legislation (Council Directive 98/58/EC of 20 July 1998 concerning the protection of animals kept for farming purposes) states that:

"Natural or artificial breeding or breeding procedures which cause or are likely to cause suffering or injury to any of the animals concerned must not be practised".

"No animal shall be kept for farming purposes unless it can reasonably be expected, on the basis of its genotype or phenotype that it can be kept without detrimental effect on its health or welfare".

However, it is rather unclear what the implications of this are for legal requirements facing animal breeders (Gamborg et al., 2005; Olsson et al., 2006) and more generally who would be liable for prosecution under such legislation. FAWC (2004) noted that legislation had not, to that point in time, been used as a basis to restrict a breeding practice and this situation seems unlikely to change. In the UK an attempt in 2004 by CIWF to challenge the legality of the chronic feed restriction required to successfully rear broiler breeders to reproductive age failed, partly because the appeal judge refused to consider that the animals' genotype contravened UK legislation (implementing the EU directive).

Over the last decade, the European Food Safety Authority (EFSA) has conducted a number of animal welfare risk assessments of different livestock industries, including pig production (e.g. EFSA, 2007). In relation to pig production, litter size was discussed as a possible risk factor for negative welfare outcomes, largely based on problems associated with low birth weight, increased teat competition and piglet mortality, but also due to concerns relating to possible welfare impacts of management responses such as cross-fostering, especially when practiced after the first day of life (EFSA, 2007). Based on these concerns they recommended that: "Genetic selection for litter size should not exceed, on average, 12 piglets born alive..." (EFSA, 2007, p3).

However, as a result of the apparent economic benefits of large litters to the industry, the ongoing development towards increased litter size in pig production can be expected to continue. The question of whether the goal of ever increasing litter size has resulted in modern intensive pig production straying beyond practices that are acceptable to the public has not been addressed. Nonetheless, in Denmark, The Pig Research Centre has launched a new campaign to improve pig welfare and one of the specific goals is a reduction in total piglet mortality by 20% before 2020.

The aim of this paper is not to judge what the public at large find acceptable but it will aim to draw together all the pertinent scientific and practical evidence which might contribute to a societal debate about the ethical acceptability of large litter size. Here we provide a comprehensive assessment of all the available information on the impact of increasing litter size on welfare allowing evidence-based conclusions to be drawn. These conclusions can inform the debate on the societal acceptability of increasing litter size within the context of other issues such as environmental goals and food security. To the extent it turns out that

the development implies increased welfare problems or raise other ethical concerns, it will be relevant and of value for both pigs, pig producers and society to analyze management or breeding strategies to meet these challenges. Consequently, we identify a number of different mitigation strategies that could allow some of the identified welfare issues to be avoided or minimised.

2. Litter size in domestic pigs

Before proceeding to an assessment of how litter size may impact on welfare and possible ways to mitigate these challenges we will firstly give some consideration to how litter size in the domestic pig has developed over time and what 'large' litter size actually refers to. Emphasis is placed on Danish pig production where litter size increases have been most rapid in recent years, and current average litter sizes are the highest seen in European production (Pedersen et al., 2010). However, given the upward trend of litter size internationally, and the export of Danish breeding stock, many of the scenarios and issues described will also apply to other countries, either now or in the future.

2.1 Litter size in wild pigs and related species

Pig species are naturally polytocous, and have been said to be the only naturally polytocous ungulate (SVC, 1997). Litter size in wild boar is normally quoted as being around 4-6 on average (see Appendix three). However, under varying environmental conditions wild boar can have litters in double figures (Bieber and Ruf, 2005; Servanty et al., 2007; Focardi et al., 2008), with litter sizes of up to 14 having been recorded (Servanty et al., 2007). Wild boar sows are flexible in their reproductive effort and respond to good environmental conditions by increasing litter size (Servanty et al., 2007). Wild boar litters sizes are actually ecologically unusual for an ungulate of their body size, where smaller litter sizes are the norm (Saether and Gordon, 1994; Carranza, 1996; Bieber and Ruf, 2005; Focardi et al., 2008). This is illustrated in Figure one, where *Sus scrofa*, and its two closest relatives *Phacocooerus aethiopicus* (the Desert Warthog) and *Potamochoerus porcus* (the Red River Hog) are clear outliers from other ungulate species. The characteristic porcine large litter size is associated in the wild with high offspring postnatal mortality, and may be part of an evolutionary strategy of over-producing. (Interestingly, the other ungulate with higher than normal litter size, the Chinese Water Deer, *Hydropotes inermis*, also shows high levels of neonatal mortality, for instance, estimated at between 20 and 40%: Dubost et al., 2011). The process is thought to be a form of parental optimism where the production of numerous neonates allows replacement offspring in the event of others in a litter dying (Mock and

Forbes, 1995; Mock and Parker, 1998) and guards against an unpredictable lactation phase, where resources may be plentiful or sparse.

In addition to high litter size, wild boar adopt a faster life history strategy (earlier reproduction) when environmental conditions are good and show substantial flexibility in life-history strategy depending on environmental conditions: as food availability declines, juvenile reproductive development is delayed and the trade-off between reproduction and survival shifts towards survival (Bieber and Ruf, 2005). In terms of classical life history theory then pigs appear more R-selected (large number of offspring, low offspring survival) but they differ from the classical pattern for R-selected species due to having relatively slow growth rate, high levels of parental care and a relatively long lifespan. The propensity of pigs for flexible increases in reproductive effort (earlier reproduction, larger litters and multiple litters over a year) may partly explain why the wild boar was such a valuable animal for domestication.

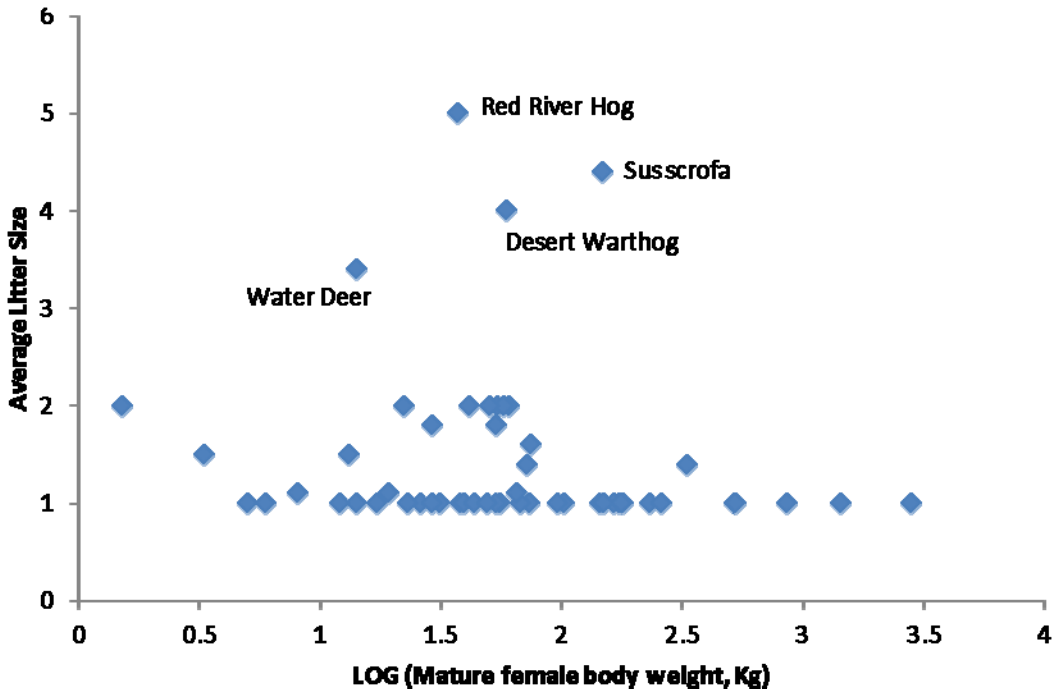

Figure 1: Relationship between female body mass and average litter size in 53 Ungulate species (Data from Saether and Gordon, 1994)

2.2. History of litter size and piglet mortality in domestic pigs

Human beings began the process of domesticating wild boar about 10,000 years ago, with several independent domestication locations being involved (Larson et al., 2011). Following the initial domestication, humans then began selectively breeding for particular traits in pigs creating a range of domestic breeds with different physical, behavioural, physiological and

reproductive characteristics. In the last century as knowledge about the principles of inheritance increased, the process of selection in pigs has been conducted in a more systematic fashion. Selection was initially focused on physical appearance but from the 1950's onwards traits relating to farm production were increasingly of selection interest (Dekkers et al., 2011). Initially major progress was seen in carcass traits and growth rate while reproductive output showed little gain. As a consequence, over most of the recent history of pig production litter size changed relatively little. In the UK at the end of the second world war the average litter size was nine (of which 7.6 piglets were reared: Ridgeon, 1993), whereas a textbook from 1811 states that average litter size then was around 7.5 (cited in Baxter 1984). Indeed average litter sizes recorded for much of the post second world war period are only at the high end of what would be biologically possible for wild boar under good conditions. As pig production further increased in intensity, improvements in litter size were achieved through better management and nutrition. More recently genetic selection for litter size has been implemented. About two decades ago, with the implementation of the best linear unbiased prediction (BLUP) using an animal model in pig breeding, substantial genetic improvement in litter size has been achieved in dam breeds. A simulation study by Roehe (1991) and a selection experiment reported by Sorensen et al. (2000) indicated that a selection response (increase) using the animal model of about 0.4 piglets per generation can be achieved. Subsequently, practical genetic improvement programmes have shown that these improvements are possible.

In Denmark, selection for litter size (total born piglets) was initiated in 1992. Between 1992 and 1996 Danish production showed a yearly increase of 0.1 total born piglets, maintaining the earlier slow upwards trend (Figure 2). From 1996 the genetic improvement had segregated from the breeding herds via the multiplier herds and reached the production herds in enough sows to affect the production level. Since then litter size (total born piglets per litter) has increased by 0.3 piglets per year on average (Table 3; Figure 2). In 2004 the selection criterion was changed from total born piglets to 'live piglets at day 5' (LP5). However, the full effect of this change will only become apparent in future years as LP5 will not yet have been fully realised in Danish production herds due to the delay in such a change transferring from breeding herds to farm production. Approximately 5 to 6 years after the introduction of LP5 a equilibrium genetic progress is expected in the production sows, in herds purchasing replacements from multiplier herds. But it will take longer in herds with other replacement strategies (Personal communication: Henryon, PRC). Since production herds differ in their use of breeding animals there will be variation in the time taken for full transfer of national changes to local production. Some farms buy in their gilts from multiplier herds (resulting in faster transferring), some produce their own gilts using 'core-management' (medium transferring) and some herds only use their own animals (slow

transferring). Further, this assumes that the genetic progress obtained in purebreds in the breeding nucleus is fully realised in the crossbred sows in production herds. Crossbreeding results in an additional increase in litter size and thus a larger risk for the individual piglets and a larger demand on the sows during parturition. Due to the lack of parental assignment identification in production herds this is not well documented.

The other obvious trend seen in the data in Table 3 is that as litter size has increased in Danish pig production so has piglet mortality. It is worth noting that there has been a disproportionate increase in prenatal deaths compared to live born mortality. Whilst total born piglet numbers increased by 33% between 1996 and 2009, the total number of weaned piglets increased by only 23%. So a significant proportion of the selection effort (prior to the introduction of LP5) has gone towards producing stillborn piglets. Between 1996 and 2009 the average number of stillborn piglets per farrowing has more than doubled from 0.9 to 1.9. This disproportionate increase in the number of stillborn piglets, and the related fact that genetic selection has led to a greater increase in the number of ovulations than in manifest litter size (Dekkers et al., 2011), raises interesting scientific and ethical questions, which will be addressed in later sections of this report.

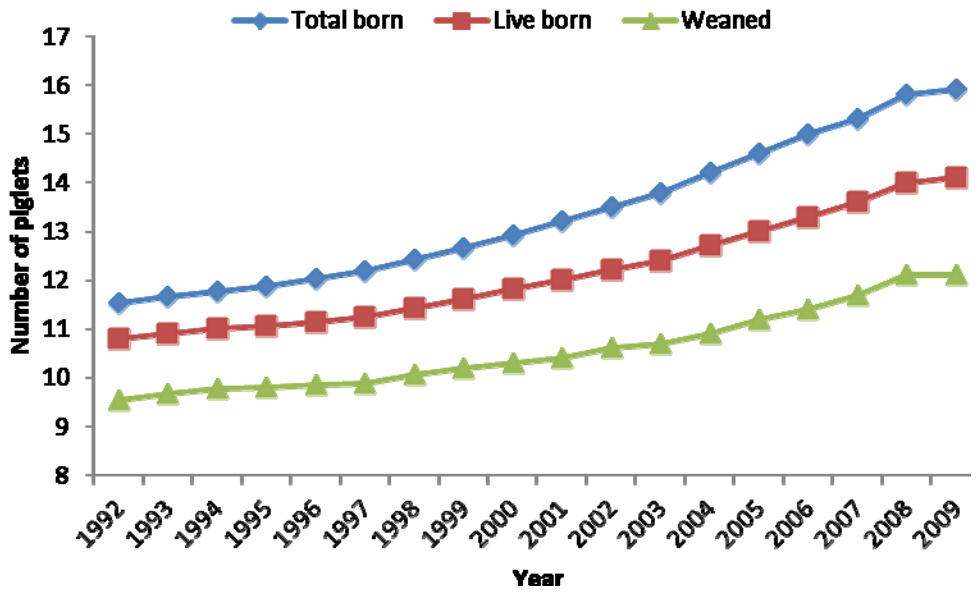

Figure 2: Developments in numbers of Total born, Live born and Weaned piglets per litter in Danish production between 1992 and 2009.

Table 3: Changes in National Litter size statistics in Denmark and UK

		1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Denmark ALL	Live born	11.2	11.3	11.5	11.7	11.9	12.1	12.3	12.6	12.9	13.2	13.5	13.6	14	14.2
	Still born	0.9	1.0	1.0	1.1	1.1	1.2	1.3	1.4	1.5	1.7	1.7	1.7	1.8	1.9
	Weaned	9.9	10	10.2	10.3	10.4	10.5	10.7	10.9	11.1	11.3	11.6	11.7	12.1	12.2
	Total Born	12.1	12.3	12.5	12.8	13	13.3	13.6	14	14.4	14.9	15.2	15.3	15.8	16.1
	Prenatal mort. (%)	7.44	8.13	8.00	8.59	8.46	9.02	9.56	10.00	10.42	11.41	11.18	11.11	11.39	11.8
	Pre-wean mort. (%)	18.18	18.7	18.4	19.53	20	21.05	21.32	22.14	22.92	24.16	23.68	23.53	23.42	24.22
Denmark Top 25% Pre-wean mort. (%)				16.92	17.56	17.78	18.84	19.72	20.00	20.81	20.92	21.66		20.86	22.69
Denmark Bottom 25% Pre-wean mort. (%)				21.31	22.58	23.2	24.22	25	24.44	25.36	26.39	26.21		26.45	26.45
UK ALL	Live born	10.84	10.89	11.01	10.98	11.02	10.90	10.97	10.75	10.75	10.89	10.90	11.10	11.58	11.05
	Still born[1]	0.95	0.92	0.93	0.98	0.98	0.95	0.89	0.93	0.88	0.79	0.80	0.80	0.83	0.94
	Weaned	9.60	9.69	9.78	9.79	9.89	9.62	9.72	9.61	9.63	9.69	9.50	9.74	9.82	9.82
	Total Born	11.79	11.81	11.94	11.96	12.00	11.85	11.86	11.68	11.63	11.68	11.70	11.90	12.41	11.99
	Prenatal mort. (%)	8.10	7.80	7.80	8.20	8.20	8.00	7.50	8.00	7.60	6.80	6.80	6.70	6.68	7.84
	Pre-wean mort. (%)	18.58	17.95	18.09	18.14	17.58	18.82	18.04	17.72	17.20	17.04	18.80	18.15	20.87	18.10

1. Calculated from prenatal mortality % of total born

2.3. What do we mean by large litter size in domesticated pigs?

Litter size is determined by three biological factors: ovulation rate, conception rate and embryonic/fetal survival. Each of these factors can be affected by a number of secondary factors (Spötter and Distl, 2006), e.g. genetic, environmental, management, seasonal, infectious, toxic and nutritional factors (Bazer et al., 2001). Litter size is defined in this report as all piglets born alive plus all piglets born dead (regardless of birth weight) that appear normally developed and coloured. This excludes fully or partly mummified piglets that did not survive to term, but includes any normally developed piglets, that were alive to term (i.e. stillborns), and piglets that possess any malformation meaning they were not viable (e.g. incomplete gut development such as blind anus). We believe that this definition is relevant as any piglet so defined has participated in any intrauterine crowding and in the birth process. Since the pig industry often focuses on viable piglets, our definition may include more individuals than are recorded under practical conditions. In addition this definition may differ from that used in other publications.

For the purposes of this report we have divided litter sizes into notional zones based on particular thresholds that affect management (Figure 3). We have firstly categorised litter sizes of six or fewer as 'abnormal', as litter sizes in this region would generally be regarded as indicating a problem with the sow's reproductive function (such as a health problem) that needed addressing. These abnormally small litters may or may not represent a welfare concern depending on their cause.

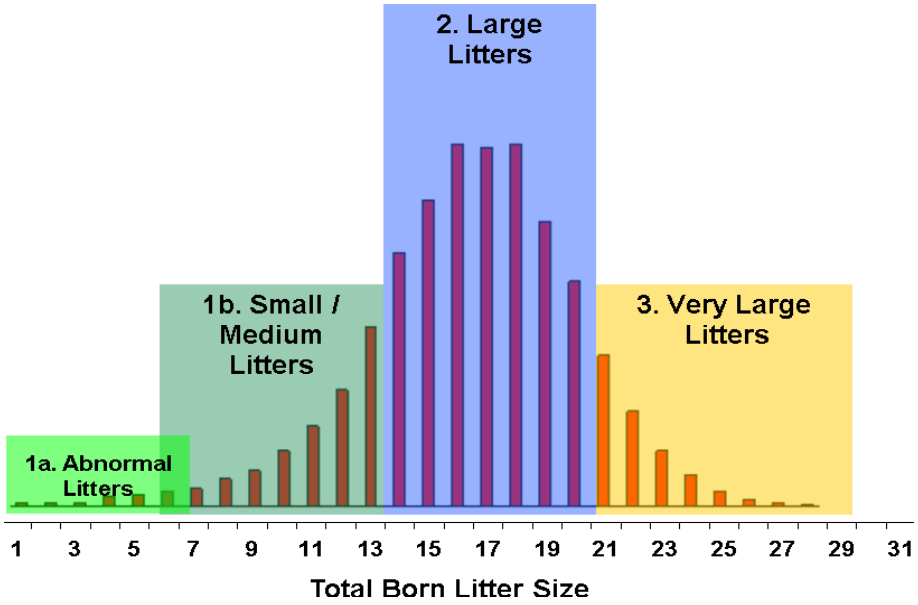

Figure 3: Distribution of litter sizes from Danish data, and notional litter size categories used for discussion in this review (see text for further descriptions).

Litter sizes of between seven and thirteen piglets have been categorised as 'small/medium'. The upper limit of this range is based on average numbers of functional teats seen in commercially available sows. For any given litter, if a sow produces fewer viable piglets than she has functional teats, then little or no intervention is necessary, as each piglet has a chance to identify and occupy a teat. Teat number generally varies between 8 and 18, with 12 to 14 being most common in Western breeds. Chinese breeds such as the Meishan and Erhulian can have above 20 teats (although ~18 is average) (Bazer et al., 2001; Ding et al., 2009), which fits very well with the litter sizes in these breeds. Dysfunction of individual teats will also often reduce the litter-rearing capacity of a sow. Temporary inability to access all functional teats can also affect the effective teat number. This could be caused by: i) the anatomical position of teats under hind legs when the sow lies on her side, ii) metal bars in crates used in many production systems, iii) sow posture during suckling resulting either in some teats not being exposed or being too high to be reached by small piglets.

Litter sizes between 14 and 20 are classified here as 'large', and litters of 21 or above are classified as 'very large'. The distinction between large and very large litters is arbitrary. In most cases litters of greater than 14 total born (presuming an average level of stillbirth) will require some form of management intervention since an individual sow gives birth to more piglets than she can sustain. When the majority of litters fall within this zone interventions such as cross-fostering and forms of teeth reduction become a routine part of farm management. For farms where the sow genetic stock is such that most litters are at the low end of this range, or in the small/medium zone, piglets can be readily fostered onto other sows because the total number of teat spaces available (i.e. the number of sows farrowing on any given day multiplied by the number of teats) will still be greater than the total number of live born piglets born minus peri-parturient mortality. However, at some point within a production system where large and very large litters are commonplace a further management threshold in relation to the total number of teat places in a breeding herd will become apparent. On many farms, a number of sows will be farrowing within the space of a few days (batch farrowing), so the next relevant threshold relates to the situation where the total number of viable piglets born to all sows in a given farrowing batch exceeds the number of functional teats of all sows in that batch. If this begins to occur regularly, fostering piglets to sows with available teats is no longer a sufficient strategy, otherwise viable piglets will die. This describes the current situation in Denmark. At these levels of litter size a different set of interventions may be required, for example the use of nurse sows (which raise their own piglets before receiving another litter to suckle), which are commonly used in Denmark or the use of artificial rearing methods (see 'management strategies' section). At such large litter sizes the requirement for tooth-reduction may actually be decreased as intra-litter

competition is reduced. The point at which the number of piglets produced is above the herd capacity of course depends on the herd size, the numbers of sows farrowing at the same time, the sow's capability of nursing large litters and the litter equalisation strategy of the herd (e.g. the number of piglets that an individual sow is expected to nurse).

As well as average litter size, variability in litter size is also important. When average litter size is low, very large litters will still occur but at a low prevalence. When they occur infrequently, very large litters can in all likelihood be dealt with by cross-fostering. However, relatively small increases in average litter size mean a disproportionate increase in very large litters (presuming there is no decrease in variability or other change to the shape of the distribution). So with relatively small advances in average litter size (which might still be within the boundaries of what a single individual sow could cope with) we quickly move to a situation where management interventions become routine.

3. Assessing animal welfare impacts relating to litter size

3.1 The Decision situation

Before considering the welfare impacts and ethical implications of large litter size in pigs, it is necessary to clarify the assessment criteria. There are a number of ethical concerns about intensive pig production in general, regardless of litter sizes; however, on the other hand, the large production volume also shows a widespread acceptance of the practice of producing and consuming pork. In this report, the ethical concerns regarding impacts of increase in litter size is separated from an ethical assessment of pig production in general.

Hence we suggest, *firstly, an ethical assessment of the development from medium/small litters to large litters* (cf. the definitions in Figure 2). Assessing this development will largely have to be based on the Danish experience, with the caveat, however, that the Danish point of departure for this development is different from that of other countries. This development in litter size is summarized by the following figures, based on Table 3:

	Total Born	Weaned	Post-natal deaths	Stillborn
DK 1992	12,1	9.9	1.3	0.9
DK 2008	15.8	12.1	1.9	1.8

The assessment will be made in three steps. *First, an assessment of the welfare impact on the different groups of animals will be performed* (Sections 4-5; See Table one for a summary). It will attempt to answer the following questions:

- Post-natal death piglets: More piglets die early in life: how does their welfare develop on average (i.e. from 1992 to 2008)? How does their lifetime welfare compare with the normal life from piglet up to finisher?
- Stillborn piglets: Do stillborn piglets represent a welfare problem?
- Weaned piglets: More piglets are weaned: how does their welfare develop on average?
- The Sow: What is the average welfare impact, of larger litters, on the sow?

Secondly, it is relevant to assess *how new management and breeding strategies for large litters are able to improve the situation for each of these groups* (Section 6).

Thirdly, *an overall ethical assessment of the development as a whole will be performed* (Section 7). The assessment of the aggregated overall welfare impacts of the development is an ethical issue. We discuss the elements that may enter into this assessment. We also discuss whether there could be ethical concerns over and above the specific welfare impacts.

The report will gather information about the biological impact of large litters and the management practices and genetic strategies used to cope with them. This collection of information will be guided by the evaluation criteria relevant for the welfare assessment. These criteria are set up below. Criteria for the overall ethical assessment will be discussed in Section 7.

3.2 Philosophical accounts of welfare

'Welfare' is a normative concept because it defines the aspects of life it is in the interest of an individual to favour or have favoured. However, there has been variation in what different authors consider a definition of animal welfare, and this reflects that 'welfare' can be understood in different ways. For humans, there is a large philosophical literature on the notion of welfare, and this is in many ways relevant for the understanding of animal welfare as well. The philosophical discussion about welfare has largely been concerned with isolating distinct views on welfare and examining their implications. Roughly, three competing views have been identified and these can be labelled as hedonism, preference-satisfaction and objective (cf. Parfit 1984).

3.2.1 Hedonism views

The hedonism view defines welfare in terms of the quality of the individual's mental states. Originally, this quality was characterized in terms of pleasure and pain, which in turn was considered opposites poles on a continuous scale of intensity (e.g. Bentham 1789). Recently, however, it has been stressed that both positive and negative mental states make up a heterogeneous field of experiences; for instance, physical pain from a specific tissue

injury and general nausea do not appear to be different intensities of the same component of mental states (Parfit 1984).

The quality of mental states may of course vary over time. Hence, hedonism may give rise to assessments of welfare at a given time; but it may also give rise to assessment of life-time welfare for an individual through aggregation of its welfare at all times throughout its life.

3.2.2 Preference-satisfaction views

The preference-satisfaction definition has been inspired by the economic notion of welfare. Sometimes, it is understood as referring to experience or feeling of satisfaction resulting from having preferences fulfilled. But to put the weight on feelings would make this view a variant of hedonism. In order to make it a distinct view, 'satisfaction' has to be understood simply as the obtaining of a certain state of affairs (like when the clause of a contract is satisfied), without reference to the experiences this may involve (Griffin 1986). However, since this view appears to play no role in the literature on animal welfare, we can leave it aside.

3.2.3 Objective views

A third group of views are *objective* in the sense that they pick out features that makes life good for the individual regardless of how the individual subjectively perceives them. An example of such an item could be 'good health' which might be considered good for the individual, regardless of whether the individual prefers to be in good health or feels better off by being in good health.

For animals, a subgroup of objective views known under the name of *perfectionism* is particularly relevant. The basic idea is that a good life involves realising ('perfecting') the potentials inherent in the individual's nature. Traditionally, human nature, or the essence of human beings, has been characterized by definitions such as rational animal, social animal or political animal. Since the Enlightenment, such definitions have been considered rather vague and arbitrary, and the focus has consequently been on the more subjective views on welfare. Recently, however, attempts have been made to revive perfectionist ideas (Hurka 1993).

These revivals have perhaps been most successful for non-human living organisms, where the concept of an individual's nature can be given a clearer meaning. According to this view, an animal's nature is how this species normally will develop without interference, if it lives under suitable and favourable conditions (roughly, in the kind of environment to which it is evolutionarily adapted with sufficient possibilities to sustain itself) (Taylor 1986).

3.3 Animal welfare

The meaning of “animal welfare” has been the subject of much discussion (e.g. Fraser et al., 1997) and given that it is used to refer to an ethical rather than scientific concept there is no single correct definition. Many authors define ‘welfare’ along hedonist lines in so far as they propose that ultimately what matters is how an animal feels and whether it suffers (Dawkins, 1990; Duncan and Petherick, 1991; Duncan, 1996). It should be noted that hedonism does not imply that pain and suffering should always be avoided. Sometimes, a painful experience in the short term may lead to more pleasurable states in the longer term. For instance, animals entering into aggressive interactions may accept some degree of pain in order to gain access to food or sexual partners. Another point about pain is that, for humans in pain, it makes a lot of difference if the person knows that the pain will only last a certain time. But an animal in pain may not know whether the pain will go away or last forever (see Mendl and Paul, 2008). Alternatively, for humans, pain can be additionally distressing when it has specific negative implications for the future that the individual is aware of.

For animals, much of the research into farm animal welfare has generally been focused on the alleviation of negative states of suffering such as fear, stress, pain and various forms of disease. However, from a hedonistic perspective, positive states are also important; and more recently there has been increasing interest in concepts of 'positive welfare' where welfare is not only achieved through an absence of negative states, but also through providing for positive experiences and emotions in animals (Boissy et al., 2007; Yeates and Main, 2008; FAWC, 2009). This trend is reflected in the UK Animal Welfare Act (2006) which requires animal keepers not only to protect their animals against cruelty but also to meet the full range of their needs including positive ones, such as the expression of normal behaviour patterns.

Some authors have taken an interest in animal preferences and set up various choice experiments to study them (e.g. Dawkins, 1983; Mason et al., 2001; see Kirkden and Pajor, 2006 for a review). However, it is our judgment that this has not been motivated by the view that animal welfare consists of preference-satisfaction as described above. Rather, preferences have been seen as an indicator of underlying motivating states. Roughly, the hypothesis has been that affective states such as pain and pleasure have served as guidance for the development of an animal’s choice behaviour throughout evolution; and therefore, an animal’s choices under suitable environmental conditions are a good indicator of its mental states. In other words, the understanding of welfare has still been hedonistic.

Others take a more objective view and regard welfare as equivalent to a lack of disease and normal physical functioning. Broom is typically put forward as a proponent of

this view. Broom's often quoted definition of animal welfare is: "The welfare of an individual is its state as regards its attempts to cope with its environment" (Broom, 1986).

Historically, the distance between these two views has often been portrayed as being larger than it really is. Few hedonists would deny that health is very important for the mental states of an animal. Even if some disease is not felt by the animal at the time, it is likely to be experienced at a later time. This appears to be the observation underlying Dawkins' (2003) proposal that welfare can be defined by two questions: "is the animal healthy?" and "does it have what it wants?" Broom also emphasizes that feelings are involved as part of the coping success of the animal (Broom, 1998).

There has also been much discussion within the literature on concepts of naturalness or telos, relating to perfectionist ideas ('telos' refers exactly to the inherent nature of an animal). Such ideas appear prominent among lay people and also within organic farming (Lund and Röcklinsberg, 2001). However, as applied to farm animals, perfectionism raises many questions because the whole idea of domestication and use of animals for human purposes seems to violate the ideals of a natural life. Even so, proponents of the view derive some clear priorities from it regarding animal welfare. These priorities are concerned with assessment of welfare on a general level rather than assessments of individual welfare. One such priority is the importance of freedom of movement. It seems doubtful to characterize the environment of farm animals as 'natural'. Still, the environment should allow the animal to express its evolved behaviour patterns. As it was expressed in the Brambell Report (Brambell, 1965, paragraph 37):

> *'…we disapprove of a degree of confinement of an animal which necessarily frustrates most of the major activities which make up its natural behaviour'.*

Some early proponents of this definition extended this from 'most of the major activities' to hold that to prevent suffering an animal needs 'to perform all the behaviours of its repertoire' (Kiley-Worthington, 1989). However, as many behaviours have evolved as an adaptation to deal with an adverse situation (distress calls in isolation, fleeing from a predator and so on), it seems that performance of the whole behavioural repertoire is not necessary, only those parts of it that the animal perceives to be important in the more protected environment of a farm (Dawkins, 1998).

Another priority is often described through the concept of animal integrity, which has been defined as

> *'the wholeness and completeness of the species specific balance of the creature, as well as the animal's capacity to maintain itself independently in an environment suitable to the species' (*Rutgers and Heeger, 1999).

Hence, we should not infringe the animal's physical wholeness (such as castration or tail-docking), but instead create conditions where the animal has a life that accords with their

species-specific capacities and adaptation patterns: conditions where the animal can flourish and its inherent potentials can be fulfilled.

A third priority concerns the handling of disease. Interference with the natural course of disease is not natural. This priority is clear in organic farming, where the organic Principle of Health implies that "[i]mmunity, resilience and regeneration are key characteristics of health" (IFOAM 2005). From this follows the organic restrictions on the use of medicine. However, this is a point where disagreements arise. Many lay people, and also many scientists inspired by the perfectionist notion of animal welfare, will insist that is better for the individual animal to get treatment in the case of disease and thereby avoid suffering (e.g. Lassen et al., 2006). This shows that many people inspired by perfectionist ideas about natural life are likely also to appeal to hedonism and thereby hold a mixed view. The perfectionist account of welfare is largely relevant for the overall assessment of different forms of practice. We shall therefore postpone discussion of development from small/medium to large litters from a perfectionist perspective until Section 7.

Welfare implications will thus largely be assessed according to hedonism. Ultimately, we cannot measure welfare as it is a private property of the individual's conscious experience. However, it is possible to assess welfare by measuring parameters within the areas of behaviour, physiology, neurophysiology, disease, and physical factors. Each of these parameters has advantages and disadvantages. It is becoming more apparent that integrating the different approaches provides a more global and thorough assessment of an animal's welfare than single parameter measurement (Webster, 1998). It is equally important that the biological basis of each of the measures used and how they relate to each other is fully understood before they are used as welfare indicators (Rushen, 2003). Such animal based measures (Whay et al., 2003) are the end result of an integration of the effects of the physical and social environment and all the experiences that the animal has in that environment, as well as the degree of immune challenge that the animal faces.

3.4 Relevant alternatives and the non-identity problem

It is often assumed that, in order for an event to have a welfare impact on an individual in hedonistic terms, *the individual should be alive and experience the event as making a difference in the quality of its mental states*. However, this assumption appears to be based on a misunderstanding. An event can harm an individual, regardless of whether this is experienced as bad or not, simply by making it less well off than it otherwise would have been; or to put it in hedonistic terms: if the event deprives the individual of positive mental states it would otherwise have enjoyed (Broome 1993).

Suppose, to give an example, that a farmer decides to change housing conditions for his finishers, and that the animals as a consequence become less fit than earlier finishers were before the change. A new finisher will never experience that this change of practice has happened. Nevertheless, it is harmed because it is deprived of the better mental states it would have enjoyed, had the change not taken place. On the assumption that the animal has to experience the event as unpleasant, there is no welfare impact of the change. But if we compare the welfare resulting from the two housing conditions, it seems clear that welfare has decreased. Hence, the assumption must be false and, in relation to the topic of this report, we can allow for the possibility that increasing litter size could be considered detrimental to piglet welfare even when no unpleasant experiences are associated with it.

Hence, all hedonistic assessments of welfare impacts are concerned with *the difference in welfare between two alternatives*. When it is said that a certain action or practice has a negative or positive welfare impact on an individual, this impact is conceived as relative to some specified alternative. *It is therefore very important to be clear about what the base-line alternative is*. As was made clear in Section 3.1, we consider two comparisons: *the development from small/medium litters to large litters*, and *various strategies for welfare improvements of status quo of large litters.*

It still appears to be a necessary condition of a welfare impact on an individual that this individual is alive, i.e. that the individual exists in both alternatives. But consider a situation like this (Parfit, 1984):

> *The 14-Year-Old Girl*. This girl chooses to have a child. Because she is so young, she gives her child a bad start in life. Though this will have bad effects throughout this child's life, his life will, predictably, be worth living. If this girl had waited for several years, she would have had a different child, to whom she would have given a better start in life.

The example implies that the child that will come to life when the girl is 14 is numerically different from the child that will come to life when the girl is older. We can assume that the exact identity of an individual is determined by the joining of a particular ovum with a particular spermatozoon. Hence, when we compare the two situations, it is not the same individual which will have a worse life by being born earlier. In either alternative, some individual is brought to life, but the girl's choice has no impact on an individual's life in the sense that this individual is worse off in one alternative than in the other. Parfit calls this the Non-Identity Problem.

Opinions divide concerning whether an example like this should make us say that bringing an individual into existence with a certain level of welfare is a welfare impact on this individual. Some authors are in agreement with this, whilst others hold to the necessity of the individual existing in both alternatives. However, regardless of whether the welfare

differences are understood as impacts on individuals, or they are assessed from an impersonal perspective, there is widespread agreement on the following points:

- When we consider 'Same Number' choices, i.e. choices where the same number of individuals exist in all alternatives, the relevant comparison is how well off the (possibly different) individuals are in these alternatives. Hence, if we compare the case, where the girl has a child at 14 with the case where she has a child later, the latter alternative is better, because the child in this alternative lives a better life. This is clearly relevant for the assessments in this report. When we compare alternatives at different times, it is obviously not the same individuals who exist in these alternatives. Thus, when we ask about the welfare impact on the sow of larger litters, it is not an impact on one and the same sow; rather, we compare the average lifetime welfare of a sow in 1992 with the average lifetime welfare of a sow in 2008.
- When we consider 'Different Number' choices, i.e. choices where a different number of individuals exist in the alternatives, it is necessary to assess the value of bringing extra individuals to life on top of comparing the welfare of the number of individuals existing in all alternatives. Hence, if we compare the case that the girl has a child with the case that she has no child at all, then, apart from the impact on the girl, it is necessary to assess the coming into existence of a child as compared with this child not coming into existence; i.e. how does living a life compare with no life?

From the perspective of this report the equivalent issue is that larger litters have more 'life' than smaller litters. Although it could be argued that given a fixed demand for a certain supply of pig meat products, there will not really be any more pigs, just fewer sows to produce the same number of growing pigs. Of course this over-simplifies a bit as the demand is not necessarily fixed. In practice, larger litters may in fact result in a larger supply of pork from the same number of farms with the same number of sows.

The assessment comparing small/medium litters with large litters is thus concerned with a Different-Number-Choice. This comparison involves comparing the lifetime welfare of the same number of piglets in the two alternatives. But in addition, it involves the assessment of lifetime welfare of the additional number of individuals. This assessment cannot be made in terms of the difference in lifetime welfare relative to the life in another alternative; it has to be made in absolute terms.

3.5 Welfare impacts of dying

What is bad about death? In this section we shall consider how, and to which extent, dying makes life worse for an individual. Answering this question raises many complications. From an ethical perspective, there is the further complication that it may make a difference whether the death is the result of a deliberate killing, or it is an unintended consequence of a practice with another motive. We shall consider this difference in section 7, but it is not an issue here. From a perfectionist perspective, the main issue about dying is to which extent the death can be considered unnatural. We consider this issue in section 7. Thus, in this section we shall look at the badness of dying from a hedonistic perspective.

All agree on the point that, if dying is experienced as bad, this will count as a negative welfare impact. But again, the assessment is a matter of comparing with the relevant alternative. Hence, dying may also be bad to the extent it deprives the animal of welfare it would otherwise have enjoyed (Yeates, 2010). This seems obvious, if we look at humans. Suppose a young person at 20 dies in her sleep without ever knowing. To say that her welfare is unaffected by this event appears absurd.

However, the view that, apart from the experience of dying, the badness of dying is a matter of the welfare of which the individual is deprived, has also been criticised. This is because it is at odds with some of our basic intuitions about the badness of dying. It implies that it is less bad if an older person dies than if a younger person dies. Most people would accept that. But it also implies that it is even worse, if an infant (with normal life expectancy) dies; and it is still worse if a fetus or even an embryo (likewise with normal life expectancy) dies. And many people have the opposite intuition that these deaths would be less bad, the earlier the better.

This observation has led to a revision of the deprivation view known as the Time-Relative Interest Account (McMahan, 2002). On this view, the deprivation by dying is a matter of, at the time of dying, how strong the individual's interest in continued life is. An individual's interest in future life is concerned with plans, expectations, hopes and intentions that connect its present self with itself at future times. To the extent that these psychological connections into the future are weak, the loss of being deprived of this future is discounted. Thus, a person at 20 may have strong psychological connections to her future self, whereas a fetus or an infant may have none or only very weak psychological connections to their future selves. Hence, their loss at the time of dying is considerably less than the loss of the 20 year old person.

There is considerable debate over the extent to which animals are capable of conceiving of the future (Suddendorf and Corballis, 2007; Mendl and Paul, 2008; Clayton et

al., 2009). However, it is highly unlikely that they have any major psychological connection to the future and are probably more akin to human infants on this measure.

The Time-Relative Interest Account is also not entirely satisfying (Holtug 2010). It is based on a new condition for negative welfare impacts of an event, namely that the individual at the time when the event happens is psychologically connected to what it is deprived of. But if there is a loss of welfare, and the experience at the time does not make a difference, why should psychological connectedness at the time make a difference?

In both cases, the relevant alternative should be specified. In general, we shall compare the early death of a piglet with the normal life expectancy of a piglet. However, for some assessments, this may not be a viable alternative. We discuss this further in connection with overall ethical assessment of alternatives in Section 7.

3.6 Summary of welfare assessment criteria used in the report

- From a hedonistic perspective, it is relevant to consider the animal's life time welfare, as compared with the lifetime welfare of a similar animal in a relevant alternative. For the assessment of the development from small/medium litters to large litters, this involves:
    - The Sow: How does lifetime welfare develop on average with larger litters?
    - Weaned piglets: How does their lifetime welfare develop on average with larger litters?
- Particularly concerning hedonistic assessment of the welfare impact of dying, it is relevant to consider how the death is experienced; to which extent is the animal's interest, at the time of dying, in continued life frustrated; and how much lifetime welfare is the animal deprived of by dying:
    - Post-natal death of piglets: For different times and causes of death: How conscious and sentient is the animal? How does it experience its death? How does its lifetime welfare compare with the normal life from piglet up to finisher? Under which circumstances could it have survived, and what life would that have implied?
    - Stillborn piglets: Is a stillborn conscious and sentient at the time of dying? Under which circumstances could it have survived, and what life would that have implied?

For an assessment of the animal's experience of dying, and for the assessment of the animal's time-relative interest in continued life, it will be necessary to make assumptions about the onset of sentience, and about the extent to which an animal at various stages of its development is psychologically connected to its future life stages. This issue is discussed in section 4.4.5.

4. Welfare impacts on the piglet

SUMMARY:

Increased litter size is associated with increased total piglet mortality.

- There is a consensus in the literature that increased litter size is associated with increased neonatal mortality. However, levels of live born mortality in Danish pig production, whilst high, are comparable to other countries, with lower total litter sizes, implying that Danish pig farmers are managing large litter sizes reasonably well.
- Neonatal mortality represents one of the most significant negative animal welfare impacts of large litter size. Although the welfare impact of different types of death will likely vary, in some cases substantial suffering may occur before death.
- The prevalence of stillbirths is seen to be higher in Denmark as a consequence of selection for large litters. The scientific arguments suggesting that stillborn piglets may not suffer are convincing but remain untested in the pig. Furthermore there remains some uncertainty about the proportion of piglets recorded as stillborn that were indeed dead before expulsion.

There are a number of additional welfare concerns relating to large litter size in piglets that survive the neonatal period.

- Many of the causes of mortality (chilling, starvation, injury, disease), may also occur in lesser forms that cause suffering in surviving piglets.
- The phenomenon of lowered birth weights and associated effects on piglets that survive the perinatal period deserves consideration from a welfare perspective. Low birth weight is associated with a variety of negative long-term effects on piglet physiology and behaviour, such as increased stress reactivity, which may impair the health and welfare of some individuals.

For some piglets being born into a large litter may have other consequences for their postnatal experiences.

- Large litters are associated with intense teat competition and increase the likelihood that some piglets may not gain adequate access to milk (which has many negative effects including limiting colostrum intake, impairing thermoregulation and causing possible hunger).
- Management responses to large litter sizes, such as ubiquitous cross-fostering and the use of nurse sows also raise several welfare related questions. However, there remains uncertainty over the extent to which these impair welfare.

4.1 Intra-uterine crowding and uterine hormone exposure

Issues relating to intrauterine growth retardation in pigs have been reviewed and discussed previously (Ashworth et al., 2001; Foxcroft et al., 2006). As discussed earlier (section 2.1) pig species have a natural propensity to conceive large numbers of offspring. Prenatally this is demonstrated with high ovulation rates providing the surplus offspring and uterine space representing the limited resource. Of the released ova, 30-50% fail to survive through gestation (Anderson, 1978; Pope, 1994; Geisert and Schmitt, 2002) and those that do survive must compete to acquire adequate uterine space for blood flow and delivery of nutrients vital for sustaining life. Several studies looking at embryonic survival have indicated that prior to and during conceptus elongation, conceptuses can alter the uterine environment by secreting oestrogen (Anderson, 1978; Geisert et al., 1991; Pope, 1994; Krackow, 1997). As a result of asynchronous elongation, some conceptuses will be more advanced than others and the more developed ones are able to release oestrogen, in the form of estradiol 17β (E2β), creating a potentially hostile uterine environment for their less developed littermates, impeding elongation and resulting in degeneration. Runt piglets may implant later than the rest and this might explain why increased crowding in the uterine horns leads to increased runting (Perry and Rowell, 1969; Dzuik, 1985). Asynchronous development means smaller embryos are disadvantaged and the proportion of underdeveloped embryos is similar to the proportion of early embryonic loss (~20-45% before day 25: Bazer et al., 2001). Asynchronous development may be part of the natural reproductive strategy of the pig. In the wild, under sub-optimal post-natal conditions litter size heterogeneity may mean that smaller piglets die off more quickly allowing their larger siblings to survive relatively unaffected (Fraser, 1990). Such an effect has also been postulated to explain asynchronous hatching as an adaptive response to unpredictable food supply in bird species (known as "Lack's hypothesis"). For those embryos that do survive, their further growth and development as fetuses may be compromised by intra-uterine crowding, since size variability within a litter can lead to higher post-natal mortality, for various reasons including teat competition. However, embryo heterogeneity is not the norm for all pig breeds. Meishan pigs have greater homogeneity in early embryo size and this could be one reason why they have greater litter sizes and lower embryo loss (Bazer et al., 2001). The same effect is seen in gilt litters of European breeds, where lower birth weight is associated with reduced variation and no impact on piglet survival (Thorup and Musse 2010).

4.2 Still births, birth difficulties and asphyxia

For humans, stillbirths are defined in the UK as: "any child expelled or issued forth from its mother after the 24th week of pregnancy that did not show any other signs of life…" (Stillbirth

definition Act 1992). As the whole litter is born at the same time, and as piglets are not considered viable if born before day 107 of gestation, then definitions are somewhat different in pig production. Stillbirths can be divided into antepartum deaths which occur before parturition (often referred to as type 1 stillbirths or “mummies”) and intrapartum deaths which occur during parturition (type 2: Alonso-Spilsbury et al., 2005). Type two stillborn piglets may have died just before expulsion was initiated, during expulsion or just after being expulsed. Type one stillbirths are recorded in some countries but not in others, making international comparisons of stillbirth prevalence difficult. More generally, in pig production individual causes of mortality can often be misrecorded on-farm (Vaillancourt et al., 1990, 1992; Edwards et al., 1994) and this raises the possibility that a proportion of the stillborn piglets are actually postpartum deaths of low viability piglets rather than true stillborns.

The amount of late fetal development and maturation is a predisposing factor in survival (Randall, 1972b; van der Lende et al., 2001). In the final days preceding farrowing, the fetus experiences an increase in growth rate (Biensen et al., 1998) and development, with final physiological preparations for extrauterine life. In the human literature, premature infants are often physiologically compromised with reports of a higher incidence of respiratory distress syndrome (e.g. Lauterbach et al., 2001). It is possible that premature induction (<114d gestation) of piglet birth may result in a compromised neonate with suppressed lung maturation or a stillborn piglet. The risk of early parturition increases with increasing litter size (Leenhouwers et al., 1999; Rydmer et al., 2008; Vanderhaeghe et al., 2010ab, 2011), possibly as a result of an acceleration in the maturation of the fetal HPA axis, resulting in the initiation of the parturition process and higher fetal cortisol levels reaching the uterus (Van Dijk et al., 2005). This shortening of gestation could be compared with the effect of farrowing induction, where when gestation is decreased by one day, birth weight is reduced by 100g on average. Despite this, several investigations (Straw et al., 2008; Olson et al., 2009) indicate that piglet survival following induction can be acceptable, thus possibly excluding the theory of immature piglets (although see Gunvaldsen et al., 2007). Premature farrowings have been suggested to affect colostrum composition and intake by piglets (Milon et al., 1983; Jackson et al., 1995). In these studies sows were artificially induced to farrow prematurely at 109d or 112d of gestation respectively.

A piglet with immature lungs will be at risk from hypoxia and may be stillborn. Hypoxia occurs when the neonate experiences oxygen deprivation generally as a result of perinatal asphyxia during parturition, or postnatally if the lung surfactant factor is not functional or if a piglet is born inside the placenta, but may also occur *in utero* as a result of poor oxygen supply via the placenta. Dystocia (difficult births) can result in hypoxia. Prolonged farrowing duration, litter size and the position in the birth order all influence the extent of hypoxia (Herpin et al., 1996). In a population genetic study, Canario et al., (2006a)

found genetic correlations showing that increasing total litter size was associated with longer farrowings and higher stillbirths. Piglets born later in the birth order are subjected to successive uterine contractions, and experience a greater risk of damage, occlusion or rupture of the umbilical cord or detachment of the placenta (Herpin et al., 1996) and are more likely to be stillborn than piglets born earlier (Baxter et al., 2008). Given the relationships described between litter size and premature parturition and the relationship between birth weight and litter size (to be discussed later), it might be presumed that low birth weight piglets are at the greatest risk from hypoxia and stillbirth, however this is not necessarily the case. There is a curved relationship between birth weight and stillbirth (Roehe and Kalm, 2000) and very large piglets can be equally at risk from hypoxia most likely as a result of birthing difficulties whilst passing through the birth canal.

Meconium aspiration syndrome (MAS) is a risk factor for stillbirth or early postnatal death either by reduced vitality (impairing behavioural landmarks such as reaching the udder and successful suckling, therefore effecting thermoregulation and colostrum intake), myocardial dysfunction or lung damage (Mota-Rojas et al., 2002; Alonso-Splisbury et al., 2005). MAS occurs when the fetal piglet experiences asphyxia and a surge in fetal cortisol levels cause the sphincter muscle to relax and thus a release of faecal matter (meconium) into the placenta ensues. When the fetus experiences severe distress (e.g. a surge in uterine pressure) it can aspirate this meconium and placental fluid. Such a surge in pressure can be a consequence of the misuse of drugs designed to speed up the farrowing process (Mota-Rojas et al., 2002). Some piglets are born alive but swallow a lot of placental fluid and/or meconium and then die – effectively these piglets drown in their own placental fluids and are often thought of as being stillborn.

The transition from prenatal to postnatal life is a critically important time point in the life of any individual. For most species it represents the most dramatic change in circumstances that will be experienced during the whole life cycle. Difficult birthing processes can impact upon welfare of both the mother and delivered offspring (depending on whether these offspring are thought to be sentient and conscious: see section 4.4.5). There is much evidence that fetal physiology alters in the lead up to birth in preparation for postnatal life. Of critical importance in that process is the level of glucocorticoid hormones (cortisol in the pig) (Liggins, 1994). There is also evidence that the process of birth itself may impact on later health and well-being. In sheep and humans the passage of the fetus through the birth canal or experiencing uterine contractions is important for the onset of breathing movements and thermoregulation. This could contribute to problems for very low birth weight piglets that may not experience the same physical stimulation compared to larger individuals. There is related evidence of long-term implications for pig physiology (Daniel et al., 1999, 2008; Carroll et al., 2000) and immune function (Daniel et al., 2008) of

being born via a natural vaginal birth or a caesarean section. Generally, piglets born by caesarean section appear less suited for life than vaginal born piglets (Sangild et al., 1995). Given these effects it follows that there may be long-term implications of variation in the birth process. Increasing litter size is associated with a longer duration of farrowing (Van Rens and Van der Lende, 2004; Canario et al., 2006a), but in a shortening of the expulsion phase of the individual piglet.

In cattle, dystocia has also been shown to impact negatively on neonatal thermoregulation (Stott and Reinhard, 1978; Adams et al., 1995), uptake of immunoglobulins (Vermorel et al., 1989; Bellows and Lammoglia, 2000; Waldner and Rosengren, 2009), behavioural vitality (Adams et al., 1995; Bellows and Lammoglia, 2000; Hickson et al., 2008) and on health outcomes (respiratory and digestive diseases: Lombard et al., 2007).

4.3 Teat competition and establishment of the 'teat order'

Piglets find and take ownership of a certain teat during the hours after they are born (Scheel et al., 1977), and then consistently return to this teat at each suckling (teat fidelity; Newberry and Wood Gush, 1985; de Passillé et al., 1988). After about the first 12 hours, milk is only let down from the teats for a few seconds once or twice an hour (Fraser, 1980). Consequently there is competition to take possession of functional teats through which a stable 'teat order' emerges in which piglets occupy the same teats at each suckling bout (Fraser, 1975; de Passile and Rushen, 1989). The heaviest piglets are more likely to win in fights for teats (Scheel et al., 1977; Graves, 1984) and these strongest piglets may occupy the most preferred anterior teats (McBride, 1963; Puppe and Tuchscherer, 1999; but see de Passillé and Rushen, 1989). Piglets massage the udder with a rooting motion of their snouts, stimulating milk production in general and at their teat in particular (Spinka and Algers, 1995; Torrey and Widowski, 2007). Once a teat order is established, piglets defend their teats at each suckling (de Passillé et al., 1988), and vocalise if their teat is not available (Appleby et al., 1999). Teats which are used remain productive while un-used teats rapidly involute (Kim et al., 2001).

In larger litters there is inevitably greater competition for productive teats or indeed for any teat (Milligan et al., 2001b). Piglets which cannot get a teat at all face a critical situation and typically starve to death in the first one to three days (English and Smith, 1975, Hartsock and Graves, 1976, Fraser et al., 1995). Occasionally more than one piglet will share one teat and this usually also causes problems for at least one of the sharing pair (de Passillé et al., 1988).

4.4 Perinatal mortality and welfare implications

4.4.1 Overview of relationship between litter size and piglet mortality

All else being equal, larger litters have higher piglet mortality (Blasco et al 1995; Sorensen et al 2000), and lower piglet weights (Kerr and Cameron, 1995; Roehe, 1999; Sorensen et al., 2000), and small piglets have a higher risk of mortality (see section 4.4.2). On the other hand, Cecchinato and others (2008) found that piglet survival chances were reduced in both small (<6), large (12-14) and very large (>14) litters compared to intermediate litters (6-11), reflecting the fact that small litters often reflect a pathology in reproduction.

Despite the association with higher mortality, if an increase in litter size increases the number of weaned piglets, then it is beneficial for farm production. If not then an increase in litter size will be economically counter-productive. Danish production data indicate that an increase in litter size from 11.5 total born piglets in 1992 to 15.9 total born piglets in 2009 resulted in an increase in weaned piglets per litter from 9.5 to 12.1 piglets. In an early consideration of the impact of large litters on mortality, Blasco et al. (1995) found that with an increase in litter size from 6-8 to 16-18, neonatal mortality increased from 10-15% to approximately 45%. The fact that today in Denmark average litter size is above 16 and yet the total mortality rate is much less than this reflects two things: 1) the relative success in Danish management, and 2) that the genetic correlation between litter size and mortality rate is <1 (i.e. genetically speaking, increased litter size is not always accompanied by higher mortality), as is evident from genetic trends in purebred Danish sows since the introduction of LP5 on the selection criterion, resulting in increased litter size and a reduced mortality (see section 6.1).

Interestingly a recent study of European organic pig farms found an even higher average level of piglet perinatal mortality (30.65%: Sundrum 2011), from a much lower average total litter size (12.4) highlighting that this issue can be a problem even for sectors of production that specifically aim to operate to high welfare standards and in tune with natural production methods.

4.4.2 Piglet birth weight and birth weight variation within a litter

The negative relationship between litter size and birth weight (on average, larger litters have smaller piglets: Wolf et al., 2008) is of critical importance to many aspects of piglet welfare and has been discussed for close to one hundred years (Hammond 1914). As well as being associated with lower birth weight, large litter size is associated with increased within-litter weight variation (Wolf et al., 2008; Quesnel et al., 2008). It is widely thought that birth weight is the most important factor for piglet survival (Gardner et al 1989; Kerr and Cameron, 1995;

Roehe and Kalm, 2000; Knol et al., 2002ab; Fix et al., 2010). Roehe and Kalm (2000) reported 40% pre-weaning mortality in pigs with a birth weight of lower than 1kg, 15% between 1-1.2kg and only 7% when birth weight was above 1.6kg. Quiniou and others (2002) have showed that increasing litter size from ≤11 to ≥16 resulted in a reduction of mean birth weight from 1.59Kg to 1.26Kg. This corresponded to a mean decrease of 35g for each extra piglet born.

Smaller piglets within a litter are often termed runts but their weight may not be the only indicator of their viability. Measures of body proportionality such as the ponderal index (birth weight/ (crown–rump length)^3) have been shown to provide a valuable indicator of mortality risk for instance (Baxter et al., 2008). Small for gestational age (SGA) piglets have more potential to recover given proper management than those that have suffered some degree of intrauterine growth retardation (IUGR) which may have other abnormalities meaning that they have low viability (Fowden et al., 2005, 2006). Although individual papers often provide unambiguous definitions of what were regarded as SGA and IUGR piglets these definitions are not applied unanimously across studies. Generally, SGA piglets are those weighing less than the tenth percentile at birth (Bauer et al., 1998), yet have reached their genetic potential for intrauterine growth, displaying normal allometry. IUGR piglets, however, do not reach their intrauterine growth potential, displaying asymmetrical growth (Bauer et al., 1998). Recent studies looking at the gross shape and size of piglets suggest that IUGR piglets are disproportionately long and thin (Baxter et al., 2008) and it is possible that such piglets are pathologically growth impaired. Older data (Royston et al., 1982) suggested that, statistically, runt piglets form a discrete subpopulation: these animals are attached to proportionately less placenta with less placental blood flow (Wootton et al., 1977), have altered muscle development (Handel and Stickland, 1987), which almost certainly impairs their growth potential, and impaired thermoregulatory abilities (Hayashi et al., 1987).

Being born of low birth weight and in a large, heterogeneous litter not only increase the risk of being born dead (see section 4.2), but also of death in the postnatal period. The main causes of neonatal piglet mortality are chilling, starvation and crushing by the sow, and these three causes interact (Edwards, 2002). Small light piglets are at risk of starvation as they are often excluded by teat competition from access to productive teats, and if they gain access to a teat, may be less efficient at stimulating and draining it effectively. Piglets are at additional risk from disease if they have failed to acquire sufficient immunity in the immediate postnatal period. In addition, low birth weight piglets show poorer thermoregulatory abilities (Herpin et al., 2002) and are therefore more at risk from chilling, which can weaken an already vulnerable neonate making it less vigorous when competing at the udder and potentially less responsive to the movements of the sow. For all piglets the udder is a

potentially risky area. Piglets seek the udder for colostrum, milk and warmth, but are at greater risk of being crushed by an unpredictable mother, often 250 times their weight. For low birth weight piglets, the risk of crushing is increased because they spend longer near the sow's udder (Weary et al., 1996). Thus it is possible that a vulnerable neonate may experience chilling, starvation and then crushing (Edwards, 2002), which highlights the considerable welfare issues surrounding piglet mortality. The majority of pre-weaning mortality occurs in the first 72 hours of life (Edwards, 2002). However, later death can occur, particularly from disease, and as such maintaining optimum hygiene is an important husbandry practice in the farrowing house.

Larger pigs at birth is, however, not only positive either, as birth weight is genetically, positively (and therefore unfavourably) correlated to proportion of stillborn piglets (Grandison et al., 2002; Damgaard et al., 2003). Moreover, larger pigs may have negative effects on the sow during gestation and labour.

4.4.3 Maternal behaviour

Due to the common causes of death, piglet mortality is clearly a welfare issue for piglets. In addition, there are possible additional impacts on mortality through effects of litter size selection on the maternal behaviour of the sow. A large litter competing for teats and fighting at the udder can cause disturbance and pain for the sow, resulting in increased posture changes and a consequent increased risk of crushing and also of chilling and starvation if she does not settle to allow colostrum intake. Not only are there immediate consequences for the piglets, but a poor mother may limit her longevity in the herd. Sows that display savaging behaviour towards their piglets are selectively culled (Chen et al., 2008) and sows responsible for high levels of crushing may also be culled. Andersen and colleagues (2005) have also suggested that the higher level of crushing seen in larger litters could be part of an adaptive strategy that sows have to limit maternal investment.

4.4.4 Comparative aspects of litter size and mortality species

Direct comparisons of mortality figures between wild boar and domesticated species are not possible. Although wild boar mortality figures can be much higher than those recorded in domestic pigs the time scales are different. Juvenile mortality figures in wild boar tend to be recorded over the first year of life, whereas mortality in domestic pigs is usually calculated to weaning. Wild boar mortality estimates (Appendix three) are highly variable. However, the generally high wild boar mortality figures do emphasise the reproductive strategy that pig species have adopted, i.e. a strategy based on high production during times of plenty and an associated high mortality level. Given that pig species have adopted a reproductive strategy based on producing a large number of expendable offspring, it has been suggested (SVC,

1997) that as a consequence of this natural biology of the pig “there may be a ‘normal’ baseline mortality in pigs, which may prove to be very difficult to get below”.

From one perspective one of the major advances of domestication has been a dramatic reduction in mortality levels. When thinking about the implications of litter size in pigs in terms of the societal acceptability of mortality it may be helpful to look at other species. Some points of comparison might come from other (litter bearing) mammals that fall under human care.

Rabbits are one species that have analogous litter sizes to pigs, and for which there are data on both wild populations and farmed populations (which have also been genetically selected for increased litter size: Mgheni and Christensen, 1985). In one study wild rabbit pup mortality was observed at 32.4% on average but reached 100% in some litters (Rödel et al., 2009). Rashwan and Marai (2000) reviewed perinatal mortality in rabbits under commercial production. Estimates varied widely across different studies, depending on circumstances, breeds, parity etc, but pre-weaning mortality figures are comparable or worse than those seen in pig production, with figures of >20% and even >30% not uncommon.

More generally across other farmed livestock species neonatal mortality figures vary widely. Within sheep production lamb mortality can be up to 20% (the majority of which occurs in the first day of life; Dwyer, 2008) but can be higher when disease outbreaks occur (figures of up to 40% can be seen in some instances, Personal communication: Dwyer, SAC). Mellor and Stafford (2004) provided estimates of maximum recorded neonatal mortality rates as being up to 25% for lambs, 51% for kids, 50% for calves, 90% for deer calves, 35% for foals and 35% for piglets. Average figures for all these species will of course be much lower and will vary considerably depending on circumstance and the timescale over which they are assessed.

An interesting perspective on mortality in the pig industry may come from data on mortality and litter size in companion animals where it might be presumed that human standards of care would be relatively high. Dogs are a litter bearing species, albeit with smaller litters than those of pigs (litter sizes up to 17 have been recorded in larger dog breeds but the average is between 3 and 7 puppies across breeds and 5.4 overall: Borge et al., 2011). Data on canine perinatal mortality suggests that figures range from lower than, to comparable with, those seen in pig production. There is considerable variation between studies of different breeds and situations but figures for pre-weaning mortality range from 2.5% to 18.5% (Gill, 2002, Hare and Leighton, 2006, Linde-Forsberg and Persson, 2007), and a stillborn rate of 6.1% according to one study (Linde-Forberg and Persson, 2007).

4.4.5 Onset of sentience

As discussed in sections 4.2, 4.3 and 4.4, many welfare issues relating to litter size are manifest in the fetal / neonatal period. To properly determine the degree to which effects around this period are welfare relevant requires that we discuss the capacity of piglets to experience suffering across this period. We might all sensibly agree that fertilised eggs are not sentient, equally the capacity of adult pigs to experience a wide range of emotional states is not particularly up for debate, so it follows that at some point between these two time points sentience increases to a point that the experiences of pigs becomes morally relevant. Therefore, an important issue that pertains to the ethics of large litter sizes and still-births is the question of the stage of development at which fetuses develop awareness and the capacity to suffer. Further to that it is relevant to consider how pain perception and other sources of possible suffering operate biologically in neonatal animals.

The question of when animals develop awareness has both relevance to animal welfare (e.g. Mellor, 2010) but also to human obstetrics and the treatment of human fetuses (e.g. Royal College of Obstetricians and Gynaecologists (RCO&G), 2010). Hence there is a reasonable literature from which we can draw conclusions relevant to the issue of perinatal mortality, morbidity and suffering in pigs. A number of writers have argued that underpinning the public concern for animal welfare is the increasing acceptance of the idea that animals are sentient and can subjectively experience poor and good welfare states (e.g. Dawkins, 1990). Hence the discussion on fetal awareness has often focused on the question of when animals (and humans) have developed a sufficiently complex nervous system to 'support' conscious experiences (awareness). The recent report from the RCO&G (2010) focuses on awareness of pain in fetuses, and concludes that as neural projections from the peripheral body to the cortical region of the brain are not completed before 24 weeks of age, and as the cortex is necessary for conscious experience, then pain cannot be experienced by the fetus prior to 24 weeks of age (see RCO&G, 2010 pages 3-10).

Diesch and colleagues (2010) have added that in the context of developing animals, both sentience and consciousness are required for animals to suffer. Recent research from David Mellor's group in New Zealand suggests that the fetus never properly gains consciousness until after birth (e.g. Mellor, 2010). This idea has emerged partly from studies of fetal electroencephalogram (EEG) in lambs (see Mellor et al., 2005 for a review). These studies suggest that for 95% of time fetal lambs, as judged by interpretation of EEG data, are in a state of sleep or unconsciousness. In order to interpret the remaining 5% of time and the question of whether the lambs are awake or altering sleep states, Mellor et al (2005) refer to a study of fetal lamb behaviour made through a plexi-glass window (Rigatto et al., 1986) that suggests that lambs never gain a true state of wakefulness *in utero,* never having open eyes or showing coordinated movements of the head. Mellor et al (2005) suggest a

number of factors that could cause this state of fetal unconsciousness including the combined effects of *in utero* adenosine (a sleep inducing agent) and allopregnanolone (an anaesthetic). However, in other research, fetal lambs have been visualised (using ultrasound) to show quite co-ordinated mouth and tongue movements and also stretching/flexing of the head and neck (Coombs et al., 2010).

Mellor and Stafford (2004) have also considered the welfare implications of neonatal mortality and morbidity. Another factor they draw attention to in this review is that the low levels of blood oxygen in the fetus before and during labour (Mellor and Gregory, 2003) are unlikely to be compatible with consciousness. They also suggest (largely on circumstantial human experience) that a relatively slow descent into a hypothermic state (a likely prelude to death in many cases of live born mortality in pigs) may not be experienced as being aversive, due to reduced levels of cognitive function and awareness. On the basis of these and other considerations Mellor and Stafford (2004) produced a ranking of neonatal welfare insults in which anoxia and hypothermia are deemed lesser threats to welfare than prolonged hunger (at ambient temperatures) and pain from neonatal disease.

This understanding of fetal and neonate awareness has already been used to inform practice. For example, The Royal College of Obstetricians and Gynaecologists report (RCO&G, 2010) concluded on the basis of the available data that there was no clear case for the use of anaesthesia in humans during fetal interventions and late abortions due to fetal abnormalities. Mellor (2010) has argued that when slaughtering pregnant ruminants, fetuses should be ideally left in the slaughtered mother until dead. This advice is based on his view that as long as breathing is never allowed to start, then the fetus will never gain consciousness and hence suffering will be avoided.

How do we then apply this knowledge to interpret the welfare impacts that may arise from larger litter sizes in pigs, involving potentially higher numbers of still-births and early post-natal mortalities and morbidities? Mellor (2010) categorises animals on the basis of their stage of neurological maturity at birth and on that basis we can regard piglets as equivalently mature at birth as sheep. Hence we could draw direct inferences from the available sheep data if we wished to assign welfare rankings to the perinatal insults facing piglets. The lowest ranking for welfare risk would be assigned to those piglets that never develop full and rhythmic breathing and hence never gain consciousness (i.e. those that die during labour or immediately after); medium ranking would be for piglets that develop full breathing, but descend into hypothermia (and hence reduced awareness) over the immediate hours following birth; highest ranking would be assigned to piglets that develop full breathing are not hypothermic, but suffer slow deaths from hunger, disease or injury as they will have developed full consciousness and hence potential to suffer.

However, these conclusions should come with caveats and cautions. This research is the product of a single research group working with a limited number of species (Mellor 2010) and replication by others and across a wider range of species would be valuable. Various criticisms of this research are summarised by Derbyshire (2010) including arguments that the cortex is not essential for the experience of noxious stimulation, uncertainty over the interpretation of EEG patterns and the unexplained significance of often complex and organised fetal behaviours (Coombs et al 2010). In addition there remain problematic questions over the nature of fetal awareness and the danger that we do not make enough of the potential differences between awareness in human adults and other non-verbal, less developed animals (Derbyshire, 2010).

In conclusion, there are data relating to the extent to which we might expect piglets to be aware, that in principle allows us to make inferences over the severity of the welfare insults experienced by fetal and newly born-piglets. However, it should be noted that this remains a challenging field of enquiry and other alternative interpretations of awareness in fetal and neonatal farm animals may develop with further research.

4.4.6 Pain experiences in neonatal piglets

Following the immediate peri-parturient period the capacity of young animals to experience states such as pain will be an important determinant of the welfare relevance of many effects (e.g. some forms of neonatal mortality, injuries from teat competition, teeth reduction). Pain is defined by the International Association for the Study of Pain as 'an unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage' (IASP, 1979 p250). The following definition of animal pain, which does not rely upon self-report, has been suggested:

> *'Animal pain is an aversive sensory and emotional experience representing an awareness by the animal of damage or threat to the integrity of its tissues; (note, there may not be any damage) it changes the animal's physiology and behaviour to reduce or avoid the damage, to reduce the likelihood of recurrence and to promote recovery; non-functional pain occurs when the intensity or duration of the experience is not appropriate for the damage sustained (especially if none exists) and when physiological and behavioural responses are unsuccessful in alleviating it' (*Molony, 1997).

Issues relating to pain perception in neonates have been the focus of much discussion in the human and animal literature. Until relatively recently it was widely presumed in human medicine that infants were not capable or perceiving pain in a morally relevant way. This led to only a limited use of analgesia during many potentially painful

surgical and other interventions (Rutter and Doyal, 1998). In the animal literature the suggestion that newborn animals are less capable of suffering from pain has actually been framed in legislation covering common farm 'mutilations' such as castration, tail-docking, beak-trimming and de-horning (e.g. Danish legislation requires that piglet castration is undertaken under anaesthetic only after 7 days of age). Partly this reflects the generally correct assumption that less tissue damage may occur earlier in life but it also reflects a general belief that very young animals are in some sense less capable of suffering. This suggestion has several roots. The central nervous system of neonate is immature, and responses to pain in neonatal animals are classically seen to be less behaviourally organised than those seen in older animals (Fitzgerald, 2005). So, for instance, in human infants, localised noxious stimulation may provoke whole body responses, which become more specific as age increases. Another part of the limited attribution of pain perception to neonates stems from our inability to consciously remember painful events experienced during very early life (MacPhail, 1998). However, it is now well appreciated that pain can be experienced in early life (Bellieni and Buonocore 2008) and indeed that it can have long-term impacts on later pain responding (Taddio et al., 1997; Grunau et al., 2006; LaPrairie and Murphy, 2010) and on other behavioural parameters. At the very least this implies that severe challenges experienced by neonatal animals may have welfare relevance even in the absence of sentience at the time of the challenge. However, beyond this possibility it is now more broadly recognised that neonatal animals can perceive pain in a morally relevant way. In fact, studies on the development of the descending pain inhibition system suggest that in some cases pain in neonates could be worse than in older animals because the inhibition system develops later than the pain system itself (Fitzgerald, 2005).

In pigs, studies have been conducted to examine age effects on pain and distress associated with husbandry procedures such as castration and tail-docking (e.g. Carroll et al., 2006;Torrey et al., 2009; see Prunier et al., 2006 for a review of castration studies). These studies tend to point to the conclusion that piglets experience noxious challenges as equally painful from the first 24hours of life onwards (more detailed assessment of how piglets react to noxious challenge over the first 24hours of life have not been conducted to allow an assessment of the possibility of carry-over effects of fetal sedation as suggested by Mellor). An earlier study (McGlone et al., 1993) found that early tail-docking was associated with a great negative impact on growth rate but it is not clear whether this reflects a more distressing experience or simply a greater negative impact caused by impaired teat competition (Prunier et al., 2006). Overall it appears reasonably safe to conclude that noxious challenges in very early neonatal life probably are associated with negative affective experiences in pigs.

4.5 Long-term effects of birth weight

Beyond the immediate effects that low birth weight may have on survival there also exists a large experimental and epidemiological literature, across many species, showing that birth weight relates to many aspects of an individual's biology throughout their lifetime. The concept of low birth weight is of course relative, for instance across breeds and many of the pertinent studies may not have properly distinguished low birth weight and physical/physiological maturity. Within the human literature there has been some discussion (e.g. Wilcox 2001) on the point that low birth weight (defined statistically in relation to the population distribution) can be statistically associated with certain outcomes (e.g. mortality, later physiology etc) without being causal related to them. So for instance, low birth weight and increased mortality may be statistically associated, but not causally connected if they are both caused by intra-uterine conditions. Such distinctions are seldom made or directly investigated in the pig literature but the relative role of birth weight and maturity in determining piglet welfare outcomes clearly deserves more study.

Human health interest in this area took off after the identification by Barker and co-workers (1993) of an association between low birth weight and an increase risk of later negative health outcomes (cardiovascular conditions, diabetes, obesity) in a cohort of British citizens. Since then, what became known as the 'Barker hypothesis', alternatively called the 'Thrifty phenotype' hypothesis, has been widely examined in a variety of different human datasets and has also triggered a number of animal studies utilising natural variation in birth weight or experimentally manipulating birth weight.

4.5.1 Stress physiology

In a number of studies, birth weight has been shown to impact upon stress reactivity later in life in pigs. Kranendonk and co-workers (2006) found that at day 41 of age larger birth weight piglets had a lower cortisol response to ACTH challenge compared to smaller birth weight piglets. Similarly, Klemcke and others (1993) found that piglets, which were small at birth (<1.2kg) had larger adrenal glands (relative to body weight) at 3 or 7 days of age. These small piglets also had increased circulating level of cortisol at both ages (and almost double the concentration at 7 days of age) compared to larger (>1.2kg) piglets. Smaller piglets also had higher cortisol binding capacity and a greater cortisol output from adrenocortical cells when stimulated with ACTH and birth weight negatively correlated with these parameters. Similar effects have also been seen beyond the immediate neonatal period. Poore and Fowden (2003) assessed pig HPA function at 3 and 12 months of age using insulin and ACTH challenge tests. HPA reactivity (to either challenge) was increased in small birth weight (<1.47kg) piglets when they were tested at 3 months of age, along with

overall adrenal size and an increased ratio of adrenal cortex to medulla in comparison to heavier piglets. However, at 12 months of age increased HPA reactivity was only seen in response to insulin. In another study, (Poore et al., 2002) blood pressure but not heart rate was found to be inversely associated with birth weight at three months of age, and more significantly with a measure of body disproportion. Furthermore, although there was no difference in basal level of adrenaline or cortisol, basal noradrenaline was higher in low birth weight piglets. Larger birth weight has also been associated with a stronger rhythmicity of cortisol release at nine weeks of age (Munsterhjelm et al., 2009). Munsterhjelm and colleagues suggest this relates to either a negative effect of being small (poor prenatal life conditions) or a positive effect of being large (larger piglets are more competitive and tolerant of thermal challenges). A blunted circadian rhythm of cortisol release is often associated with chronic stress and has been shown to relate to negative health outcomes in humans (Sephton et al., 2000).

Overall, these findings suggest that low birth weight piglet have a permanent alteration to the functioning of their HPA axis, implying that they are likely to show increased stress reactivity throughout their lifetime. In addition to welfare implications of elevated HPA reactivity, increased cortisol levels (whether basal or through repeated acute responses) could also have negative economic implications, through impaired growth or lowered meat quality (e.g. Yoshioka et al., 2005). There may be wider implications of such increased stress reactivity for disease transmission since even relatively mild or short-lived stressors can increase faecal excretion of enterotoxigenic *E. Coli* (Jones et al., 2001; Dowd et al., 2007) or *Salmonella* (Isaacson et al., 1999; Callaway et al., 2006). There are also food safety issues since catecholamines are known to stimulate bacteria in gut mucosa to penetrate muscle raising concerns for meat safety (Humphrey, 2006).

Pig studies have not however addressed directly the question of whether litter size impacts upon HPA function. In rodents, Rödel and others (2010) found an effect of litter size on offspring HPA function. At 17 days of age basal corticosterone levels were negatively correlated with litter size and at day 33 (two weeks post weaning) corticosterone response to a 10 minute elevated plus-maze test was also negatively correlated with litter size (although basal values were not at this age). The authors suggest that this outcome either reflects a delayed maturation of the HPA axis in offspring from large litters (an effect also found in other biological systems: see section 4.5.3) or that the increased competition for maternal resources led to a down-regulation of HPA function.

Associations between birth weight and later HPA reactivity have also been found in humans (Phillips et al., 2000) and it has been suggested that this effect might be causally implicated in the link (Law and Shiell, 1996) between low birth weight and high blood pressure. The negative link between blood pressure and birth weight has been questioned

(Huxley et al., 2002) and gestational age at birth may be one possible confounding factor in this relationship (Kajantie et al., 2002). This further emphasises the points raised earlier in section 4.4.2 on mortality that assessment of body shape and or gestational age may need to be taken into consideration to allow for a proper assessment of the outcome of litter size or other prenatal effects.

4.5.2 Behaviour

The possible impact of large litter size on intra-litter competition was discussed in section 4.3. A separate question is whether there might be longer-term effects of high levels of teat competition later in life. It has been suggested that in some species there is early life 'programming' of particular biological responses, where the early life environment is taken as a 'forecast' of future environment (e.g. Bateson et al., 2004; Gluckman et al., 2005). How such theories might apply in the case of large litter size is unclear. Being born in a large litter could be taken as a signal of plentiful food (as the dam has produced a large litter), or teat competition could be taken as a signal that resources are scarce. Regardless of this 'forecast' theory, severe protein malnutrition may alter brain development and thus behaviour (e.g. Morgane et al., 1993). Given that some piglets may starve to death without intervention, there may be some piglets that undergo severe (near-fatal) under-nutrition at some stage in early life and this could have implications for later behavioural strategies.

For instance, aggressive experiences at the teat could affect future aggressive behaviour. In mice, animals from larger litters were initially more aggressive, but then ended up subordinate (Ryan and Wehmer, 1975). In pigs, a detailed study by D'Eath and Lawrence (2004) of 125 pigs from 16 litters found that those pigs from larger litters in which there was more competition were more aggressive at mixing soon after weaning. However, we have failed to repeat this result in a larger dataset of 1132 pigs which were mixed into new social groups at around 7 weeks post-mixing (Turner et al., 2006). Drickamer et al (1999a) reported that litter size and sex ratio were not predictive of social dominance in gilts. D'Eath (2005) found that pre-weaning mixing of piglets from different litters resulted in lower attack latency during later post-weaning mixing, but that the resulting aggression ended up causing fewer body lesions, suggesting that these pigs might be more socially skilled (i.e. rather than being more aggressive they were better able to resolve contests quickly). Some suggestion of a similar finding in relation to litter size comes from Chaloupkova et al (2007) who found some evidence of a relationship between increasing litter size and decreased likelihood of post-weaning mixing agonistic interactions ending with one pig chasing and biting at another, and also with a decreased number of wounds. This might suggest that, along similar lines to that suggested by D'Eath (2005) as a consequence of pre-weaning mixing of piglets, that piglets from larger litters are more socially skilled than those from smaller litters.

It is widely appreciated that experiences during early life can have long-term impacts on emotionality in later life. Litter size could impact upon later emotionality through consequences of social competition, through altered nutritional state or more generally if associated with a lower level of individual control over the environment (e.g. Chorpita et al., 1998). There are some indications of possible litter size effects on emotionality in rodents. When compared to mice from smaller litters, those from larger litters took longer to begin moving in an open field (Ryan and Wehmer, 1975), suggesting they were more anxious. Janczak and co-workers (2000) found that mice selected for large litter size were more fearful in an elevated plus-maze test. More recently, Dimitsantos and others (2007) assessed the impact of litter size on later emotionality using natural variation rather than artificial manipulation of litter size. They found that rat litters of <10 pups had heightened signs of emotionality (e.g. increased anxiety) compared to larger litters. They also noted that different studies have found an increase (Hinz et al., 1983; La Barba and White, 1971; Ryan and Wehmer, 1975), decrease (Gamallo et al., 1988, Robinson, 1975) or lack of effect (Grota and Ader, 1969; Milkovic et al., 1976) on emotionality as a consequence of large litter size depending on species, breed and other experimental conditions. However, similar outcomes have not been widely examined in pigs. The fact that stress physiology variables (section 4.5.1.) have been seen to change as a consequence of birth weight does suggest that wider behavioural reactivity may be affected in a way that could be detrimental for welfare. There is some suggestion of behavioural outcomes of birth weight. D'Eath and Burn (2002) found an effect of weight within litter on struggling in the back test, for instance. However, Van Erp-van der Kooij et al (2001) found no effect of litter size on struggling.

An increase in 'emotionality' resulting from early life sub-optimal nutrition is a common finding in other species (Levitsky and Barnes, 1970, 1972). Learning deficits can also result from early life under nutrition for example in mice (litter-size manipulation study, Nagy and Porada, 1991) and in humans (Grantham-McGregor, 1995). Spencer and Tillbrook (2009) found that increased neonatal feeding as a consequence of artificially reduced litter size caused female mice to have a less anxious behavioural profile. A more recent study has demonstrated the converse effect: male offspring reared in large litters (and therefore fed less) also showed lowered anxiety levels and a reduced level of stress reactivity (Bulfin et al., In Press).

Moinard and others (2003) in an investigation of risk factors for tail biting found that farms where cross-fostering was practiced had a higher incidence of tail biting. However, since this was an epidemiological study whether fostering contributed directly to later likelihood of tail-biting occurring or whether this association was related to a different causal pathway (for instance herd size increasing the likelihood of fostering) is unclear. Large litter size might contribute to the relationship, but was not included in the analysis. Beattie and

colleagues (2005) found that piglets that spent more time engaging in tail chewing behaviour were lighter at weaning (but not at birth), and other studies suggest that pigs that have experienced a postnatal growth check may be more likely to tail-bite (reviewed by Taylor et al., 2010).

Low birth weight piglets were found to have a decreased willingness to play when presented with a ball in the creep area at various ages before weaning (Litten et al., 2003). Play represents a useful indicator of positive welfare and its absence is often associated with situations of decreased welfare or fitness (Held and Spinka, 2011).

4.5.3 Health implications

The pig has been extensively studied as a model of the health effects of intrauterine growth retardation in humans. Small piglets, studied using either the natural variation in within-litter birth weight in modern genotypes, or through artificially induced growth retardation, show alterations in the trajectories of growth and development of major biological systems. The accelerated maturation of some of these systems may be seen as evidence of developmental adaptation to a compromised uterine environment. For example, the rapid morphological development and enhanced contractile ability of skeletal muscle and an increased cardiac output have been described in low birth weight piglets (Bauer et al., 2006).

However, the majority of biological functions appear to be impaired by a low birth weight thus large litter size and its associated uterine crowding and compromised placental efficiency may be expected to exacerbate these developmental abnormalities. There is evidence of compromised growth of the gastrointestinal tract, liver, kidneys, thymus, ovaries, muscles and skeleton in low birth weight piglets (Handel and Stickland, 1987; Xu et al., 1994; Bauer et al., 2002; Da Silva-Buttkus et al., 2003, Mollard et al., 2004; Wang et al., 2005; Morise et al., 2008; Cromi et al., 2009). The tissue-specific decrease in expression of proteins that regulate immune function, intermediary metabolism and tissue growth may explain the abnormal growth and functioning of these systems (Wang et al., 2008). Examination of the health impacts of a low birth weight has primarily focussed on the incidence of chronic cardiovascular and metabolic diseases of human adulthood. Of more immediate relevance for pig production are observations in humans of heightened risk for infectious diseases associated with a low (SGA) birth weight (Moore et al., 1999; McDade et al., 2001; Amirilyo et al., 2011). Although these effects have been little studied in pigs, there is evidence of increased adhesion of bacteria to the poorly developed ileum and colon of piglets born after intrauterine growth retardation (D'Inca et al., 2011) and such piglets show a reduced lymphocyte proliferation in response to a standard pokeweed mitogen challenge (Tuchscherer et al., 2000). Important renal functions are also compromised by a low birth weight leading to a reduction in glomerular filtration rate (Bauer et al., 2002) which could

heighten the risk of urinary infection. Increased litter size heightens the risk of premature parturition with the attendant health risks discussed earlier.

The fetal brain may also be susceptible to developmental modification leading to poor prenatal growth. For example, lambs that have experienced chronic placental insufficiency appear to show structural abnormalities in the brain (Duncan et al., 2004), whilst Leitner and others (2005) showed compromised spatial orientation in 6 year old children that had experienced intrauterine growth retardation. Impaired spatial memory in undernourished low birth weight lambs at about 7 months of age has been found (Dwyer unpublished). Delayed neonatal behaviours such as reaching the udder and sucking have been described in lambs with a low birth weight or from a larger litter size (Dwyer, 2003). Similarly, delayed physical and behavioural development in mice has been reported (Dwyer et al., 2007). In fact, in lambs there is a separate effect of litter size over and above birth weight for behaviour and thermoregulation that suggests larger litters are affected more than would be predicted from birth weight alone (Dwyer 2003). If such effects are manifest in piglets, they may contribute to the delay and attendant risk for survival of achieving key behavioural milestones such as finding the udder and suckling.

An important postnatal effect of the diffuse epitheliochorial nature of the porcine placenta is that piglets are born without immune protection, and have to acquire maternal antibodies through the ingestion of colostrum (Gaskin and Kelly, 1995). The difficulty of acquiring colostrum, particularly in a large litter, has been described above. Some have argued that the competency of the passive immune response acquired in this way in practice differs little between piglets (Fraser and Rushen, 1992; Damm et al., 2002). However, the sow's colostrum yield appears to be independent of litter size (Devillers et al., 2007; Quesnel 2011) and competition between large numbers of littermates would on average be expected to result in a smaller quantity of colostrum intake per piglet (Le Dividich et al., 2005), although it is not clear whether this lesser quantity is still sufficient for piglets. In combination with physical and mental developmental immaturity and the low vigour of small piglets from large litters, this competition may constitute a further risk factor for disease. However these risk factors combine, the preweaning mortality rate from infectious disease is seen to be disproportionately high in low birth weight piglets compared to heavier piglets (Bilkei and Biro, 1999; Tuchscherer et al., 2000) which we can predict may become worse as litter size rises.

Although there are no data available on litter size and immune function in pigs, we might predict that there would be some impact since HPA axis activity is affected and immune measures may change down stream as a consequence. There is some evidence in rats that litter size can impact on later immune function. Prager and colleagues (2010) found evidence of negative correlations between litter size and aspects of adaptive immunity and

positive correlations with measure of innate immunity. They suggested that this outcome may be due to offspring in large litters having to invest more resources in growth at the expenses of immuno-competence (adaptive immunity being more energetically costly for the individual). They hypothesised that the effect could be a consequence of differential transfer of immune components from mother to offspring (either prenatally, or via milk intake) depending on litter size. Alternatively these authors speculated that enhanced maternal care of smaller litters may have benefited immune system development, or that increased competition in larger litters acted as a stressor, impairing immune function.

Litter size was found to be a risk factor for piglet knee abrasions (Norring et al., 2006), which are both a direct welfare problem and a risk factor for pathogen entry to the body. Low birth weight has also been found to have a negative impact on bone development (Romano et al., 2009).

Splayleg has been suggested to occur as a myopathy associated with a poor intrauterine environment (Holl and Johnson, 2005) or as a consequence of a reduced gestation length (Sellier et al., 1999), and both of these could be affected by litter size. Splayleg is the most common birth defect seen in pig production (Partlow et al., 1993). Large litter size and lower birth weight are associated with increased prevalence of splay-leg (Sellier and Ollivier, 1982; Vogt et al., 1984; VanDerHeyde et al 1989; Holl and Johnson, 2005). Holl and Johnson (2005) found that the odds of splayleg occurring increased with decreasing piglet birth weight. VanDerHeyde et al (1989) found that 6.7% of litters of 8 piglets or smaller were affected by splayleg whilst 21.1% of litters above this cut-off where affected. However, it should be noted that levels this high are not seen in current commercial production in Denmark (Personal communication: Moustsen, PRC).

4.6 Sex ratio effects

Some studies have shown a relationship between litter size and litter sex ratio. Large litter sizes have been associated with a reduced proportion of male piglets (Górecki, 2003; Tse et al., 2008). Servanty et al (2007) also found that sex ratio varied with litter size in wild boar; with a male bias in small litters and a female bias in large litters. However, another study of wild boar litters failed to find any association between litter size and sex ratio (Fernández-Llario et al., 1999), and we have been unable to find any relationship in large datasets of domestic pigs available to us (SAC, unpublished data). If the suggested association between litter size and sex ratio holds true, this could have a number of impacts, either positive or negative, on later welfare and productivity. One possible benefit is that a lower proportion of males born will mean less piglets being castrated, with associated benefits to welfare of minimising pain, the risk of infection and other welfare impacts of castration (Prunier et al.,

2006). Penny and Hill (1974) found that castrated males were more likely to be the victim of tail-biting than females (as assessed through degree of tail inflammation at slaughter). Some studies have also found an increased disease prevalence in castrated males compared to females or uncastrated males (deKruif and Welling, 1988), A more female biased population could also result in less mounting behaviour, which is mainly performed by males and has a variety of possible negative impacts on pig welfare (e.g. stress, but also possible increased risk of lameness etc). However, the impact of having fewer males in a population on mounting levels is unknown (for instance if mounting is performed by the most dominant boars in a group then having fewer males may have no overall impact). Male biased mortality has been observed (Baxter et al., In Prep.) and the incidence of splayleg is substantially higher in male piglets compared to females (Sellier and Ollivier, 1982; Holl and Johnson, 2005).

4.7 Management responses to large litter sizes

Where an individual litter reaches a size where the sow is unlikely to be able to successfully rear all the piglets (i.e. viable piglets outnumber functional teats), there are a number of management options that the stockperson can take and a number of possible consequences for the maternal or nurse sow(s) (see section 5.4), nurse and for the piglets.

4.7.1 Tooth reduction

Piglets are equipped by evolution for fighting with their littermates for access to teats, having sharp needle teeth protruding at an angle from the jaw (Fraser and Thompson, 1991). Fights between piglets result in lesions to piglet faces although these are not usually severe enough to impact on piglet growth or survival (Brown et al., 1996) and to the sow's udder (Weary and Fraser, 1999). To reduce facial lesions on piglets and sow udder damage, full or selective clipping of some piglets within a litter can be used as a management tool (Weary and Fraser, 1999).

In countries such as Denmark where selection for litter size has advanced the most the use of teeth reduction may actually be reduced since in most cases more advanced management practices are required as routine. Indeed, tooth clipping is prohibited in Denmark and the grinding of corner teeth is only permitted if there previously have been problems. However, in other countries one consequence of the move from medium to large litters is an increase in the use of some form of tooth reduction to minimise the damage that piglets inflict upon each other or the sow when competing for a teat. With increasing litter size, and a finite number of functional teats teat disputes are likely to intensify. Fraser (1975) and Hutter et al. (1993) identified relationships between facial wounding and litter size. They noted that when teeth were left intact, piglets from large litters (>11 piglets) were more likely

to be severely injured. EU legislation permits tooth resection by either tooth clipping or grinding (Directive, 2001/93/EC), but it discourages it and only allows the practice where "there is evidence that injuries to sows' teats or to other pigs' ears or tails have occurred". This stance is taken because there is evidence that tooth resection is in itself behaviourally and physically damaging. There are two main methods to resect the needle teeth; i) clipping to removing all or just the pointed tip of the teeth (Weary and Fraser, 1999) and ii) grinding using a rotating grindstone. Both methods involve restraint of the piglet and in systems where the sow is loose, a commonly practiced observation is to restrict the vocal cords of the piglets whilst clipping in order to reduce distress vocalisations and reduce the chances of the sow becoming aggressive (Personal communication: Baxter, SAC). Handling piglets is a known stressor and plasma cortisol concentration increases with restraint duration (Rosochacki et al., 2000). For tooth grinding the heat generated by the grinder may be a concern. Using a thermal imaging camera, Baxter et al. (unpublished observations) demonstrated that a tooth ground for 3 seconds rose to 45°C, and after 6 seconds the tooth reached 83°C. Opinion is divided in the literature on how grinding or clipping compare, to each other, in their impact on animal welfare (see Marchant-Forde et al., 2009 for a discussion). Tooth clipping also has significant welfare implications. Although physiological assessment of stress parameters suggest the impact is not as great as castration or tail-docking (Prunier et al., 2005; Marchant-Forde et al., 2009), the procedure is stressful (Marchant-Forde et al., 2009) and there is substantial likelihood of pain associated with the procedure (Hay et al., 2004) Incorrect clipping can lead to deep wounds of the tongue and lips (Burger, 1983; Bruckner, 1986) and splinters caused by clipping may become embedded in the gums (Hutter et al., 1993). Thus there is a risk of infection, reduced milk intake and therefore reduced weight gains. The evidence for an effect of clipping on weight gain may depend on the stage of lactation: a decrease in weight gain of piglets with clipped teeth is seen in early lactation (Robert et al., 1995, Weary and Fraser, 1999), while those of piglets with intact teeth may be decreased in late lactation (Hutter et al., 1993).

4.7.2 Cross-fostering

A common management practice to deal with large litter sizes and heterogeneous litters is to cross-foster. Cross fostering can be limited, if only a few extra piglets are fostered, or extensive, if all sows are expected to have the same number of piglets. Transfer of piglets between litters is usually carried out when a sow is producing insufficient milk (for example due to illness), or where a sow has a large litter (especially when there are more piglets than functional teats). If done correctly cross-fostering gives piglets enhanced survival prospects (Cecchinato et al., 2008) and could reduce further management interventions for piglets that

are suffering from remaining in a large litter or those low birth weight piglets that are failing to compete for a productive teat with their larger littermates.

Cross fostering can be performed with a number of aims, at different times after birth, or involving different strategies: i) litter standardisation to achieve even litter size; ii) litter equalisation to achieve piglets of the same size within each litter; iii) sorting piglets into same sex litters; iv) transferring unthrifty piglets to a new litter; v) keeping back small piglets at weaning; vi) collecting surplus piglets at nurse sows (section 4.7.3).

i) Litter standardisation to achieve even litter size. This management tool is used in most commercial productions (Straw et al., 1998). It includes transferring piglets between sows to achieve the same litter size at all sows, or to achieve a desired litter size at some sows. This gives all piglets the same chance to have access to a teat, despite being born in a small or a large litter. One additional factor to this strategy is that with high litter size, nurse sows (see 4.7.3) may be included, to ensure enough functional teats for all piglets. At the other end of the spectrum with low litter size "skip-a-sow"-strategies may be used, where old sows and/or sows having farrowed few piglets are culled immediately after farrowing, after the new born piglets have been transferred to other sows (Personal communication: Tom Gilesby, Renselaer Veterinary Practice).

ii) Litter equalisation to achieve piglets of the same size within each litter. This strategy is widely used in pig production irrespective of litter size (Straw et al., 1998). Normally this includes transfer of more piglets than the previous mentioned "litter standardisation". Performing "litter standardisation" will often involve transfer of the smallest or largest piglets born thus may partially be a form of equalisation.

iii) Sorting piglets into same sex litters. Sorting piglets into litters of the same sex is commonly practiced in some countries such as Brazil (Personal communication: Thorup, PRC) to improve efficiency of certain tasks, such as castration and to save time at weaning when the sexes may be split to allow different feeding strategies for gilts and boars.

iv) Transferring unthrifty piglets to other litters. As more piglets at the sow will increase the risk for some piglets falling behind, higher litter size may facilitate the use of this technique (Thorup 2010b). One unthrifty piglet can be exchanged with a thrifty piglet in another litter ("swapping"). This will increase the chances of survival for the unthrifty piglet, but can reduce growth rate in both piglets (Straw et al., 1998). In the case of more unthrifty piglets, a litter of unthrifty piglets may be transferred to a sow, that early weans her own piglets (nurse sow), or to some form of artificial nursing system, such as a Nurtinger. In the case of these latter

strategies there may be some controversy as these piglets are effectively being early weaned before the stipulated age (26 days). However it can be argued that this is “first-aid” for a challenged piglet that might otherwise die. Very little research has been conducted into the health and welfare issues for animals artificially reared (see section 4.7.5).

v) Keeping back surplus piglets at weaning. Piglets vary in size at birth, and as the largest piglets at birth grow faster than their smaller litter mates this difference increases during lactation. Additionally, disease and differences in sow milk production may increase both the proportion of small piglets and increase the differences. Being small at weaning can thus either be an indicator of being born small, or of being a challenged piglet. Farmers are often conscious of issues relating to poor health in small weaned piglets so they often aim to wean even batches of piglets. As a consequence, if there is not a focussed strategy for segregated weaning procedures, small piglets may be held back until they achieve a higher weight. This normally involves collecting small piglets and putting them on a sow that should have been weaned.

There are various possible welfare concerns relating to these different reasons why piglets may be moved from their birth litter to a different grouping. In general challenges to welfare become greater as the piglets get older, which means that the earlier fostering takes place the more likely it is to be successful (Straw et al., 1998). Very early moves to a new litter may deprive the piglet of access to colostrum, which is important to achieve maternal immunity (Bandrick et al., 2011), thermoregulation and energy (Herpin et al., 2002). Late transfer will challenge the piglets by introducing them into litters where the rank, teat order and maternal bonds are already fixed. The transfer window is generally recommended to be only after the piglet suckles from its own mother to ingest colostrum for 6 to 12 hours (Thorup et al., 2004) and not after 2 days post-partum, where the ranking process has been relatively fixed (De Passilé et al., 1988). *Ad libitum* availability of colostrum only occurs for the first 12h after the onset of farrowing when it is let down continuously, thereafter it is available for approximately 30 hours during cyclical let downs. Piglets need to ingest colostrum as soon as possible, to acquire maternal immunoglobulins, nutrients and sustenance for adequate thermoregulation. Gut closure takes place between 24-48h old and after that immunoglobulins can no longer be absorbed (Gaskin and Kelley, 1995). If piglets are fostered without gaining sufficient colostrum they risk compromised immunity, chilling and starvation. If they are fostered onto a sow that is still producing colostrum these risks are significantly reduced and acceptance of fostered piglets is greater. It is, however, likely that even if they have six hours with their mother suckling before being transferred to a foster

mother that they will become hungry and cold during the transition period and this will influence their initial behaviours with their foster mother.

An advantage of fostering at 6 hours old is that piglet behaviours will be less risky in terms of acceptance by the nurse sow because they are unlikely to have bonded sufficiently with their mother before separation. Price and others (1994) showed that piglets fostered within 9 hours of being born showed similar behaviours to resident piglets and aggression or sniffs towards them by the sow were no different to behaviours directed towards her own piglets. However piglets fostered after 2 days of age showed a greater reluctance to engage in suckling, higher rates of ambulation, and more frequent vocalisations. Additionally, sows tended to be more aggressive toward older fostered pigs. Similarly, Straw et al. (1998) reported higher pre-weaning mortality in piglets fostered over 3 days old.

Piglets are able to recognise the odours, vocalisations, and home pen of their dam and prefer to approach these cues rather than those of an unfamiliar sow (Morrow-Tesch and McGlone, 1990; Horrell and Hodgson, 1992b). As such, fostered piglets are likely to experience stress when removed from their sow and pen (similar to the experience of a weaned piglet). Not only do newborn piglets form quick bonds with their mother, they also establish fidelity for a particular teat, or a specific teat pair (Pedersen et al., 2011) during the first 24 hours of life, often defending ownership of this teat aggressively during nursings. When foster piglets realise that they cannot reach their own dam, they go to the udder and seek out the teat in their previously preferred position (which may involve competing with the incumbent piglet for it) rather than identifying an unused, productive teat and establish a new place in the teat order (Horrell, 1982). This can lead to disruption of the teat order and aggression between piglets over teats, resulting in facial injuries to piglets, and fostered piglets do not grow as well as resident piglets (Horrell and Bennett, 1981). Although Kirkwood and colleagues (1998) found no effect on weight gain and pre-weaning mortality for cross-fostered piglets. Piglets that are not growing well may put themselves at greater risk of crushing by spending longer at the udder (Weary et al., 1996). The sow is more likely to terminate a suckling bout (to the detriment of all piglets), in response to piglet screams, which are likely to occur during teat order disruption (Horrell, 1982, Appleby et al., 1999; Pedersen et al., 2011). Thus if piglets are fostered after these bonds become established, they show behaviours indicative of separation distress. When separated from their mother, piglets perform high pitch vocalisations, with younger piglets often “quacking” (Weary et al., 1999) and during fostering, fostered piglets are observed to “wander the pen” performing these vocalisations (Horrell and Bennett, 1981) and often failing to suckle initially or fighting over a preferred teat in order to re-establish teat fidelity.

Depending on the age at fostering, foster piglets may face aggression from the existing litter away from the teats, as piglets are capable of recognising their littermates by

around 7 days of age (Horrell and Hodgson, 1992b) and will fight with non-littermates at this age (Jensen, 1994; D'Eath, 2005). Foster piglets also risk aggression from the sow as sows are capable of discriminating between their own piglets and foreign ones by odour at about 7 days of age (Horrell and Hodgson, 1992a), and sows selectively show aggression towards fostered piglets, which may try to escape the new pen (Horrell 1982). Some farm managers will repeatedly cross-foster piglets and move them from sow to sow in order to manage growth rates for weaning. However such practices are very disruptive for both the sow and piglets and have been reported as injurious and counter-productive with repeatedly cross-fostered piglets failing to suckle and acquiring facial lacerations and showing no improvement in weaning weights (Robert and Martineau, 2001).

With litter equalisation, producers expect the even piglets to thrive better, as small piglets are not inferior to larger litter mates. However it has been argued, that fighting may be increased in equalised litters, as piglets that are even in weight may have difficulties establishing a stable social hierarchy. Indeed, Milligan and co-workers (2001b) found that piglets fought more when cross-fostered into new groups with piglets closer to their own size than they did when moved to groups with much larger piglets. However, Deen and Bilkei (2004) found that in litters of 12 piglets low birth weight piglets spent more time in teat disputes when littermates were larger, and as a consequence missed more nursing opportunities. This was not the case in litters of 8 piglets.

The long-term impact of cross-fostering is uncertain. Stewart and Diekman (1989) found that gilts reared by foster dams had lower reproductive success in their first parity (poorer conception and farrowing rates and fewer live born piglets). As mentioned earlier Moinard and others (2003) found that farms where cross-fostering was practiced had a higher incidence of tail biting. Although the causal relationships underlying these effects are uncertain such studies do suggest that a closer look at the short- and long-term impact of cross-fostering on piglet behaviour, production and welfare is merited.

4.7.3 Nurse sow systems

One practical consequence of increased litter size is the increased use of wet nurse sows. A nurse sow weans her own piglets, and then has 12 to 15 functional glands available for a new litter of piglets. According to EU legislation, piglets cannot be weaned until 28 days after birth, unless there is a risk for health problems for sow or piglets. Piglets can be weaned at 21 days, if they are weaned to cleaned sections, where they are not mixed to older animals. The use of nurse sows, as a solution to the challenges of large litters is now close to ubiquitous in Denmark but has yet to be widely used in other countries.

There are two main types of management processes that involve using nurse sows; one-step and two-step. One-step management involves weaning at least 21 day old piglets

from a “chosen” nurse sow and then fostering on surplus piglets from newly farrowed sows when the piglets are at least 12 hours old. The nurse sow then rears this second litter to at least 21 days of age when they are weaned and she returns to a dry sow facility for service. Two-step management involves the use of two lactating sows. An intermediate sow is identified and her litter is weaned at 28 days old (potentially at least 21 days old) and then a two-step nurse sow is identified whose piglets are 4-7 days old. These piglets are all fostered onto the intermediate sow. The two-step sow is then given surplus, large newly farrowed piglets that are at least 12 hours old to ensure they have received enough colostrum from their natural mother to acquire maternal antibodies (Thorup et al., 2006).

The welfare implications for the sow are described below. The welfare implications for the piglets are likely to be similar to those experienced by cross-fostered piglets (see 4.7.2 above) and also piglets that experience early weaning (discussed below in 4.7.4). The separation distress and aggression involved in re-establishing teat order may be less in one-step or two-step nurse sow management than in cross fostering because the whole litter is fostered on and off or because the young piglets have yet to form a teat order or bond to their mother. The main welfare detriment experienced by piglets during nurse-sow management is the risk that the 6 hour old fostered piglets suffer starvation and chilling whilst they wait for their foster mother to accept them. Successful sucklings can take 6 hours after piglets are given to the nurse sow (Thorup and Sorensen, 2006). This may result in the piglets becoming frantic for milk.

Weaning can be a traumatic event, particularly for piglets as it involves changes in diet and in the social and physical environments (Fraser et al., 1997). Recently attention has also been drawn to the possible psychological and long-term consequences of early weaning (Newberry and Swanson, 2008; Weary et al., 2008). Although in this fostering scenario, piglets are not being weaned onto solids, they are being weaned onto a strange sow and potentially into an unfamiliar farrowing crate (albeit often one similar to their previous accommodation). Thus still a potentially stressful situation. When separated from their mother, piglets perform high pitch vocalisations, with younger piglets often “quacking” (Weary et al., 1999). Such vocalisations are also reported when fostering occurs, with the fostered piglets observed to walk around the pen periphery performing these vocalisations (‘wandering-squealing syndrome’: Horrell, 1982) and often failing to suckle initially or fighting over a preferred teat in order to re-establish teat fidelity.

4.7.4 Weaning age

Weaning can be thought of as the withdrawal of maternal care and of the milk supply. Litter size might affect weaning age in two (opposing) ways depending on management decisions. If larger litter size requires more nurse sows, then fewer pens are available for farrowings.

This can be solved by having fewer sows farrowing per day, which can be achieved by reducing the number of sows, increasing the number of available farrowing pens or by weaning earlier. Alternatively since high litter size at the sow will reduce growth rate, when piglets are being weaned at a fixed weight, piglets often need to be weaned later. Late weaning can be negative for sow welfare as discussed with respect to the use of nurse sows and prolonged lactation (see section 5.4). The former issues regarding early weaning have also partially been discussed in relation to nurse sows, as some form of early weaning is a necessary component of nurse sow systems.

Arguably, the artificial weaning which is practiced universally by the pig industry is 'early', since under natural, free-ranging conditions the age by which piglets are fully weaned is around 60-137 days (Newberry and Wood-Gush, 1985; Jensen and Recen, 1989). Although part of pre-industrial agriculture, such practices are obsolete and common practice in the EU is to wean at 28 days of age. Organic herds often wean at 40 days old, and in Denmark at 49 days at least, however the sows are loose and it is likely that a natural weaning process has already begun in animals kept in this way (since the sow has more control). Some extreme early weaning strategies remove piglets between 7-14 days and are still practiced in the USA. These strategies were initially introduced to control diseases amongst finishers. However, there are well reported performance disadvantages of such early weaning management systems including; inconsistent growth performance throughout the finishing phase (Wiseman et al., 1995), decreased post weaning weight gain (Leibbrandt et al., 1975) and abnormal feed intake that may affect metabolism (Pittaway and Brown, 1974). In addition, there are increases in aberrant behaviours such as belly nosing and flank biting, which can be important indicators of stress (Fraser, 1978; Metz and Gonyou, 1990; Bøe, 1993; Gonyou et al., 1998).

Many of the welfare challenges of early weaning are because it is abrupt, with no introduction of solid food and no gradual separation from the mother. Abrupt weaning involves a complete change in both the form and pattern of delivery of food, requiring both behavioural and physiological adaptations by the piglet. If supplementary food is available from at least the third week of lactation, when milk production starts to decline, expression of foraging behaviour has functional consequences for changes in gastric enzyme secretions and gut development (Cranwell, 1995), allowing the piglet to experience a more gradual weaning process. If weaned before three weeks of age such adaptations are unlikely to occur and abrupt weaning causes nutritional challenges for the young, can slow growth rate and compromise immune function (Algers, 1984; Pajor et al., 1999). There is concern that animals exposed to maternal deprivation during the neonatal period could show an altered response to stress during adolescence (e.g., Liu et al., 1997; Lay et al., 1998). Hohenshell et al. (2000) found altered hypothalamic-pituitary-adrenal (HPA) axis activity in early weaned

pigs. The specific cause of this is unclear, as early weaned piglets are being subjected to maternal deprivation, as well as a location and nutritional change. Work looking at the behavioural consequences in female pigs of being weaned at three different ages (12, 21 and 42 days) demonstrated that although the early weaned pigs showed behavioural inhibition in an open field test, the impact on their brain neurobiology could not be unambiguously interpreted as dysfunction (Sumner et al. 2008). Both papers suggest further investigation is needed.

A further potential longer term consequence of early weaning is the possible influence removal from the mother might have on the maternal behaviour of female offspring that go on to be breeding gilts. Young animals learn key behaviours during the neonatal period and maternal behaviour can be transmitted from one generation to the next (for instance through non-genomic transfer: Francis et al., 1999; Champagne and Curley, 2009). In mice, early weaning deprives mouse pups of maternal care, increases their anxiety and decreases their maternal behaviour as adults (Kikusui et al., 2005). Also in this study of mice, other changes in neonatal environment, including handling and changes in feeding competition altered adult behaviour. It is unknown whether similar effects would be seen in pigs, where maternal care is substantially different to rodent species, however there may be long-term consequences of early weaning and/or management procedures which alter the neonatal environment.

4.7.5 The use of artificial rearing systems

An alternative management strategy to nurse sows for rearing surplus piglets is to use an artificial system. One such system widely used in the Netherlands, the USA and increasingly in Germany is the Rescue Deck system. This is a specially designed unit that is recommended to sit above the farrowing crates in traditional farrowing houses and to house either surplus or low viability piglets. The decks are fully slatted, heated and lit and have artificial milk, water and, when piglets are older, a creep feeding system. Piglets are typically housed there from 3-20 days old and often this system does indeed “rescue” piglets that would otherwise die. One of the welfare and ethical issues is whether some of these piglets should be kept alive. With traditional fostering the recommendation is to move the larger piglets onto foster sows and leave the weaker piglets with their mother, thus limiting stressors on a vulnerable animal. There is very little scientific evidence as to the pros and cons of rescue decks. Reports suggest that piglets reared in rescue decks have poorer growth rates and work looking at long-term impacts on performance suggest rescue deck piglets take a longer time to reach slaughter weight and have poorer average daily gain (Futterkamp, 2011). Other reports suggest they do save piglet lives but question the effects on long-term health and behaviour (Müller, 2011). Piglets removed from their mother as

early as 3 days old will inevitably be subjected to the same welfare detriments that any early weaned piglet would be, as already described above. Such systems are likely to require very careful management. One German study on growth rate, demonstrated that artificially reared piglets were 2 kg lighter at 22 days compared with piglets reared by sows (Tolle and Meyer 2008).

5. Welfare impacts of large litter size on the sow

SUMMARY:

From the sow's perspective increasing litter size may impair welfare

- Increased production pressure placed on sows may produce health and welfare concerns if the sow does not receive appropriate levels of management.
- The extent to which the experience of farrowing is affected by litter size requires further research
- Longer farrowing durations associated with larger litters may be more painful for sows.
- Sows may also experience more discomfort during farrowings that involve passing dead piglets.

5.1 Gestation

Although numerous studies have addressed welfare issues surrounding the housing and husbandry of gestating sows (e.g. Marchant-Forde, 2009), these have not focused on issues specifically to do with the fact that the animals concerned are pregnant. Furthermore they have not given any consideration as to whether the fetal litter size being borne has any impact on sow welfare. However, when we consider the process of pregnancy and birth in women, society expects that these women should be cared for and given extra special treatment. This is particularly the case if the woman is carrying twins or more babies as there is a feeling that this is a more difficult pregnancy with a greater energetic demand, and also the fear that any insult to the mother has potentially greater effects in terms of the number of lives involved and the greater fragility of the fetuses. Pregnant sows also have many challenges to face, which include the energetic demands and nutrient requirements of her growing fetuses, hormonal changes, the effects on sleep and rest and the general discomfort and restriction of movement. In addition, within commercial farming systems there are additional challenges such as group dynamics, access to resources and resting areas and of course the issue of feed quantity and delivery. Increased metabolic loading on sows during pregnancy could also increase the risk of heat stress in countries where this is an issue.

Some of the common complaints in pregnant women are nausea, sleep disturbance, pain and discomfort, constipation and heartburn. These complaints are often reported to be exacerbated in women carrying multiple offspring (Campbell, 2001). These symptoms have rarely been considered in pregnant farmed animals and given the pressure to increase maternal output (either by size and/or number of offspring) we should consider the impact of these symptoms on pregnant farmed animal welfare. Nausea is reported to be greater in

twin pregnancies than singletons (Louik et al., 2006). Hormonal effects of pregnancy may be exacerbated due to increased number of fetuses.

For much of the pregnancy the developing litter takes up only a small proportion of the mother's nutrient supply (Whittemore, 1998), and the litter is relatively well protected from nutritional decreases (Pluske, 1995). However, sows may still feel increased hunger motivation when carrying a larger litter (due to physical and hormonal signals of litter size) which could make the feed restriction experienced through gestation more distressing. However, the difference (from the sow's perspective) of a small, large or very large litter may only be really meaningful in late gestation when sows naturally shift towards a catabolic physiology. It might also be speculated that if modern hyper-prolific sows are fed more to meet the demands of their developing litter that they could be less chronically hungry.

Any discomfort as a result of pressure on the stomach or other organs from the uterus is also unclear. Sow size has increased (Moustsen et al., 2011) in recent years and in association with the carrying of very large litters this could create issues relating to access to resources such as drinkers and feeders. Any issues relating to physical comfort during resting and sleeping are unknown. Although piglets represent a much smaller percentage of maternal birth weight compared to other species, the overall ratio of litter weight to maternal weight in pigs is equivalent to other domesticated species bearing smaller litters (7-9%: sheep: Gardner et al., 2007; dairy cattle, Personal communication: Barrier, SAC). Since gilt and sow weight at farrowing has increased in Danish sows, in recent years in order to remedy problems relating to shoulder sores etc, it is unlikely that increased litter size will have led to a significantly increased fetal: maternal weight ratio. Women bearing twins often report that, especially in late pregnancy, they have difficulty achieving comfort in any body position and back and abdominal pain are common (Campbell, 2001), although such concerns differ between quadruped and bipedal species. Although Danish research suggests late stage pregnancy sows are often dominant in social groups (Hansen et al., 2009), size and discomfort could also impact on social behaviour if for instance sows carrying large litters have a poorer ability to move, and so are unable to gain access to resources, defend sleeping areas etc. Equally, an increased requirement for rest when pregnant with a large litter might not be fully satisfied in large sow groups, or where space allowance is restricted. Sows have been shown to be only weakly motivated to obtain social contact in preference tests (Kirkden and Pajor, 2006), but the impact, if any, of their fetal litter size, on motivational priorities (e.g. for environmental comfort, social circumstance, food etc) remains unknown. Beyond purely physical effects of litter size on gestation behaviour there may be theoretical reasons for thinking that large litters could cause sows to behave differently. In mice, litter size during pregnancy has been shown to impact upon behavioural characteristics of the mother: both maternal aggressiveness and anxiety increased with

increasing litter size (D'Amato et al., 2006). The authors hypothesised that, based on hormonal signals, mothers are able to evaluate the reproductive value of their unborn litter and adjust behaviour accordingly (i.e. by being more protective of a larger litter). Rodent studies have shown that, following birth, aggression towards a nest intruder is also increased in mothers with larger litters (Maestripieri and Alleva, 1990; Koskela et al., 2000).

In humans multiple pregnancies require a greater cardiovascular workload (Nizard and Arabin, 2005), which could also be reflected in sows bearing large litters. Hypertension and associated complications are more common in human multiple pregnancies and increase in incidence with increasing number of fetuses (Smith-Levitin and Vohra, 2005). Up to 25% of multiple pregnancies in women are complicated by hypertension (Long and Oats, 1987). Pre-eclampsia has a 3 fold higher risk in twin pregnancies than singletons, and triplets have a 3 fold higher risk then twins (Duckitt and Harrington, 2005). Constipation is reported as being worse in women bearing multiple fetuses (Campbell, 2001). In pigs the level of constipation has been associated with farrowing duration (Oliviero et al., 2010), so any additional constipation induced by a large litter size could exacerbate the litter size effect on farrowing duration. However, allowing the sow to move freely before and during farrowing, reducing constipation in the sow and avoiding excessive fattening of the sow during late gestation all seemed to be key factors in shortening the sow's farrowing time, and thus reducing perinatal mortality (Oliviero, 2010). Haemorrhage and urinary tract infections are more common post-natally in women carrying multiple fetuses (Carlin and Neilson, 2006).

Whilst it is clear that there are limits to how far we can attempt to extrapolate the experiences of human mothers to those of pregnant sows (especially since twins or triplets represents a far greater increase in fetal load than the difference between say a large and very large litter of piglets), it is equally clear that a number of possible welfare detriments of bearing more fetuses are suggested by this comparison. Further research could be focussed on assessing the welfare impact (and altered gestation needs) associated with large litter sizes.

5.2 Parturition

Giving birth, from human experience, is reported to be an extremely painful process (Melzack, 1992) and research has resulted in numerous different analgesic and anaesthetic drugs administered via various routes to alleviate pain (Brownridge, 1991). The pain experienced by non-human animals during parturition has received little scientific interest; however the research carried out on non-human animals has provided information about the anatomy and neural input to the uterus and cervix. Studies of the intrinsic nerve supply of the uterus indicate that sensory fibres are more numerous in the cervix and the lower uterine

segment than the main body of the uterus (Bonica, 1986). Neural supply to the uterus and cervix is mainly via the hypogastric and pelvic nerves which enter the spinal cord through dorsal roots predominantly in the lumbar region (Steinman et al., 1992; Berkley et al., 1993). Labour pain is initiated in the uterus due to dilation of the cervix and contraction of the lower uterine segment and there is a correlation between the degree of dilation of these structures to the intensity of pain experienced by humans (Bonica, 1986). There is also a correlation between the onset of uterine contractions and the onset of pain (Corli et al., 1986). Endogenous opioids are released in response to nociception, and have potent analgesic properties (Dalayeun et al., 1993). Studies have shown that an endogenous opioid-mediated analgesic system exists in parturient rats (Gintzler, 1980; Sander and Gintzler, 1987). Hypogastric neurectomy results in reduced analgesia suggesting that stimulation from the lower uterine segment and cervix induces this analgesic system (Gintzler et al 1983). This pregnancy-induced analgesia has since been shown to exist in parturient women (Cogan and Spinatto, 1986; Whipple et al., 1990) and in the pig (Jarvis et al., 1997). Opioid-mediated analgesia at parturition may act as a defence against the pain of labour but increased release of opioids in response to nociception may also interfere with parturition and maternal behaviour by the inhibition of oxytocin (Lawrence et al., 1992). This could be applicable to domesticated animals as the increase in the size or number of offspring could cause increased release of opioids in response to nociception and thus impact on maternal-offspring bonding.

As litter size increases, average piglet birth weight decreases (Johnson et al., 1999; Roehe, 1999). This may reduce pain at expulsion of each fetus but parturition may last longer and the cumulative effects may be greater. Evidence from human research suggests that the aversiveness of a painful experience relates more to how bad the experience was at its worst and at its end point (peak-end effects: Kahneman et al., 1993). This may suggest that duration of farrowing is not the most pertinent variable in determining the overall severity of the experience. However, if longer farrowing durations are associated with greater inflammation or tissue damage to the sow, post-farrowing pain could be an issue. Pain experienced by the sow during farrowing is of obvious welfare concern in its own right, but may have several additional consequences. Anecdotal reports suggest that pain may be involved in the aetiology of savaging (White, 2008) and could also have an impact on other aspects of poor mothering, such as likelihood of crushing (Haussmann et al., 1999), as sow discomfort is associated with increased postural changes (Mainau et al., 2010). In humans pain at childbirth is associated with later physical and psychological health outcomes. For instance, the experience of increased acute pain associated with giving birth increased the likelihood of later experiences of both pain and postpartum depression (Eisenach et al., 2008). Mainau and co-workers (2010) produced a behavioural ‘ease of farrowing score’

(EFS) based on multivariate analysis of multiple behavioural measures. Sows passing stillborn or mummified piglets were found to have a lower EFS possibly indicating that they experienced more discomfort during farrowing when passing dead piglets. Colostrum yield was also found to be negatively related to the proportion of stillborn piglets (Quesnel, 2011). Larger litter size and more stillborn piglets were both associated with longer farrowings durations (VanDijk et al., 2005).

It is unclear whether larger litters of on average smaller piglets would produce more direct tissue damage to a sow than smaller litters of larger piglets. Greater tissue damage, if associated with larger litter (and this is undetermined) may provide a route for the entry and spread of infection. Sickness behaviour (Weary et al., 2009; Dantzer, 2009) associated with infection could be a significant risk both to sow welfare and the welfare of her piglets. Even sub-clinical infections can impact on behavioural function, for instance depressing activity or inducing fear/anxiety (Lyte et al., 1998). Difficult or extended farrowings may also cause other welfare detriments relating to increased fear levels, generally and increased levels of fear expressed towards offspring piglets. This may be particularly true in gilts where increased restlessness and responsiveness to piglets at farrowing is predictive of piglet-directed aggression (Ahlström et al., 2002).

In the above section the parturition process and its impacts on the sow in terms of pain have been described. In addition to this pain, the sow could experience uterine and maternal fatigue, which can lead to dystocia, otherwise described as a difficult farrowing (Lay et al., 2002) or the cessation of farrowing. Uterine fatigue or secondary uterine inertia means the uterus ceases to perform meaningful contractions and this can affect the piglets with increased risk of asphyxia and stillbirth. Maternal exhaustion refers to the inability to sufficiently increase intrauterine pressure by contractions of the abdominal muscles and diaphragm. This inability may not only be affected by the sow's physiological state but perhaps also by her perception of effort and exhaustion (van Kempen, 2007). Serious health complications may arise in the sow from exhaustion during labour. These include retention of placenta and piglets, hypocalcaemia, hypomagnesaemia, metritis, and ketosis. This can result in health complications that require attention during parturition (e.g. assistance to pass the last piglets either manually and/or medically with intra-muscular injections (sometimes administered into the vulva) of a drug such as Oxytocin to restart contractions) or after parturition (e.g., hypocalcemia). Oxytocin has the potential to actually increase the risk of stillbirth and may cause additional stress for the sow, and thus be counter-productive (Mota-Rojas et al., 2002; 2005; 2006). It can produce uterine spasm rather than rhythmical contractions resulting in premature umbilical occlusion or rupturing, thus increased asphyxia and stillbirth.

The birth process is energetically demanding and increasing litter size has the potential to increase those energy demands, particularly if it causes prolonged parturition and the complications described above. If sows are exhausted they may refuse food and water, which could lead to further complications such as agalactia, which again impacts on both sow and piglets, with a failure to let down milk requiring further interventions and the potential to impact on future longevity. However, small piglets may be expelled more easily, which could reduce some of the impacts on the sow.

Barrier and Haskell (submitted) found evidence that dairy cows that experienced a difficult calving where more likely to experience calving problems at subsequent calvings (although not in sheep, Dwyer and Lawrence, 2005), and also had impaired fertility. In dairy cows, dystocia also reduces milk yield, increases the risk of mastitis and increases the chances that a cow will be culled (Tenhagen et al., 1999; Rajala and Grohn, 1998).

5.3. Lactation and post-weaning

Raising a large litter not only has immediate welfare impacts for the sow during lactation, but could also have longer term impacts on her health, behaviour and ultimate longevity in the herd.

5.3.1 Sow health

During the immediate post-parturient phase, before any management interventions such as fostering might relieve the pressure of a large litter, the sow will be required to nurse her newborns. During farrowing, colostrum is let down continuously for approximately 12 hours before cyclical let-down starts, with colostrum and milk delivery approximately every 20 minutes. Colostrum production is highly variable between sows (LeDividich et al., 2005), but colostrum quantity does not increase with increasing litter size (Devillers et al., 2007; Quesnel, 2011), resulting in piglets in larger litters having on average less colostrum each. However, there is some uncertainty about what level of colostrum intake can be considered enough. As cyclical let down starts, competition for teats becomes apparent. Disputes at the udder will influence maternal behaviour (by causing discomfort: Fraser 1975), but could also influence maternal health. Piglets are born with their deciduous canines and third incisors or “needle teeth” fully erupted and angled in such a way that the biting actions piglets use to displace siblings from teats can result in serious facial lacerations (Fraser, 1975; Drake et al., 2008) and teat damage. Such damage to the udder could lead to infection; causing mastitis which if not treated could result in culling. Gerjets and Kemper (2009) quote a German study where litter size and farrowing duration where both found to be risk factors for the occurrence of sow infections in the peri-parturient period (Bostedt et al., 1998). Teat damage and infection are likely causes of this but interrupted sucklings may affect udder

health as teat disputes cause the sow to terminate milk let-down before completion, resulting in inadequate drainage from the teats and the potential of a distended udder, as is seen in newly weaned sows.

During parturition, lactation starts and the sow's metabolism changes from an anabolic to a catabolic state, facilitating the mobilisation of fat into milk (Uvnäs-Moberg, 1989). As lactation progresses and the energy demands become more intense sows will further mobilise their body reserves (Quesnel and Prunier, 1995). Milk production plateaus by the third week in lactation, before gradually declining (Elsley, 1971). These demands increase with litter size and if sows cannot maintain a high feed and water intake they will start to lose body condition and may be at greater risk of developing injuries such as shoulder sores. Shoulder ulcers normally develop during the first and second week of lactation in sows that are too lean at farrowing. They start healing during the third and later weeks, when lactation peaks. Shoulder sores result from persistent and constant compression of the blood vessels in the skin around the tuber of the scapular spine resulting in insufficient blood circulation, necrosis, and subsequently ulceration. Sows with a low body condition score are considered more likely to develop shoulder sores because they have less covering or cushioning around the tuber of the spine of the scapula (Zurbrigg, 2006). The force and duration of the pressure, as well as the robustness of the skin are likely to influence the development of ulcers (Herskin et al., 2011). Sows kept in restrictive systems, where posture changes are limited are more at risk of developing such injuries and a recent epidemiological survey conducted by Bonde (2008) on 3831 Danish sows from 98 herds found shoulder ulcers in 17% of lactating sows kept in conventional farrowing systems. In the same study, weaning weight of the litter was shown to significantly contribute to the prevalence of shoulder sores. This latter result could be as a consequence of better nursing by the sow and therefore more lateral recumbency or a result of the energetic demands of raising a larger litter and its subsequent effect on body condition score. However shoulder sores have a multi-factorial aetiology and occur in other countries – such as Sweden – where average litter size is much lower, and lactating sows are loose. The Danish recommendations have changed to increased number of feedings per day, especially in the late part of the lactation period, where herds are feeding 3-8 times a day, both to increase feed uptake and to limit the time the sows spent lying without moving. The issue of shoulder sores has become a matter of concern in Denmark; a large-scale study at Danish abattoirs in 2001 recorded the prevalence of shoulder ulcers (Christensen, 2001). As a consequence, Danish slaughterhouses began to pressurise pork producers to reduce the number of sows delivered to their plants that have or have had shoulder ulcers, and Danish legislation requires that sows with severe shoulder ulcers are destroyed.

5.3.2 Sow rest / irritation

We have already discussed maternal fatigue during parturition, however, particularly in confinement farrowing systems a large litter size will result in a greater frequency of piglet behaviours (nosing, nibbling, exploratory) orientated towards the sow that may interfere with rest or cause irritation (De Passillé and Robert, 1989; Arey and Sancha, 1996). De Passillé and Robert (1989) suggested that since sows use posture changes to stop piglets annoying them, they may experience fewer proper rest periods when litters are large or the farrowing environment is restricted and barren. Whatson and Bertram (1982) suggested that the level of irritation for the sow could be decreased by providing alternative enrichment for the piglets to focus their attention towards. Alternative housing, where the sow can be loose for lactation could reduce irritation by allowing the sow the ability to move away from the litter. Again this would be an issue for large litters maintained on a single sow as compared to small litters. Presumably large litters are no more of a concern because the piglets above the individual sow's maximum capacity would be removed, for fostering or culling.

5.3.3 Sow longevity / burn out

Large litter size has the ability to impact on a sow's longevity in the herd. The physical impacts described in the above section, relating to poor body condition, development of shoulder lesions, lactational oestrus, increased weaning-to-oestrus interval, udder and teat health will all impact on a sow's longevity in the herd. According to available national production statistics sow cull rates have increased over the last 10 years (see Table 4), with sow mortality showing significant increases particularly in North America. Though national statistics for sow cull and mortality rates are not published in Danish annual reports, a recent survey by Fowler (2009), reporting European statistics for 2008, recorded sow mortality in Denmark at 14.5% and sow replacement rate at 53.1%, with the European averages at 5.8% and 44.9% respectively. These high levels of mortality reported in Denmark have resulted in a public concern about sow longevity prompting the initiation of research into management and breeding programmes to improve these figures, with a goal to reducing the level by 25% by 2013. Sow longevity is included in the current Danish selection criterion.

Common reasons for culling include reproductive problems, old age, and udder problems (Stalder et al., 2004; Engblom et al., 2007). Epidemiological studies of sow longevity and the factors that contribute to it often show that low litter size is one of the reasons sows get culled (Abiven et al., 1998; Anil et al., 2008) and conversely that litter size tends to be associated with length of productive life (Serenius and Stalder, 2006, 2007; Hoge and Bates, 2011). However, large litter size could still be an underlying cause in many of the other reasons sows are culled after only a relatively limited number of parities. The period immediately following farrowing is when the highest number of sows die on farms

(Engblom et al., 2007). It is not known whether the frequency of sow on-farm deaths (i.e. non-cull deaths) has increased in association with litter size selection. A recent epidemiological study (Willgert, 2011) found that farm prevalence of sow lameness increased with numbers of piglets produced by sows per year.

Table 4: Changes in sow cull and mortality average and top 10% rates over 10 years for the UK and North America.

	UK*		USA†		Canada†	
	2000	2010	2000	2010	2000	2010
Average mortality (%)	3.9	4.01	6.9	9.48	4.7	9.34
Top 10% sow mortality	3.4	3.43	2.7	4.04	1.5	4.24
Average cull rate (%)	38.1	45.95	44.6	47.48	41.1	42.73

* Data from MLC/BPEX Pig Yearbooks
†Data from PigCHAMP database

5.4 Welfare impact on foster or nurse sows

For a lactating sow the move to being a foster or nurse sow can be a significant transition. There are a number of potential welfare implications for all sows involved in the fostering process. The impact depends on the time in lactation when the transition is performed, how many piglets are involved and how well the management around the transition supports the sow's need for nutrients. During the first days of lactation milk production from specific teats is not dependent on the sow being nursed or not (Theil et al., 2006), nor is the sow bonded to specific piglets (De Passillé et al., 1988). Later in lactation the sow may experience a build up of milk with out being nursed at normal intervals (Thorup and Sørensen, 2006b), and the sow may be relocated to the new batch of piglets to reduce disease transmission in segregated systems (Thorup and Sørensen, 2006a). An extended lactation period will increase the period, where a crated sow is in the crate. If sows are not fed well, extended lactation may reduce backfat level and protein resources in the sow. However, Danish investigations indicate that the sow prospers on the extended lactation period, as lactational oestrous is frequently seen in nurse sows, and as litter size was increased by two piglets in the subsequent litter (Thorup, 2007). Pedersen and others (2010) found no increase in shoulder ulcers in nurse sows.

An immediately obvious welfare consequence (in current systems) for the nurse sow is that her confinement within the crate environment will be extended beyond the normal weaning period. This may raise issues for welfare relating to both the behavioural restriction associated within the crate and also to potential physical damage such as shoulder lesions, already described. However, shoulder lesions are more likely to occur if backfat in P2 is below 15 mm at farrowing (Thorup, 2006). Sows chosen as nurse sows tend to be in good condition so may not develop shoulder ulcers as often as other sows (Pedersen et al., 2010), however this is an area where management – good or poor - has potential impact on sow

welfare. For the one-step and intermediate sows, they are early weaned at the height of lactational output (approximately 21 days: Elsley, 1971) and are then expected to rear another litter for at least 21 or 14 days respectively. For the two-step nurse sow, her natural litter is transferred after 4-7 days after which she rears another litter for at least 21 days leading to a total lactation of at least 25 days. If the intermediate sow's litter is weaned at 21 to 28 days and she rears the two-step sow's litter for another 21 days (if the piglets were 7 days when transferred, 14 days will do), she has the potential for 42 to 49 days in a farrowing crate, not including the pre-farrowing period when she is transferred from dry sow accommodation to the farrowing house. One study of crated sows suggested that by 29 days in a crate, they were beginning to show a higher cortisol/adrenocorticotropin ratio following corticotrophin-releasing hormone injection, suggesting changes in the Hypothalamic Pituitary Adrenal axis indicative of chronic stress (Jarvis et al., 2006a) and assurance schemes such as RSPCA freedom foods in the UK have placed limits on the duration of crate confinement to 28 days because of such concerns. This extensive period of restriction also prolongs lactational output, impacting on body condition (Kim and Easter, 2001; Prunier et al., 2010), with potentially injurious consequences already described. In practice, since nurse sow generally rear a litter of smaller piglets at a high feed intake, they may come onto heat, which suggests they are in an anabolic state since heat during a catabolic state is not expected to occur (Kuller et al., 2007; Kuller, 2008). In addition to the physical and behavioural restrictions imposed, there are also potential impacts because of the parent-offspring conflict regarding lactational output: Early on in lactation the needs of the sow and her litter may be quite well aligned in terms of milk production, with the sow still investing energy in her current litter. However, during the latter stages of lactation the needs of the sow and her litter become increasingly divergent. A power struggle over maternal resources develops with each party operating an evolutionary strategy for survival. The piglets must consider their own survival and soliciting as much milk as possible from the sow will aid in their growth and development. The strategy adopted by the sow is one of balance: she must balance the needs of her current litter with the needs of possible future litters and thus her lifetime reproductive success. Therefore, in order to maintain body condition whilst still providing for her current litter, she will reduce the number of milk let-downs per day. This can only be efficiently accomplished by a gradual separation from the litter, thus a control of her lactational output. In environments where the sow is kept loose for lactation, she is better able to control her output (Pajor et al., 1999), however even in farrowing crates sows are observed attempting to limit the piglets' suckling in the few ways possible: by standing or sitting and by spending more time resting on their sternum (thus, covering the teats) (De Passillé and Robert, 1989; Rantzer et al., 1995; Pedersen et al., 2011). In these examples the behavioural responses of the sow are seen as an adaptation to favour her future

reproductive output (Weary et al., 2008). For the intermediate and one-step sow, she will be receiving a litter whose needs are very different to her own and are likely to impact on her future reproductive success. Evidence from Danish research lends supports to this argument by demonstrating that nurse sows, on average, take one extra day to come on heat (Thorup, 2007). However, this could be due to the occurrence of lactational heat (anabolic state) and not due to a catabolic state, since it was also found that nurse sows subsequently had two piglets more in the following litter than control sows. The delay in return to oestrus could also be explained by occasional lactational heats. However, a large literature has shown that an energetically expensive lactation is associated with subsequent fertility problems (Quesnel and Prunier, 1995; Close and Mullan, 1996; Prunier and Quesnel, 2000; Thaker and Bilkei 2005; Quesnel, 2009; Prunier et al., 2010), but the extent to which this affects nurse sows is unclear.

When a sow is transitioning to become a nurse sow, the limited literature available reports that she does not lactate for an extended period of time (3-12 hours), which is likely to cause significant discomfort in the udder and could initiate lactational oestrus (Thorup, 2007). Whilst this transition probably results in some acute pain for the sow, there could be ongoing chronic pain as her milk yield has to adjust to the smaller demands of a younger litter. Farmer and others (2007) looked at the incidence of mammary gland involution and endocrine changes in early and late weaned sows. Mammary involution is the process by which the fully functional lactating mammary glands regress to a quiescent, resting state (Monks et al., 2002). This process is associated with drastic endocrine changes and during forced weaning milk accumulates rapidly within the glands and hormonal withdrawal is immediate and complete (Monks et al., 2002). This latter impact has potential consequences for the sows when they are early weaned from their own piglets and are waiting for their new piglets. In fully weaned animals the process of involution is inevitable and potentially functional; in diary cows for instance, changes occurring in the gland may be required for the gland to redevelop fully for maximal milk yield in the subsequent lactation (Hurley, 1989). In an experiment with rodents Hanayama and Nagata (2005) demonstrated that when involution of mammary glands was impaired, these glands showed periductal mastitis and their redevelopment for the next lactation was poor. For nurse sows then, there may be detrimental effects on mammary tissue because of the interruption in let-down when they are early weaned and in transition.

There are likely to be welfare concerns with the issue of early separation from the natural litter and the stress of accepting a foreign litter, some of which is exacerbated by distress that is often displayed by the foster litter (see sections 4.7.2 and 4.7.3). Fostering whole litters may lessen disruptive behaviours, however the actions of the foster piglets will influence the sow's behaviour and when performing the fostering process, researchers have

reported that sows experience stress and often do not nurse their new litter for 6 hours after being given them (Thorup and Sorensen, 2006b). Such behaviour will cause the piglets to become more frantic for milk, which may enhance their disruptive behaviour; in an experiment where piglets were separated from the sow, they vocalised more frequently if they were chilled or hungry (Weary and Fraser, 1995). Work by Horrell and Hodgson (1992) showed that piglets appear to be able to distinguish their own sow from an alien sow from 12 hours old. Thus the initial behaviours with the nurse sow maybe disruptive if they are calling for milk, but less disruptive than if they are calling for milk and suffering from maternal separation. For the 4-7 day old piglets in these management scenarios the process is likely to be more difficult because mother-offspring bonds have been formed and a teat order has been developed. Additionally, handling stress for the sow is likely to occur because nurse sows are usually moved to the new litter to minimise disease transfer. However this movement further delays the acceptance of the litter. In the one-step nurse sow management routine this stress may manifest itself in poor maternal behaviour, with 18-20% piglet mortality rates reported (Thorup and Sorensen, 2006b).

6. Mitigating the welfare impacts of large litter size

SUMMARY:

Several possible approaches to mitigating health and welfare issues associated with large litter were identified and are summarised in Table 2.

- To truly address the issue will likely require a global approach where several different strategies are implemented all with the ultimate goal of improving pig welfare in Denmark and in other countries using Danish genetics.

At a national level an important mitigation strategy is genetic selection encompassing traits that promote piglet survival, vitality and growth

- With the introduction in Denmark of the breeding objective LP5 (selection for number of piglets alive at 5 days rather than total number born) neonatal survival has improved in breeding and multiplier herds and is expected to improve in the commercial herd, as dissemination of the new genetic stock increases.
- Several other options for genetic strategies also show promise and are discussed in the report.

Nutrition for gilts and sows, through rearing, gestation, lactation and subsequent reproductive cycles could also contribute to improving piglet outcomes.

- Several components of gilt and sow diets have been shown to improve piglet outcomes (both early life vitality and survival and later health and welfare).
- Given that variability of piglet birth weights is associated with piglet mortality sow nutritional changes aimed at more uniform birth weights may be worthwhile.
- Assessment of how viable some of these are for practical implementation will require consideration of cost and sustainability, in addition to wider demonstrations of beneficial effects.

At an individual farm level, management can be improved to promote piglet survival and subsequent life vigour. An important concept is that management at all stages of the reproductive cycle, not simply in the farrowing accommodation, can impact on piglet outcomes.

Understanding the attitudes and behaviours of stockhandlers that contribute to variable farm outcomes and designing intervention training could be an important source of progress.

- Farrowing supervision and early interventions such as drying and heating piglets can play a role in improving piglet survival.
- However, irrespective of the quality of management in the farrowing house poor stockhandling at earlier stages of the reproductive cycle can create fearful animals with increased likelihood of showing poor maternal behaviour.
- Minimising the stress that sows experience during pregnancy will help support the later health and welfare of their developing offspring.
- Stockhandler attitudes and behaviours are susceptible to improvement through on-farm training, and such training can have clear benefits for piglet survival.

A selection of possible mitigation strategies to reduce the welfare impact of large litter size and its knock-on consequences, over the short, medium and long-term, are presented in Table 2. These strategies include genetic, nutritional, environmental and management approaches to deal with large litter sizes and their welfare consequences. Many of these strategies relate to the central issue of piglet mortality. However, we should keep in mind the other consequences of litter size for welfare and consider strategies to address these also. It should be stressed that different strategies may be more or less effective in different cases and with regard to different purposes. Genetic strategies are mainly important in the long term but will result in a permanent, cumulative and potentially high dissemination of response. Further, for most survival-type traits, 0-15% of the variation is genetic, whereas 85-100% is environmental. This implies that environmental factors are generally more important than genetic, and that efforts to reduce piglet mortality should focus on environmentally focussed strategies. This section of the report aims to provide a broad overview of possible areas where improvement might be made and is not comprehensive in its scope.

6.1 Genetic strategies

Current breeding strategy. The current pig-breeding strategy in Denmark has had a favourable impact on both litter size and piglet mortality (Figures 4 and 5). An indirect selection strategy was implemented in the Danish breeding programme in 2004, where the selection criterion was changed from litter size (total number born) to LP5 (number of live piglets at day 5). An observable response is now apparent in the purebred gilts with an increase of ≥1.5 live piglets at day 5 in 2011 compared to 2004 (Figure 4; Nielsen and Berg 2011). This improvement has been accompanied by a 6% better survival rate (corresponding to ≥20% less mortality; Figure 5; Nielsen and Berg 2011). As dissemination of genes (Figure 6) from the purebreds to the crossbred sows increases over the next years, this response should also become apparent at the production level. Dissemination of selection response to production herds is a slow process though. It is estimated based on gene-flow principles that initially small changes are seen until an equilibrium rate of change corresponding to the breeding nucleus is reached five to six years after changes in the breeding nucleus, in herds pursuing replacement gilts in multiplier herds (Personal communication: Henryon, PRC). So, genetics can help, but progress takes years and depends on the replacement strategies of the production herds.

The current strategy is to increase litter size simultaneously with reducing piglet mortality, because LP5 has a high, positive genetic correlation with number of weaned pigs as well as moderate, positive genetic correlations with survival rate at birth and survival rate until 5 days. Selection for LP5 should therefore increase both litter size and survival.

Moreover LP5 is not genetically correlated to survival rate from day 5 until weaning, so selection for LP5 should not have negative effects on survival after day 5 (Su et al., 2007). So, LP5 appears to be a well-suited trait for selection.

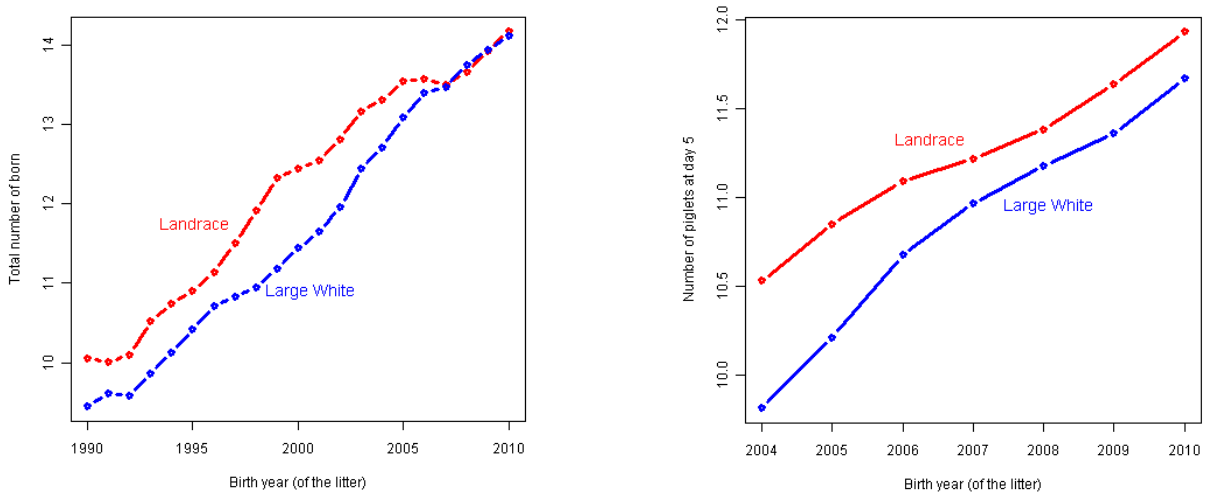

Figure 4: Development in the total number born and number of live piglets at day 5 from 1990/2004 to 2010. Based on litters from all purebred gilts (only first parity litters) in the Danish breeding- and multiplier system.

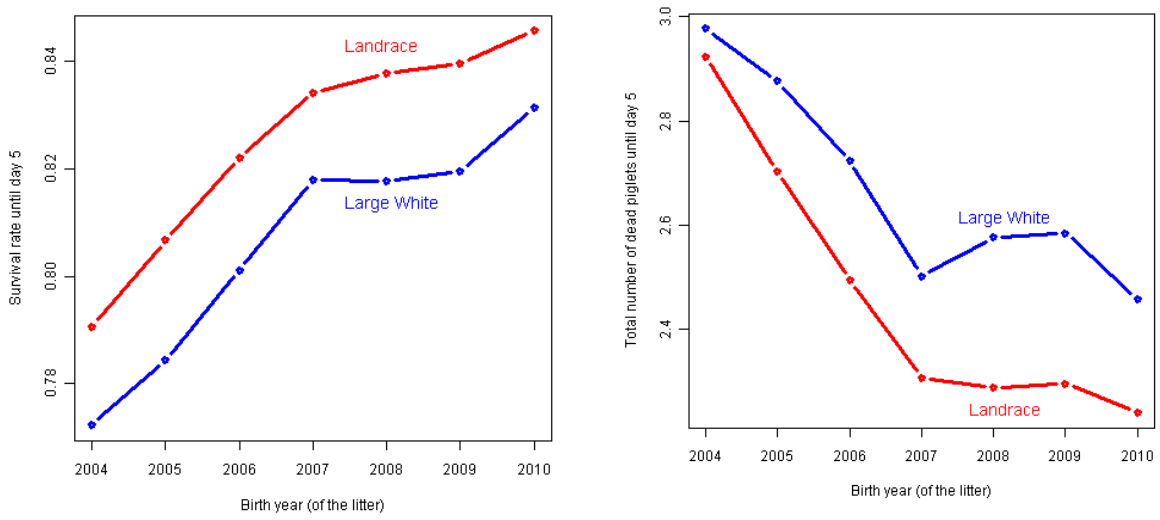

Figure 5: Development in the survival rate and number of dead pigs at day 5 from 2004 to 2010. Based on litters from all purebred gilts (only first parity litters) in the Danish breeding- and multiplier system.

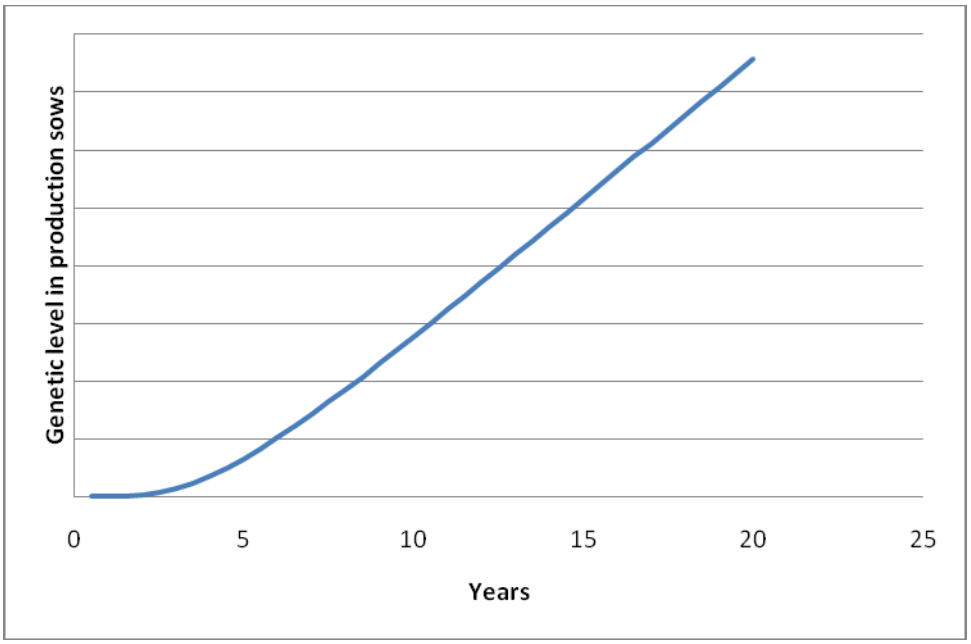

Figure 6. Genetic level in production sows, in herds pursuing replacement gilts in multiplier herds, in years after a change of selection criterion in the breeding nucleus herds.

Principles of selection for litter size and piglet survival. The feasibility of genetic strategies depends on many factors. Genetic response can mostly be achieved provided that the traits are heritable and sufficient genetic variation is present. Obtaining genetic response is not a trivial task though. It requires large amounts of information on phenotypes and pedigree information to estimate accurate heritabilities, genetic correlations among relevant traits, and breeding values to rank animals for selection. The genetic response depends on the accuracy of these parameters. The parameters will be more accurate with more phenotypes on selection candidates or more genetically-related animals. Higher prevalence (of e.g. mortality), informativeness (continuous vs. categorical scale of measure), and measurability (objective vs. subjective) also lead to higher accuracy and response. The genetic response also depends on the genetic correlations among traits in the breeding goal (e.g. growth, litter size, survival) and their relative economic/non-market values. For example, even though there is a positive (unfavourable) genetic correlation between litter size and mortality, it is possible to both increase litter size and reduce mortality as long as the genetic correlation between the two is <1. A correlation close to 1 will cause response to be very slow and costly in terms of lost genetic response in other traits. Feasibility of genetic strategies is currently limited by all these factors. In the future, there is hope among quantitative geneticists that Genomic Selection can enable more efficient use of phenotypes (Mark and Sandøe, 2010), for example from crossbred pigs on production farms. Knowledge on how

and whether this will be possible is still limited, but in the Danish breeding programme, a large-scale research-project on e.g. the ability of sows to nurse piglets (thereby improving survival) is currently running.

Piglet survival can be improved genetically through different strategies: by direct selection for survival or by indirect selection for related traits. The current pig-breeding strategy in Denmark uses indirect selection by selecting for LP5.

Alternative strategies. There are several alternatives to the current breeding strategy that are worthy of consideration.

(i) Direct selection for piglet survival. Survival or mortality traits are already to some extent recorded by breeding organisations, which would be an advantage for implementation in breeding programmes. Unfortunately, they are statistically very difficult to handle. 1) Because of their categorical nature and censoring, complex statistical methods are necessary (survival analysis and threshold models.) Such methods have not been available in standard software for estimation of genetic parameters and breeding value estimation until very recently (Ødegård et al., 2010). The prevalence of mortality is relatively low which makes it difficult to distinguish and rank the selection candidates. 3) Piglet survival is affected by two genetic components, firstly direct genetic effects on the potential of the piglet (with respect to it's vitality, growth, resistance, etc.) for survival, and secondly maternal genetic effects on the mother's potential to provide optimal conditions (birth conditions, milk yield, mothering ability, etc.) for piglet survival. The direct effect of piglet survival tends to be less heritable than the maternal effect under indoor conditions (Lund et al., 2002; Arango et al., 2006; Su et al., 2008; Kapell et al., 2011). Moreover, there are negative genetic correlations between direct genetic and maternal genetic effects (Arango et al., 2006; Su et al., 2008; Roehe et al., 2010; Kapell et al., 2011). For postnatal survival, cross-fostering of piglets has to be considered so that genetic models with biological and nurse sow effects may influence the accuracy of the genetic evaluation of all genetic effects. However, the direct effect is difficult to distinguish from the maternal since all piglets are fostered at least for a short period at the biological mother, and it will currently be a challenge to obtain correct and precise information on the nurse sow. These complexities make the current selection strategy more appealing than direct selection for piglet survival. If faster selection response on survival than the current is desired, then direct selection for piglet survival (e.g. overall, depending on underlying causes or different ages; Table 2) is a good additional strategy.

Selection for overall survival in the weaning period has the advantages of a relatively high prevalence and ease of recordings. Heritabilities of overall survival are relatively low:

e.g. direct: 0.03 and maternal: 0.05 and 0.09 (Grandinson et al., 2002; Arango et al., 2006). Mortality due to underlying causes, such as crushing, has the advantage of reflecting a specific biological background, but the prevalence becomes low and phenotypes will be subjective. Heritability estimates of mortality due to underlying causes are low for the maternal genetic component (0.03-0.06) and even lower for the direct component (Grandinson et al., 2002; Hellbrügge et al., 2008). In a recent Danish study, the maternal heritability for overall mortality (stillborn + piglets dying pre-weaning; 0.09) was higher than the heritabilities for underlying causes (e.g. 0.002 for crushing and 0.02 for stillborn; Strange, 2011). This suggests that selection for overall mortality (stillborn + pre-weaning mortality) will yield a higher genetic response than selection for underlying mortality traits. Selection against mortality in different age periods yields slightly higher heritabilities perinatally (direct and maternal: 0.01-0.06; Su et al., 2008, and maternal: 0.15; Grandinson et al., 2002) than after 5 days until weaning (0.02-0.03; Su et al., 2008). Genetic correlations between perinatal and postnatal survival of direct as well as maternal genetic effects are reported to be low which indicates that postnatal piglet survival is under different genetic control compared to perinatal survival (Arango et al., 2006; Su et al., 2008; Roehe et al., 2009; Roehe et al. 2010). This supports research examining phenotypic traits of piglet survival under outdoor conditions (Baxter et al., 2008; 2009), where the authors showed that perinatal survival was explained by piglet shape and size, whereas postnatal survival relied heavily on piglet and maternal behavior. Thus different biological traits relate to the different types of mortality. Treatment of postnatal survival into traits of early (e.g. to day 5 of age) and late postnatal piglet survival was suggested by Arango et al. (2006) and Su et al. (2008) because their genetic correlations were low suggesting that different genetic effects control also these traits. Similarly, in a recent Danish study, stillborn mortality was found not to be genetically correlated with mortality after birth until weaning (Strange, 2011). Generally, negative correlations between direct and maternal genetic effects within survival traits have been estimated, with larger negative correlations for postnatal than for perinatal survival (Arango et al., 2006; Su et al., 2008; Roehe et al., 2010; Kapell et al., 2011), which has to be considered to maximize overall selection response in piglet survival. Given the genetic parameters, the best potential strategy to increase the current selection response for survival further seems to be to focus on the maternal component of overall perinatal mortality.

(ii) Selection for survival in challenging environments. Heritabilities of piglet survival traits are reported to be low under indoor conditions. Under outdoor condition, Roehe and others (2010) found that in particular the direct heritability was substantially higher than those reported under indoor conditions. This indicates that piglets were highly environmental challenged under outdoor conditions and showed greater genetic differences than those

kept in an indoor environment (crate systems) which highly protects piglets. Furthermore, the selection took place based on EBVs of boars estimated for performances obtained under indoor conditions whereas the sow performances were obtained under outdoor conditions, so that the obtained selection responses under outdoor conditions may indicated that this shift in heritabilities did not result in genotype-environmental interactions associated with genetic re-ranking. Here the environment (lack of challenge) restricts the amount of information available for genetic evaluation. Selection for survival in outdoor conditions or challenging environments in general is not a viable strategy unless pig farming in general will become outdoor farming.

(iii) Indirect selection for higher birth weight. Phenotypically, individual birth weight is closely associated with piglet survival (Kerr and Cameron, 1995; Roehe and Kalm, 2000; Canario et al., 2006). Genetically, the relationship between individual birth weight and survival seems to be complex. For example, Knol et al., (2002) found no or even unfavourable genetic relations between birth weight and survival. Grandinson (2003) found a favourable correlation between crushing and birth weight, but an unfavourable correlation between still birth and birth weight. Knol et al., (2002), Grandinson et al. (2002) and Su et al. (2008) all concluded that breeding for increased birth weight will not necessarily result in higher overall survival rate. Furthermore, higher birth weight might cause problems for the sow during gestation and labour. Indirect selection for higher birth weight is, therefore, not a recommendable selection strategy for improving piglet survival. Alternatively, selection for an optimum birth weight (i.e. birth weight associated with lowest stillbirth) may be of advantage for survival, growth of piglet and even litter size (see Alternative Strategy (iv) below).

(iv) Indirect selection for lower within-litter birth weight variation. Given the association of high neonatal-weight variation with lower survival and more variable weaning weights (Roehe, 1999; Milligan et al., 2002; Quiniou et al., 2002), there is an impetus to select for more homogeneous litters (Damgaard et al., 2003). Increased litter size increases the heterogeneity or within-litter birth weight variation (Roehe, 1999; Milligan et al., 2002; Quiniou et al., 2002) and increases the risk of mortality (Roehe and Kalm, 2000). Reducing the heterogeneity of litters could potentially be more important than the increase of individual birth weight and this is not a new observation (English and Smith, 1975), yet it has not been effectively addressed. Recent work in this area in other polytocous species has utilised canalised selection strategies to aim for an optimum birth weight, which effectively pulls in the extremes in the population (i.e. the runts and the giants) to aim for a more homogenous litter. In a selection experiment with rabbits, selection for within-litter homogeneity lowered mortality levels compared to more heterogeneous litters (Garreau et al., 2008). Selection for

increased uniformity would imply selection for reduced phenotypic variance. This can in principle be achieved in two ways: 1) by reducing the additive genetic variance for birth weight, or 2) reducing the environmental variance for birth weight. Reducing the additive genetic variance is not desirable due to a reduced ability of the pig population to respond to environmental changes. Reducing the environmental variance by selection is in principle possible, but very difficult due to e.g. low heritabilities (Mulder et al., 2008). Moreover, direct selection on a combination of survival rate and litter size is likely to entail reduced within-litter variation of birth weights (Knol et al., 2002; Grandinson et al., 2002). Keeping in mind that piglet survival is the actual breeding goal and survival data are more readily available than birth weight data, direct selection, therefore, seems more straightforward.

(v) Indirect selection for sow nursing ability. Another possible strategy would be to breed for the sow's ability to nurse her piglets, i.e. to focus on the sow factor in survival rather than the piglet factor. The genetic potential to select for good mothering ability was shown by Baxter et al. (2011), where selecting for improved piglet survival resulted in these selected gilts displaying significantly less crushing behaviour than a control population. Selection for sow nursing ability could, for example, be done through selection for more teats (Hirooka et al., 2001). Teat number has a moderate heritability (Pumfrey et al., 1980) but is also susceptible to environmental influences in early development (e.g. proportion of males in birth litter: Drickamer et al., 1999b). Apart from the practical difficulties, selection for greater teat number may have undesirable side effects i.e. if it is associated with a longer spine and associated defects. It has also been suggested that genetic and phenotypic correlations between teat number and other genetic traits are negative (Pumfrey et al., 1980). Another option would be to select for a more general ability of the sow to nurse her piglets. Currently, PRC is investigating the potential of selecting for the sows ability to nurse 14 piglets in a large scale study. Litters of all sows are equalized to 14 piglets and the number of piglets still alive at weaning will be the trait for selection. This trait is simple to measure (objective), and the idea is that this trait includes several underlying traits (some subjective), such as milk yield and –composition, teat number and sow maternal behaviour. The potential of this trait for improving piglet survival remains to be seen.

(vi) Indirect selection for general robustness. Selection for a generally more robust neonate (Knap, 2005) may allow for increased litter size with fewer complications. Such a strategy may also deal with some of the broader issues for surviving pigs in which litter size has a contributory role. Given the possible negative impacts on stress responsiveness and increased disease risk, breeding for improvements in these traits has been explored in experimental studies with pigs. However, there is high uncertainty as to what is the best trait

to breed for (e.g. Knap and Bishop, 2000; Morméde et al., 2011) and care has to be taken that such changes do not have unintended side effects (D'Eath et al., 2010). Furthermore, the relationship between physiological or behavioural parameters putatively related to stress, and underlying affective states is unclear and these parameters are often difficult to measure. Therefore, the concept of breeding for robustness has been suggested in a number of livestock species (e.g. Star et al., 2008). Knap (2005) has defined robust animals as animals "that combine high production potential with resilience to external stressors, allowing for unproblematic expression of high production potential in a wide variety of environmental conditions". The Meishan breed of pigs appears to be able to support a greater litter size (of smaller piglets) to term compared with its occidental conspecifics due to the decreased pre-implantation growth rate and oestrogen biosynthetic activity of the Meishan conceptus compared with European and U.S. breeds, which allows more conceptuses to survive beyond day 18 of gestation (Wilson et al., 1998). Meishans are also thought to have more efficient placentas. Selection for increased placental efficiency (i.e. grams of piglet produced per grams of placenta - piglet birth weight/placental weight) is a possible way of improving survival (Mesa et al., 2005, 2006), but it is also a complicated trait, which should be treated with care (Van Rens et al., 2005). Meishans potentially have an extra advantage over Western breeds because of the maturity of the piglets at birth (Le Dividich et al., 1991; Herpin et al., 1993; Leenhouwers et al., 2001). Large White and Landrace breeds are selected for a leaner meat, which has a negative impact on the neonatal piglet which is born with less physiologically mature organs and little or no adipose tissue. The on-going public demand is for lean meat and therefore the Meishan, being a fattier breed, is less commercially viable despite its more physically capable piglets. However, lessons could be learned from the success of this breed and the physical characteristics of its piglets, although it is not immediately clear, how breeding should be done for general robustness. One possibility is through phenotypic plasticity or the environmental sensitivity of the expression of genetic production potential (De Jong and Bijma, 2002; Knap, 2005). Existing statistical methodology to deal with phenotypic plasticity is highly complex (e.g. reaction norms; Kolmodin and Bijma, 2004), and there is a lack of clarity on the effect of this approach on survival. Selection for robustness may, therefore, have some potential in the future, but the current strategy or direct selection for survival are more likely to be successful strategies.

There are at least five important questions regarding the genetic strategies against piglet mortality in relation to litter size:

i) How can sufficiently reliable and informative phenotypes be collected for successful direct selection on health traits such as piglet survival?

ii) Do sow nursing ability traits affect litter size and piglet mortality and how much?
iii) Which phenotypic trait(s) appropriately describes sow nursing ability or in other words incorporates the full maternal genetic effect on piglet survival?
iv) How can robustness be measured and/or modelled in a feasible manner in a breeding program?
v) What is the relationship between robustness, litter size and piglet mortality?

i) Selection in pig breeding is largely based on phenotypic information on purebreds in breeding herds rather than the crossbred products in production herds. For selection for improved survival, phenotypes collected in the production herds would be desirable, because health status is generally lower than in breeding herds. There are at least three reasons why selection cannot currently be realized based on phenotypes from production herds. Firstly, the crossbred animals are so remotely genetically related to the breeding stock that the phenotypic measurements in the crossbreds are not informative for estimation of breeding values in the breeding stock. Secondly, even if this problem of distant genetic relationships could be solved, there is still need for a reliable and economically viable system for tracking the genetic relationships. Thirdly, collecting the phenotypes would be a massive amount of work and difficult to streamline with risk of phenotypes not being trustworthy due to e.g. errors and subjectivity of producers or technicians. It has been suggested that genomic selection might help to solve the first and the second problem, but this area still needs further investigation. Genotyping is also still relatively expensive and thus optimizing on which animals to genotype would also still be necessary. Among others, studies on marker informativeness in both pure- and crossbreds and on how many and which crossbreds genotyping would help to clarify the potential of genomic selection to solve these issues. In the future, the third problem can potentially be solved by the use of digital chips that can measure phenotypes automatically and on an individual basis. This is an area under immense development, but for most phenotypes it is not yet available, and the current costs still limit the potential for large-scale use. It would be useful to develop small, easy to use and maybe reusable chips that can measure traits of direct importance in pig breeding goals, such as body weight, feed uptake or time of death.

Ii & iii) Selection for improved sow nursing ability might improve piglet survival even in large litters, but it is not currently clear how such selection should be done; i.e. which trait(s) should be measured and how should they be modelled statistically. There is clear evidence that the maternal impact on piglet survival is larger than the direct effect of the piglet. The relationship between specific traits that reflect sow nursing ability and litter size or piglet survival is not known, though. Studies to investigate the relationship between a variety of

sow nursing traits, litter size and piglet survival would be useful for effective implementation of selection for improved sow nursing ability.

iv & v) Selection for increased robustness in pigs has been suggested as a means to not only improve piglet survival, but also to reduce stress and piglet morbidity. How to define robustness as a trait to include in the breeding goal of a pig breeding program is still a matter of discussion. Examples of definitions are: “Pigs that combine high production potential with resilience to external stressors, allowing for unproblematic expression of high production potential in a wide variety of environmental conditions” (Knap, 2005), ‘‘The minimal variation in a target feature following a disturbance, regardless of whether it is due to switching between underlying processes, insensitivity or quickly regaining the balance” (Ten Napel, 2006), “an animal under a normal physical condition that has the potential to keep functioning and take short periods to recover under varying environmental conditions” (Star et al., 2008). Studies on how implementation of robustness given any of these definitions will actually affect litter size and survival are still needed to enable effective implementation of selection for robustness.

6.2 Strategies from early life to conception

6.2.1 Staff attitudes and behaviours towards pigs

People remain the most important contributor to animal welfare outcomes within any given farm system. Standards of care in the peri-partum period can contribute greatly to piglet welfare outcomes (see section 6.4.2). A wider issue relating to farm staff is the important concept that staff actions at all stages of the reproductive cycle from gilt rearing onwards can impact on piglet outcomes. Care and attention to gilt sow management before and during gestation has been shown to impact on piglet survival and lifetime welfare outcomes in a number of studies. Such effects may not be apparent because cause and effect are separated in time, and particularly in large units staff may specialise in particular parts of the farm (so for instance staff responsible for sow management may not feel any responsibility for piglet survival).

Hemsworth and colleagues over a number of studies have clearly demonstrated the sequential links between the attitudes that stockhandlers have towards pigs, their subsequent behaviour towards pigs, the impact this has on pig fear levels and finally the consequences of increased fear for production and reproduction (Hemsworth et al., 1995). A variety of characteristics such as job satisfaction, personality, general attitudes to animals and external recognition combine to influence attitudes and behaviours and these also can shift and become more embedded through mutual reinforcement (e.g. negative behaviours

increase pig fear reinforcing the attitude that pigs are difficult to handle (Hemsworth et al., 1995).

A number of these studies have investigated consequences for reproductive variables in addition to production variables such as growth rate. For instance, a strong negative relationship was found between sow fear towards humans and the number of piglets born per sow per year (Hemsworth et al., 1981). Hemsworth and others (1989) also found a clear link between sow fear of humans and reproductive outcomes. They furthermore demonstrated a link between stockhandler attitudes or behaviours and sow reproductive outcomes. The proportion of physical interactions with pigs that were negative was significantly related to both total litter size and number born alive. The attitude of stockhandlers on verbal effort required to move pigs also significantly correlated with numbers born alive. In another study, 18% of the variation, between farrowing units, in the proportion of stillborn piglets was accounted for by variation in how sows responded to approach from an unfamiliar human (Hemsworth et al., 1999). The implication of all this work is that farms using the same genetic stock, the same nutritional strategy and with the same housing and husbandry conditions can still vary widely in piglet outcomes as a consequence of how gilts/sows are handled before they ever reach the farrowing accommodation.

Training to improve stockhandler attitudes and behaviours towards pigs on Australian farms was shown to improve the number of piglets weaned per sow per year by 5% during a period when control farms showed a 2% decrease in that measure (Hemsworth et al., 1994). This training program involved providing information on how pig productivity and welfare are impaired by the action of stockhandlers and information on how to behave towards pigs to minimise fear. There may be additional benefits of implementing staff training schemes and staff retention six months after a training intervention was found to be increased (Coleman et al., 2000). Stockhandler behaviour during lactation can also impact on how successfully piglets cope with weaning (Sommavilla et al., 2011). Interestingly, Hemsworth and colleagues (1989) refer to one of their own unpublished studies which showed a poor link between how farm managers assessed their staff (in terms of competency/skills/attitudes and experience) and the behaviour of those staff towards pigs. This implies that in many cases management may have an inaccurate picture of their staff and may not realise the potential role they play in poor piglet outcomes.

Hemsworth and co-workers (1995) noted that the impact of human presence on piglet mortality probably interacts with general fear levels on a farm. Particularly for crushing and savaging related deaths human presence may be a risk factor when sow fear levels are high. A relationship between a shy or anxious behavioural profile and later impairments of maternal behaviour was shown in a study (Marchant-Forde, 2002) that classified gilts on a behavioural ‘shy-bold’ continuum on the basis of their response in a human-approach test

conducted during pregnancy. Gilts at the shy end of the spectrum were more likely to savage their offspring. Increased fearfulness may be a significant risk factor for piglet-directed aggression, particularly when sows are farrowing in a loose environment. Indeed, piglet-directed aggression has been proposed as a fear reaction towards the newborn piglets (English et al., 1977). More general detriments to sow maternal behaviour as a consequence of maternal anxiety were reported by Janczak and colleagues (2003) who found associations between behavioural measures of fear and anxiety at around two months of age and later quality of maternal care as reflected by piglet mortality. Neophobia and nervousness towards humans has also been found to be associated with piglet crushing (Lensink et al., 2009).

Although there is no direct evidence that increasing litter size is related to maternal fear, a study in rodents suggests such an effect can occur (D'Amato et al., 2006). However, irrespective of whether litter size or other factors are causally related to fear or not, efforts to optimise maternal emotionality – using genetic selection or rearing conditions that promote the development of calm temperament – may go some way to ameliorate the outcomes of litter size. Just as large litters require the highest possible standards of stockhandling, they also require that sows are produced which have the highest possible quality of maternal care. Reducing general fear levels in reproducing females may go some way towards mitigating the negative effects of being born in a large litter on mortality risk.

The studies from Hemsworth and colleagues clearly show not just that staff outside of the farrowing unit can have a major impact on piglet survival but that training interventions can beneficially impact on this relationship. This suggests that the development of similar materials and a training program for stockhandlers could be highly beneficial as part of a national program to address piglet mortality and welfare consequences of large litter size. Large litters place greater emphasis on skilled labour, not just more labour *per se*. However, some of the issues identified here in relation to large litter size could be effectively mitigated by good quality management. For many of these possible solutions it is not enough that industry leaders and representatives know what needs to be done. Communicating that effectively to farmers in order to cause change requires interactions with social science and psychology. Recent work with dairy cow welfare (Leach et al., 2010ab) and specifically the pressing issue of lameness has suggested new routes of communication that can better act to provoke actual change in farm practice. This work starts with an effort to fully understand all possible barriers to farmers implementing change and has highlighted the fact that to change behaviour in any scenario requires more than the simple transfer of information. Perhaps surprisingly, from a farming perspective this work has also shown that communicating information on financial benefits of altering behaviour is not all that effective either. It is important to remember that individual farm owners and staff will be motivated by different things (Edwards-Jones, 2006; Leach et al., 2010b) and in some cases financial

reward can actually be quite low down the list of farmers' goals. In fact communication methodologies closer to those practiced in advertising and marketing may be necessary. A key concept here is the importance of communicating information in such a way that the person receiving the information comes to believe they thought of it themselves. Additionally farmers are more likely to change when they understand that benefits outweigh barriers and when they know other farmers are also making similar changes.

An important step that could be taken, therefore, is making an effort to better understand attitudes of stockhandlers to piglet mortality. A significant danger with welfare issues that develop slowly over time in any particular production system is that the individual people involved gradually shift their perception of what is normal and accept the current situation as inevitable. Within the dairy industry a gradual disconnection has developed between cow lameness levels and farmers perception of how bad the situation on their farm is (Whay et al., 2003; Leach et al., 2010a). Similarly, Danish pig farmers may not perceive piglet mortality as a welfare issue, and some of the other tangential welfare issues of litter size may not be noticed at all.

6.2.2 Pre-conception nutrition and other factors

Gilt nutrition prior to conception may also contribute to outcomes in her first litter. Feeding gilts a diet with slightly reduced vitamin A content during conception and the first 30 days of pregnancy had no impact on litter size but lowered within-litter weight variation at birth and tended to lead to fewer low birth weight piglets being born (Antipatis et al., 2008). Inclusion of sugar beet pulp prior to conception or in sows from lactation through to service has been shown to improve embryo survival (Ferguson et al., 2006, 2007). Antipatis and colleagues (2008) concluded that nutritional strategies, such as manipulating maternal vitamin A status, to increase litter weight homogeneity need to be implemented either before mating or during the early pregnancy period. Quesnel and others (2008) found that the coefficient of variation for birth weight increased from 15% to 24% as litter size increased from less than ten piglets to greater than 15. However, their statistical model which included litter size, parity, year of sow birth and season at conception, only explained 20% of the overall variation in birth weight uniformity. Even allowing for the proportion of variation that may be due to genetic sources (Kapell et al., 2011), the implication is that a substantial proportion of birth weight variation is due to other maternal/environmental factors. Some of these may be amenable to manipulation to produce more uniform litters. Maternal diet before conception can also impact on offspring behavioural traits (Ashworth et al., 2009). For instance, in mice a pre-conception low protein diet was found to increase levels of fear/anxiety in later offspring (Watkins et al., 2008).

A recent finding in mice, showing that air pollution prior to conception can impact upon prenatal survival and fetus size (Veras et al., 2009) points towards the possibility that wider aspects of the environmental experience of animals during their rearing stage can also impact upon the development of their offspring. However, little is known about this in terms of pig reproduction.

6.3 Strategies to support sows and fetal piglets during gestation

6.3.1 Minimising maternal stress

Maternal stress during gestation has been shown to lead to higher pre-weaning mortality of live born piglets (Otten et al., 2001; Tuchscherer et al., 2002; Kanitz et al., 2003; Kranendonk et al., 2006). Couret and others (2009b) also showed a negative effect of social mixing in the final third of gestation on the number of mummified piglets and Weng and co-workers (2009) showed that group-housed sows had fewer stillborns than stall-housed sows. The results concerning still born piglets were not seen in Danish studies comparing loose housed and confined sows (Fisker 1994; Nielsen 1995). Despite the risk of social stress when sows are mixed, group housing in stable groups is likely to be less stressful for a majority of the sows than stall-housing and group housing with continuous mixing. Kongsted (2006) could predict sows that would not stay pregnant by observing their eating behaviour in systems with competitive feeding. The relationship between maternal stress and birth weight is more complicated with different studies findings either lowered (Kranendonk et al., 2006; Haussmann et al., 2000), increased (Otten et al., 2007) or unchanged (Jarvis et al., 2006b; Lay et al., 2008; Rutherford et al., 2009, Couret et al., 2009ab) birth weight under different forms, timings and severities of maternal stress. Stress during pregnancy can also impair piglet colostrum uptake (as assessed through immunoglobulin levels) (Tuchscherer et al., 2002).

There is also the potential for trans-generational effects in relation to piglet outcome such as survival. The experience of grandmothers has been shown to affect neonatal survival in some litters. As evidence of this, gilts born to mothers that experienced stress during their pregnancy show impaired maternal behaviour (Jarvis et al., 2006b; Rutherford et al., submitted), which can be associated with increased neonatal mortality in their own litters (Rutherford et al., submitted). Since maternal stress can also act to increase offspring stress reactivity (e.g. Jarvis et al., 2006b, Haussmann et al., 2000) optimising maternal housing and management to minimise maternal stress may also help to minimise the stress reactivity of offspring. There may be a variety of different ways that maternal experiences during gestation impact upon offspring outcomes. For instance, regularly exercising stalled sows during gestation improves litter total weight at birth (Schenck et al., 2008).

These studies provide a wealth of empirical data supporting the premise that maternal stress during gestation could act to exacerbate many of the problems associated with large litter size. Combined with the evidence, described above, on the impact of maternal temperament (as dictated by rearing conditions) this suggests that close attention to gilt and sow management and the minimisation of fear and stress in reproducing females could help reduce some of the problems of large litter sizes. The two most important components of this will be stockhandling and social interactions but other aspects of housing design and management may also be important.

6.3.2 Nutrition to support fetal development

The impact of various supplements to gestation diets will obviously depend on the quality of the underlying diet. Most investigations where supplementation has an effect on piglet survival seem to be compared to insufficient mixes as control feed. Thus the results are rarely implemented in commercial mixes for more than a year. This suggests the need for a fuller assessment of the relationship between maternal diet and piglet welfare (both overall mortality but also longer-term development). There is a concern that information on sow nutrition may have lagged behind genotype developments (Long et al., 2010). A feeding regime that was appropriate for a sow ten years ago will not in all likelihood meet the requirements of a breeding sow today. Piglet health and welfare can be supported by sow nutrition in a number of different ways. Many of the beneficial effects of pre-conception diet on litter size appear to act through improving the quality of the oocyte (Ashworth et al., 2009). Sow gestational nutrition can impact upon birth weight and litter uniformity.

Beyond birth weight sow nutrition can have an impact on body energy reserves, which may be critical for supporting early life thermogenesis. Furthermore specific supplements of a sow's diet may act to support piglet behavioural vitality early in life and improve piglet uptake of colostrum and important immune components. Sow gestational nutrition may also impact on milk and colostrum quality directly (see Farmer and Quesnel 2009 for a review). Finally, other aspects of piglet biology such as gut function can be affected by maternal nutrition during pregnancy. Some studies have also shown that supplements to maternal diets through lactation and after weaning can impact on the well-being of subsequent litters. Edwards (2005) provides a useful overview of some of the gilt/sow nutrition work which relates to reproduction and piglet viability.

Since over-feeding during gestation can lead to lower lactational feed intake, feeding supplementation of the sow during gestation for the benefit of her offspring has to be carefully considered. However, a number of studies have shown beneficial effects of sow gestation diets on piglet outcomes in very early life and also beyond the weaning period.

One widely investigated aspect of sow gestational nutrition is dietary fibre. Sows are feed restricted during gestation and may feel hungry if only fed small quantities of concentrate feed. Managers on farms with high litter size may be keener to feed larger quantities during gestation, to ensure enough nutrients to the embryos. This will have a positive effect on sow welfare. Dietary fibre promotes longer feeding times and may result in sensations of satiety (D'Eath et al., 2009). Andersen and colleagues (2007) investigated factors contributing to piglet mortality on 39 Norwegian farms. They found that herds where sows were fed a moderate (0.5kg – 1.5kg) amount of roughage during gestation had lower levels of piglet mortality. Sows receiving increased fibre diets during gestation have been reported to be behaviourally calmer during early lactation (Farmer et al., 1995). Twenty-four studies (reporting 41 experimental comparisons) on the effects of gestational dietary fibre for sows published between 1975 and 2007 were recently reviewed by Reese and colleagues (2008). Across all studies the average effect (mean, weighted by number of litters in individual studies) was an additional 0.2 live born piglets per litter and an additional 0.3 pigs weaned per litter. On average there was no impact on piglet birth weight. Studies varied in their outcomes substantially: for instance 29 comparisons reported a positive effect of dietary fibre on live born piglet numbers but 11 reported a negative effect. The authors emphasised that effects of feeding increased levels of dietary fibre during gestation may only become apparent over several parities. For instance, when they divided the studies up into those that assessed outcome over a single reproductive cycle versus those that looked across multiple cycles substantial differences were seen. The average single cycle response to dietary fibre was a reduction of 0.1 live born piglets per litter and a reduction of 0.2 weaned piglets per litter. However, studies that assessed treatment of more than one reproductive cycle found an increase of 0.4 and 0.5 live born and weaned piglets per litter respectively. They suggest this may be because nutrition prior to conception is important and studies that only assessed one reproductive cycle in most cases introduced that diet in the gestation period. From a Danish point of view, it is important to distinguish between non soluble fibres (straw) and soluble fibres (sugar beet pellets).

Other studies have investigated particular dietary supplements. For instance:

- Rooke and colleagues (2001) supplemented sows' diets with Salmon oil and found a reduction in piglet mortality.
- Supplementing sows during gestation with L-carnitine did not impact upon litter size but was found to increase average birth weight, and lower the number of still born piglets (Musser et al., 1999).

- Eder et al., (2001) also found increased birth weights and fewer low viability piglets as a result of gestation L-carnitine supplementation of gilts (where the birth weight effect was more pronounced) or sows.
- Corino et al., (2009) found that a conjugated linoleic acid (CLA) supplementation (0.5%) from day 7 of gestation resulted in a higher piglet IgG level at 21and 34 days of age.
- Patterson et al., (2008) found that a 2% CLA supplement from d85 of gestation improved piglet scouring following an experimental *E. coli* challenge
- Jean and Chiang (1999) found that supplementing gestation diets with medium-chain tri-glycerides from day 84 onwards lowered mortality in the first three days after farrowing. They found that either medium-chain tri-glycerides or coconut oil supplementation over the same period improved survival of small birth weight piglets, but that only the tri-glycerides improved survival for medium sized piglets.
- Long et al., (2010) questioned whether recommendations for sow gestation dietary energy content were still suitable for more modern hyper-prolific breeds. They investigated the effect of four different levels of dietary energy. Although total litter size was not affected, the number of piglets born alive was greater at an energy input of 6,730 kcal ME/kg live weight compared to lower or higher levels. Overall litter weight at birth increased with increasing energy input.
- Piao et al., (2010) also found that the method of feeding across gestation can impact on piglet mortality. They found that compared to flat feeding increased feed allowance in the second third of pregnancy caused an increased rate of still born piglets at farrowing.
- Laws et al., (2009) found that supplementing sow diets with olive oil between insemination and day 60 of gestation lowered the proportion of low birth weight piglets born (and conversely that sunflower supplementation over the same period had the opposite effect).

Maternal diet may also have a role in supporting offspring welfare beyond the immediate farrowing and lactation period. Oostindjer et al (2010) found that adding an Anise flavouring to sow diets beneficially altered piglet post-weaning behaviour. This study is interesting because it highlights the valuable point that gestation nutrition can potentially contribute to more than prenatal or neonatal survival. Maternal nutrition can also potentially aid aspects of piglet health beyond the immediate perinatal period. However, this role of maternal diet has not been explored widely.

6.3.3 Maintaining maternal health through pregnancy

Keeping sow lameness under control will also contribute to lower piglet mortality as sows are better able to control their movements during lactation, reducing the risk to piglets of crushing. In addition to the physical benefit of preventing lameness there could also be prenatal benefits for the developing offspring. One area that has received little consideration is the possible impact of painful conditions experienced by gestating females on their fetal offspring. Since many other stressors can have a negative impact on piglet development and lameness is likely to be a significant stressor for some animals, it can be assumed that maternal pain could impact on piglets. Some evidence for this possibility comes from a sheep study (Wassink et al., 2010), which found that 17 extra lambs were reared per 100 ewes in flocks where ewes were treated for footrot, a production benefit that meant treatment was financially beneficial for the farmer. They suggested the effect might be mediated by improved body condition in healthy ewes, which in turn improved lamb birth weigh and subsequent survival. Also, in sheep Sargison and others (1995) found that a mid-pregnancy outbreak of sheep scab significantly lowered lamb birth weight. Maternal lameness may be less likely to impact on body condition in sows where any form of lameness that prevented feeding should be dealt with quickly, however, the possibility that painful conditions such as lameness could represent a maternal stressor for fetal piglets remains. Focussing on sows that milk well has led to some interest in hoof trimming on some Danish farms where the challenge of keeping piglets in large litters alive leads to stock people focussing more on sows health.

6.4 Peri-partum strategies

6.4.1 Farrowing environment

Following on from the EU ban on sow stalls from 4 weeks after mating (due to be fully implemented across the EU in January 2013) there has been a move towards increasing implementation of group gestation housing systems in a number of countries. In Denmark around 70% of sows are now kept in social group pens during gestation, partly as a result of movement towards the post 2012 ban on stalls and also because of the specification for this within the contract for UK production. However, this change to gestation housing has not been matched by the much slower move towards loose farrowing pens. As a consequence the majority of sows move from a group pen to a farrowing crate immediately before farrowing. There is some evidence to suggest that this contrast between gestation and lactation accommodation can be negative for sow welfare and piglet mortality (Beattie et al., 1995). Transition from loose gestation housing to confinement in a farrowing crate can also delay farrowing (Weng et al., 2009). However, this same study also found the highest rate or

stillborn piglets when sows where housed in a sow stall and then moved to a farrowing crate. In some investigations, there was a negative impact on the farrowing and increase in stillborn, when young sows experienced housing in crates for the first time when being moved to the farrowing unit – both when inserted in time before farrowing (Gustafsson 1983, Cronin et al., 1996) and when inserted late before farrowing (Pedersen & Jensen 2008). In Danish investigations crated and loose housed gilts and sows did not differ in still birth rate, when farrowing in crates (Fisker 1994).

.

6.4.2 Farrowing supervision and piglet treatments

There is no clear consensus of opinion in the literature on whether farrowing surveillance is of benefit or not. Whilst, Friendship and others (1986) observed no relationship between time spent in the farrowing house and piglet mortality, Hoshino and co-workers (2009) recommended farrowing assistance for gilts and high parity sows to improve piglet survival. Cutler and colleagues (1989) provided data showing the benefit of a staff training intervention to reduce piglet mortality in Australian pig farms. Holyoake and others (1995) found that supervision for three hours after the start of farrowing increased numbers weaned due to both decreased numbers of still births and decreased neonatal mortality (attributed to fewer crushings and better survival specifically of low birth weight piglets). However, Vanderhaeghe and others (2010b) found a negative relationship between still births and farrowing supervision. In most studies the exact focus points for surveillance, observations leading into action and the cascade of actions taken are seldom described. Musse (2007) found significantly fewer stillborn piglets in the case of farrowing assistance 1hour after the last piglet born than after 3 hours. In the same study the frequency of piglets dying after birth was significantly higher when piglets were dried after farrowing, than if the piglet was transferred to the udder or left behind on the sow (Musse, 2007). It is likely that on a farm where sows are particularly fearful of human interaction then increased human presence could have this negative effect (Hemsworth et al., 1995). This may primarily apply to sows crated during gestation that are not used to positive human interaction. An adverse effect of oxytocin use may also have the same effect. The benefit or otherwise of supervision may also depend on what the attendant does. In a small scale study no benefit of piglet drying or warming was seen on behavioural landmarks such as latency to contact the udder or suckle, but piglet mortality was reduced by both treatments (Christison et al., 1997). White and colleagues (1996) developed a more extensive protocol where all piglets were dried, had their airways cleared of mucus, and received an oral dose of bovine colostrum. In addition all low birth weight piglets received oxygen through a face mask for 30 to 45seconds (see also Herpin et al., 2001). This protocol lowered pre-weaning mortality from 18.2% to 10.1% and increased piglet weaning weight. In an observational study of 39 Norwegian farms

(Andersen et al., 2007) piglet mortality was reduced when piglets were helped to find a teat shortly after birth. In this study they found no benefit of drying or placing piglets under a heat lamp for reducing subsequent mortality, although they did in a later study (Andersen et al., 2009). In these studies, the control group was not observed at farrowing and the piglets thus not helped in any way. Other piglet treatments could potentially be applied if farrowings are supervised. For example, 2-IminoBiotin, an inhibitor of NitricOxideSynthase (which is believed to play a critical role in brain damage associated withy hypoxia) has been investigated as a treatment for neonatal piglets (Peeters-Scholte et al., 2002ab, Van Dijk et al., 2008).

Attending farrowings has the additional welfare benefits of quick treatment or euthanasia for injured piglets. The financial benefit of providing extra staff cover to supervise farrowings will depend on a number of factors including the wage requirements of staff, the skill of staff at improving production figures, the numbers of sows covered by each staff member and the value of increasing the number of slaughtered pigs for a set number of sows. High levels of farrowing supervision are more common in countries where labour costs are lower, however they may still be financially viable in other countries. This is particularly true if farrowings are artificially synchronised (which in itself may raise some ethical and welfare concerns), occur in clear batches or are predicted through automated technology. Several groups have investigated the use of technology to allow stockhandlers to predict farrowing time more precisely in order to deliver better care to the sow and her litter (e.g. Bate et al., 1991; Oliviero et al., 2007; Wang et al., 2007)

The positive studies certainly suggest that if done well supervision can improve litter mortality figures; however, if done badly supervision can produce a worse outcome than doing nothing at all (which probably explains the lack of consensus in the literature regarding advice on best practice). The benefit of supervision (in terms of ability to intervene to help individual piglets) may also be reduced in non-crate farrowing systems where safe access to piglets by human stockhandlers is greatly reduced (although Andersen et al's (2009) study was conducted in loose housed sows).

6.4.3 Sow treatments during lactation

Pain and discomfort during farrowing and in the period following completion of farrowing may contribute to negative piglet outcomes. As noted earlier (section 5.2) there is some uncertainty about whether large litter sizes could contribute to more pain in the peri-parturient period. However, irrespective of whether litter size is a causal factor or not, addressing the pain experiences of pigs after farrowing (interventions during farrowing will most likely be counter-productive by interfering with the normal progression of farrowing) could improve neonatal piglet outcomes. Haussman and others (1999) found that supplying

the sow with analgesia following farrowing reduced posture changes, which could lower the risk of crushing. Improvements to maternal behaviour, as a consequence of better pain management, would have both direct (reduced crushing and savaging deaths or injuries) and indirect (improved suckling and colostrum intake) impacts on neonatal mortality and also longer-term health and performance of piglets. Treating sows with Meloxicam following farrowing has also been shown to improve behaviour and had a particularly beneficial effect on low weight piglets, which showed better growth when their sow was given meloxicam (Manteca, 2009). In contrast, Cassar and colleagues (2010) recently suggested that there was no benefit to providing analgesia around farrowing. However, this study involved both a pre- and post-farrowing treatment of ketoprofen so negative impacts on farrowing itself cannot be discounted. In any event further work in this area could be merited.

Along similar lines, although not addressing pain experience it has recently been claimed that a single injection of Azaperone (Stresnil: Janssen Animal Health) after farrowing promotes piglet survival and is particularly beneficial for promoting the survival of low birth weight piglets (Miquet and Viana, 2010). However, little information is available to verify this claim as yet.

Sow water intake has been shown to be highly correlated with piglet growth over the first three days post-farrowing (Fraser and Philips, 1989). Various issues could impact upon water intake including physical condition (lameness causing a reluctance to stand), feelings of pain and sickness post-farrowing or poor nipple drinker design or function. Although feed intake of sows during lactation may be monitored on-farm water intake is rarely assessed because it would require fitting flow rate monitors etc. However, checking the colour of sow urine provides a good proxy indicator for water intake.

Van den Brand and co-workers (2006) investigated the impact on subsequent litter performance of supplementing sow diets with dextrose between weaning and oestrus. They found that adding dextrose to the diet lowered within-litter weight variation at birth, but did not impact on litter size or on overall average birth weight. In a subsequent study, addition of dextrose and lactose to the diet of sows during the final week of their pregnancy, through lactation and up to the next oestrus was also found to increase average birth weight and lower within-litter birth weight variation and pre-weaning mortality in the next litter (Van Den Brand et al., 2009). The treatment also increased litter size in sows that had had a previous litter of <12 but had not effect on litter size when the previous litter had been >12 piglets.

7. Ethical perspectives

SUMMARY:

In addition to specific welfare issues, there are also other ethical concerns relating to the increased occurrence of large litters

- From a biological perspective pig species have adopted a reproductive strategy based on overproduction of offspring and likely high neonatal mortality. Farming of pigs has actually reduced natural levels of mortality substantially.
- However, there may be a concern that the development from small/medium litters to large litters involves crossing a border into an unnatural state of affairs.
- There may be a concern that breeding for larger litters is too costly in terms of wasted life.

The overall ethical assessment of welfare implications is complicated by the fact that there are no widely accepted evaluation criteria concerning the evaluation of adding lives to the world.

- However, it seems hard to avoid the conclusion that the Danish development, from small/medium litters to large litters is likely to have had an overall negative impact.
- Even so, the overall Danish average level of welfare compares well with other countries in absolute terms.

7.1 Introduction

So far, the concern has been with the welfare impacts on larger litters on the sow and piglets, and on strategies to meet the challenges raised by those impacts. However, a welfare assessment does not tell us what an acceptable level of welfare for the animals is. The issue of acceptability is an ethical matter, where the interests of the animals have to be balanced against human interests.

An ethical assessment of a practice, such as an instance of pig production, is concerned with, firstly, an evaluation on the impact of the practice on all affected parties, as compared with the impact of available alternatives; and secondly, whether the practice involves actions that could be considered wrong in themselves.

As for the evaluation of impact, it makes a clear difference, which alternative the practice is compared with. Animal production is a practice characterized by using animals for the benefits of humans. Hence, it is based on a positive answer to the most fundamental question of animal ethics: is it justifiable to use animals for human purposes, i.e. raise them solely for this purpose and, in an early age, either kill them for their meat or dispose of them, when they have served their purpose? There is a long practice for using animals, and it is

widely accepted in most societies. However, there is also a minority of ethically motivated vegetarians and vegans in most societies, and use of animals is increasingly under pressure for justification.

Given that the practice of using animal is considered acceptable, the main ethical problems concerning animals are: to which purposes, and under which conditions can they be used? The purpose of producing food is probably among the most widely accepted purposes. However, as other uses, this involves a potential conflict of interests between humans and animals. Up to a certain point, good conditions for the animals typically also serve the human interest in production; but then increased productivity often involves higher pressure on the animals with risk of impaired welfare as a consequence.

However, the concern here is not to assess in general what is an acceptable level of welfare for farm animals. As was pointed out in Section 3, the concern is rather with the specific consequences of increased litter size. This assessment compares different alternative forms of pig production, and only the difference between these alternatives is of interest. Hence, the assessment is made in the context of actual pig production, and the overall assessment of this practice itself is not raised as an issue here. Hence, the focus will be on *an overall ethical assessment of the consequences for the animals of larger litters.*

7.2 Overall assessment of welfare impacts

How should we assess the overall welfare implications of the development from small/medium litters to large litters? Part of the answer to this question is relatively straightforward, but it also contains complex issues dealing with how to evaluate that more individuals are brought into existence. Perhaps surprisingly, there are no clear and consistent criteria for this type of evaluation. We cannot present a comprehensive overview here, but we shall introduce some of the most important points of view. Consider the figures from the Danish development:

	Total Born	Weaned	Post-natal deaths	Stillborn
DK 1992	12,1	9.9	1.3	0.9
DK 2008	15.8	12.1	1.9	1.8

To compare these two situations is a Different Number Choice. One way to deal with such a choice is to split it up in two: a Same Number Choice and a Different Number Choice comprising the additional individuals. To do this depends on a not entirely innocuous assumption to the effect that the welfare of each individual contributes to the overall

assessment independently of the welfare level of the others – we return to this assumption later. The split up looks like this:

Same Number	Total Born	Weaned	Post-natal deaths	Stillborn
DK 1992	12,1	9.9	1.3	0.9
DK 2008	12.1	9.9	1.3	0.9

Different Number	Total Born	Weaned	Post-natal deaths	Stillborn
DK 1992	0	0	0	0
DK 2008	3.7	2.2	0.6	0.9

The Same Number comparison of course also involves the sow. Given that we have an indication on the development of the average welfare for each group, this comparison is relatively straight forward. The complicated issue is how to evaluate that additional 3.7 piglet are born, of which the larger fraction is weaned, some are stillborn, and others die early.

A widespread intuition is that of neutrality: *It is ethically neutral whether an additional individual comes into existence or not* (Broome 2004). Of course, it is not neutral to the individual itself; but it is assumed that the world, from an impersonal perspective, gets neither better nor worse. Consider the case, where a woman either gives birth to one child or to twins. It seems intuitively right to say that, ethically speaking, this makes no difference. (Of course, twins may involve more work for the parents and take away resources from siblings, but that is not the issue here).

However, the intuition involves a clear asymmetry: whereas it is considered neutral whether an additional *good* life is created, most people would consider it wrong to create an additional life destined to be bad. It seems likely that the coming into to existence of a piglet which dies painfully within 24 hours, or even a fetus which does not come to life, would *not* be considered neutral. Ultimately, the intuition about neutrality is difficult to uphold, because it lead to intransitive assessments of alternatives (Broome 2004).

The Different-Number-Choice comparison involves an assessment of a life in absolute terms. In his example about the girl, Parfit uses the expression ‘a life worth living’. By this he appears to mean a life worth living for the person who lives it. On hedonism, a life seems worth living, if it contains more good than bad experiences. A life with no good and no bad experiences, or a life where the good and bad experiences are exactly on balance, would define an absolute zero on the hedonistic scale of welfare.

However, the assessment about whether adding a life to the world is better than not adding it is ultimately an ethical assessment. The hedonistic scale implies that for the individual, living a life with no good and no bad experiences is equally good as not living at all. But from an ethical perspective, it may be said such a life is worse than not living, because it would be meaningless. Hence, from an ethical point of view, it could be required that, in order for life to be better than not living, this life has to be better for the individual who lives it than some minimal positive level of welfare.

Another assessment criterion is the *Total Welfare* view. From this perspective, we should assess the total welfare contribution from the additional individuals and compare with the difference in total welfare between the Same Number alternatives. Thus, very simply, larger litters are a good thing if they result in more pigs in the world that live happy lives, but a bad thing if those pigs live miserable lives. It seems likely that the additional individual make a positive welfare contribution (of course, this depends on how exactly the overall lifetime welfare of the additional individuals are assessed). Then, this positive contribution has to be compared with the likely negative development in the total welfare for the Same Number individuals to see whether the net effect is positive or negative. We have no definite opinion on how to strike this balance.

Although the Total Welfare view covers some of our intuitions, it is also ultimately doubtful, because it allows free trade offs between quality and quantity. A decrease in average welfare can always be weighed up by an increase in the number of individuals; but most people find that 'repugnant' (Parfit 1984).

The third major point of view is the *Average Welfare* view: we should compare Different Number alternatives by looking at the average level of welfare. Consider this figure:

	Total Born	Weaned	Post-natal mortality	Pre-natal mortality
DK 1992	12,1	9.9	10.74%	7.44%
DK 2008	15.8	12.1	12.03%	11.39%

Even excluding the stillborn from the calculation, the overall average is likely to have decreased, because post-natal mortality has increased and the average welfare of piglets and the sow has decreased. However, the Danish average compares quite well, in absolute terms, with that of other countries. For instance, the similar UK figures are:

	Total Born	Weaned	Post-natal mortality	Pre-natal mortality
UK 1992	11.8	9.6	10.5%	8.1%
UK 2008	12.4	9.8	14.19%	6.8%

It is striking that Denmark has achieved a considerable increase in productivity, as compared with UK, while still keeping post-natal mortality lower.

Also the Average View has been cast in doubt, because it violates the assumption noted above: Whether it is valuable to add an individual with a certain lifetime welfare is not independent of the welfare level of others, but actually depends on their average welfare level. In the human sphere, this consequence has been deemed unacceptable (Parfit 1984, Broome 2004). However, in the sphere of animals, it may seem more plausible.

7.3 Perfectionist assessments

As noted in Section 3, the perfectionist account of welfare is largely relevant for the overall assessment of different forms of practice. We believe two points are of particular interest for this report.

The first point is the assessment of increased litters as such. From a perfectionist perspective, it seems clear that there is an important limit by the number of piglets the sow is able to care for by herself. When the number of piglets is larger than the number of functional teats, this limit has been crossed. *Hence, many people are likely already to consider large litters (cf. Figure 1) an unnatural state of affairs, and therefore problematic.*

However, similar arguments might be made about layer production where the concept of a mother hen rearing a normal clutch of eggs, has long since disappeared in layer production. Societal concern over the egg industry has largely focused on specific welfare issues rather than the larger issue of how inherently unnatural the production system is. The key difference is perhaps that the massive alternation to normal biology represented by this change do not so obviously imply a welfare detriment to offspring.

The second point is an assessment of mortality related to increased litters. As piglets die in nature, dying of piglets is not in itself a problem. The important base-line of comparison is thus mortality rates for pigs living naturally. This comparison is made in sections 4.4.4. It has been argued that pigs may have evolved a strategy of having ‘spare’ young which may survive if food is plentiful, but which will be killed in competition with stronger siblings if not (Fraser, 1990, Fraser et al., 1995, Drake et al., 2008). Pig producers are to some degree struggling against a certain amount of inevitable wastage. To quote Fraser et al (1995):

> *“The hypothesis also puts the practical problem of piglet deaths in a different light. It implies that when we try to keep large litters alive, we are battling not just against disease, harsh weather and other external challenges, but against an evolved reproductive strategy of the species.”*

Whilst the natural reproductive strategy of pigs in general appears to be to maximise the number of offspring produced when times are good there is also some suggestion that litter heterogeneity may also be a natural reproductive strategy of the pig, (e.g. an equivalent of hatching asynchrony in birds) that allows at least some individuals to survive at the expense of their littermates when times are poor.

Overall, as compared with natural conditions, mortality for domesticated pigs, even in very large litters, has actually decreased. Hence, it does not appear to represent a problem for a perfectionist perspective.

7.4 Other ethical concerns

Here, we shall consider the issue whether increased mortality among piglets involves ethical concerns over and above its welfare implications. And there might be a worry about whether increased mortality might be seen as an unnecessary waste of lives.

This concern could be seen as secularized version of the sanctity-of-life principle. Over and above its value for the individual who lives it, life has an impersonal value. The killing of animals for the purpose of food production is considered acceptable. But killing as well as death as an unintended consequence is only justified to the extent they are necessary for the fulfillment of this purpose. Killing or letting animals die for no good reason is *not* acceptable. This means that deaths that could be avoided without disproportionate costs are considered an unacceptable waste of lives.

This view is comparable with the view many people have on abortion. Abortion is considered acceptable, but only when weighty reasons favour it. Abortion should never be mere routine. This is often coupled with the view that abortion is more problematic, the older the fetus is. A similar assessment may be relevant for animals: An unnecessary death is worse the older the animal is.

From this perspective, the development from small/medium litters to large litters brings more piglets to life, but it happens at the cost of more stillborn and increased mortality for live born. Some people might consider this cost too high; too much life is wasted for the sake increasing productivity.

Death is an event happening to the animal, and it is often assumed that, in order for an event to have a welfare impact on an individual in hedonistic terms, the individual should be alive and *experience the event as making a difference in the quality of its mental states*. It follows from this assumption that the welfare impact of dying is how the individual experiences the event of dying. If this event is painful and/or frightening, these experiences have a negative welfare impact. If there is no experience of the event (as is suspected to be the case with stillborn piglets: section 4.4.5), it has no welfare impact. However, the

underlying assumption appears to be plainly false. An event can harm an individual, regardless of whether this is experienced as bad or not, simply by making it less well off than it otherwise would have been. Or to put it in hedonistic terms: if the event deprives the individual of positive mental states it would otherwise have enjoyed. From this perspective stillborn pigs are not ethically neutral, even given the likelihood that they have no possible mental expectation of their future life.

7.5 Summary of ethical assessments

- The overall ethical assessment of welfare implications is complicated by the fact that there are no widely accepted evaluation criteria concerning the evaluation of adding lives to the world.
- However, it seems hard to avoid the conclusion that the Danish development, measured on its own standards, has been overall negative. At least, this seems to follow from two evaluation criteria, whereas the verdict of a third is more uncertain.
- Even so, the overall Danish average level of welfare may still compare well in absolute terms. At least, the Danish post-natal mortality compares well with that of other countries, in spite of larger litters.
- From a perfectionist perspective, there is concern that the development from small/medium litters to large litters involves crossing a border into an unnatural state of affairs
- Some people will consider it too costly in terms of wasted life to breed for larger litters.

8. Conclusions

SUMMARY:

The range of welfare and ethical issues associated with litter size increase place the good image of Danish pig production at risk, both nationally and internationally.

- The Danish pig industry deserves credit for its willingness to address the issues associated with large litter size.
- Danish production operates to good welfare standards that are comparable or higher than many of its competitors. So even given the problems associated with large litter size Danish pigs may be thought to have as good a life as those in many other countries.
- However, the issues associated with large litter size have been seen to raise public concern in Denmark where the pig industry is already viewed poorly by many consumers and animal welfare is societally important.
- Irrespective of any relationship to large litter size levels of neonatal mortality are high in Danish production, as they are in many competitor countries.
- Addressing these concerns provides a potential win-win scenario of both improving public opinions on pig production, whilst at the same time improving the technical efficiency of Danish production.

A full economic analysis (including inclusion of 'ethical costs') is necessary to properly identify both economic costs and benefits of further increases in litter size as opposed to moving to a focus on keeping conceived piglets alive to weaning and beyond. This is beyond the scope of this report.

8.1 Welfare impacts of large litter size on piglets

For piglets, the three main areas where litter size was identified as negatively impacting on welfare and that demanded high priority for action were piglet mortality, piglet pain and suffering and low term outcomes of birth condition and early life experiences. In addition, some areas where management responses to large litters could impact on welfare were suggested.

The most obvious welfare relevant outcome of increasing litter size in pigs is increased neonatal mortality. Large litter size tends to be associated with increased levels of prenatal and neonatal mortality. Piglets born into large litters are smaller on average and variability within each litter is greater. Furthermore, the consequences of intrauterine crowding mean that overall piglet viability may be reduced. Piglet mortality is certainly a central issue where societal concern has been clearly expressed. It is also the main area where improvements could provide a win-win scenario, where both farm economics and

animal welfare were benefited. Although piglet neonatal mortality in Danish production is high it is within the range seen in other European countries (with lower average litter sizes) suggesting that comparatively Danish pig producers deal quite well with large litters. However, the wider welfare issue is whether mortality levels across all these countries could be reduced to improve piglet welfare and also to increase the efficiency of pig production.

There is clearly potential for suffering as a consequence of the high levels of piglet mortality seen in Danish production. It is highly likely that piglets are capable of experiencing negative emotional states, particularly pain from close to the moment of birth. However, a the general understanding of the welfare impacts of different types of neonatal death for piglets is limited. To more clearly assess the scale of the welfare detriment associated with piglet mortality requires a fuller understanding of the ontogeny of sentience in the piglet.

In relation to litter size increases have been seen in both prenatal and neonatal mortality. Even if the theory that stillborn piglets are unlikely to suffer (section 4.4.5) is correct, the increased prevalence of stillborn piglets associated with increases in litter size still represents a negative welfare impact on the sow, since farrowings involving stillborn or mummified piglets seem to be more uncomfortable for sows (Mainau et al., 2010). In addition higher proportion of stillbirths is associated with lower colostrum yields (Quesnel 2011) so there may be welfare detriments to surviving littermates in litters with many stillborn piglets.

In addition to actual mortality, and possibly actually involving a greater welfare impact, is the possibility that due to being born into larger litters some piglets, whilst surviving the peri-partum period, bear some morbidity associated with for instance, a difficult birth, partial crushing, trampling or savaging or intense teat competition. These conditions might involve sustained or intermittent pain.

Further to sources of suffering in the first few days of life, the increased prevalence of low birth weight piglets may have longer-term implications for pig welfare. Low birth weight is associated with a range of possible detriments to welfare, including increased stress reactivity. Overall, the evidence suggests that low birth weight piglets that survive the perinatal period are more likely to be of lower vitality throughout their lifetime. They may be more susceptible to disease challenges and also to other challenges to their welfare. These suggest that, in so far as large litter size increases the proportion of low birth weight offspring that some offspring in large litters will have their welfare impaired. However, few studies have properly attempted to disentangle outcomes of birth weight and litter size and the extent to which negative outcomes depend on relative or absolute birth weight remains largely undetermined.

Management interventions such as cross-fostering, the use of nurse sows and associated early weaning may have implications for piglet welfare, particularly when they are

poorly managed. However, further study is necessary to properly identify the welfare implications under current management conditions in Denmark and other countries (such as the Netherlands) where conditions are similar. There seem to be strategies for nurse sow production, where neither piglet growth nor survival is impaired (Thorup and Sørensen, 2006b). However even in these investigations, there was a certain amount of hunger experienced by the piglets as it took approximately 6 hours before the transferred piglets had their first milk intake.

8.2 Welfare impacts of large litter size on sow

The impacts of large litter sizes on sow welfare are more uncertain. However, possible welfare impacts of increasing litter size for sows, whether as part of the natural process of carrying, delivering and raising a large litter, or through artificial management intervention to use nurse sows, were identified. Although it is largely unknown whether bearing a large litter decreases sow welfare during gestation, work from other species suggests that there could be an impact. Assessment of the relative welfare impact of carrying varying litter sizes for sows during gestation has not been attempted. The possible negative outcomes identified here do suggest some studies which could address this issue. Behavioural studies of sows in late gestation (when the impact of litter size will be at its greatest) could identify whether rest, resource use, social behaviour and signs of discomfort are altered depending on subsequent litter size at parturition. Possible impact of litter size on the parturition experience could also be investigated through studies of farrowing sows. Sows may also suffer impairments to their welfare due to the increased pressure placed on them by selection for large litters. Although some of this burden may be reduced by improved nutrition, theories of allostatic load (Korte et al., 2007) and resource allocation theory (Rauw, 2009) suggest that pushing animals towards the limits of their physiological capacity to cope is often associated with health and welfare problems.

8.3 Strategies to reduce the welfare impacts associated with large litters

Referring back to Table 3 we can see that there is immediate room for improvement in piglet mortality by reducing the gap between the best and ‘worst’ performers within the Danish industry. The bottom 25% of Danish herds have overall pre-weaning mortality levels around 6 percentage points higher than the best 25%. Clearly then management has a major role to play in improving piglet outcomes. Future work should focus on identifying best practice followed by the best 25% of producers that are better able to keep mortality in check, despite using similar genetic stock and consequentially similar large litter sizes.

A number of possible strategies to mitigate negative effects of increasing litter size were identified. None of these are the sole solution, but there is good reason to believe that a combination of different strategies could be highly effective in remedying at least some of the potential negatives (see also Lawlor and Lynch 2005).

Perhaps the largest issue might be whether the continued goal of increasing litter size should be reconsidered, especially if the negative consequences of large litter size cannot be mitigated through improved management. However, it should be noted that breeding in Denmark has already shifted to selection for number of piglets alive at day 5. Whilst, it is too early to tell whether this will reverse the upwards trends in mortality seen since litter size selection was first implemented the early signs seen in breeding and multiplier herds are very promising. More generally, genetic selection strategies that improve piglet survival are demonstrably possible and would be of wide-scale benefit to all farmers. Breeding goals that reflect not only economic benefit but factors of wider societal importance are becoming more prevalent in a number of animal breeding industries (Kanis et al., 2005). However, genetic selection programs often take many years to have an effect on production at a farm level. This also means that changes to remedy problems can also take some time to implement. Some traits with great potential for genetic selection to improve piglet welfare are hampered by difficulties in measurement. This can be because traits are complex, or take a long time to assess, or are manifest at a time or place which makes their assessment difficult. Behavioural traits are commonly seen as following within this. Other difficulties include the fact that heritabilities are generally low and due to the often categorical nature of health related traits, such as mortality, the certainty with which available statistical tools can evaluate the breeding stock for selection is also relatively low. Any genetic response will therefore be slow, and the difficulties increase as the prevalence of mortality decreases. Therefore the investigation of non-genetic strategies to mitigate the possible problems associated with increasing litter size is of continued value. Numerous studies suggest that maternal diet, particularly through gestation, but perhaps during rearing or in the previous lactation, can impact upon piglet mortality and overall vitality. Management strategies to promote good temperament (low fearfulness in particular) in sows could also greatly contribute to welfare outcomes for the piglet. Critical to this process, under any system of management, will be standards of stockhandling at all stages of the reproductive cycle. Finally, farrowing supervision has substantial potential, if defined and practiced well, to improve piglet survival.

8.4 Assessing the economic implications of litter size.

Some of the studies discussed in this review have highlighted the possibility that there could be hidden costs for farm efficiency of ever increasing piglet litter sizes. At some point, before the biological limit to litter size is reached, it may well be the case that increasing litter size is no longer economically sensible. This is particularly true where increasing litter size may require increased labour inputs, better sow nutrition, and result in offspring piglets that are of a poorer quality on average. Maximum production of piglets per sow may not ultimately prove to be the optimal level of production for any given farm. However, the point at which increasing litter size is no longer economically advisable would need to be assessed through a full economic analysis of overall farm efficiency but this can only be assessed under actual conditions and management – so at the end of the assessment, the conclusion is historical. Quinton and others (2006) found that the economic value of increasing litter size decreases as average litter size in the population increase, and that conversely the economic importance of piglet survival increases. This suggests that to achieve maximum economic benefit breeding programs that initially focus on litter size inevitably need to switch emphasis to survival once litter size becomes reasonably large. This is due to the fact that as litter size increases previous estimates of optimal economic weightings may no longer apply. This appears to be the case even when some of the potentially hidden costs of increasing litter are not accounted for. A full consideration of all relevant costs could suggest a lower transition point. This is also before any societal benefit, expressed in a breeding program as non-market value (e.g. Gourdine et al., 2010), is considered. Overall, the suggestion is therefore that balanced breeding between litter size, piglet vitality and survival is necessary. Even in the absence of further increases in average litter size through selection the high figure for piglet mortality recorded in Denmark provides a ready made way to improve financial performance if it could be ameliorated.

Cost of production in Denmark remains amongst the lowest in Europe, which has enabled the Danish pig industry to be highly competitive internationally. This competitiveness has been at least partly due, in recent years, to increased litter sizes and numbers weaned per sow per year. However, it is a fallacy to imagine that the process of increasing litter size is never ending or that the economic benefit of increasing piglet output per sow will persist as animals are pushed towards the far extremes of what they can cope with.

8.5 Balancing animal welfare against other societal concerns

Society continues to express concern over animal welfare issues and although litter size is not high on the agenda *per se*, some of the consequences of it may become important. Given the recent adverse public reaction in Denmark it is possible that societal concerns about ethics may become a limiting factor (to further increases in litter size in the future) before biological or economic limitations. Negative opinions about welfare in pig production in Denmark are amongst the highest in Europe (Eurobarometer229, 2005). Overall, animal welfare was the second highest concern for Danes, just behind "quality and freshness of food" at 77%. Sixty-three percent of Danes had negative views on pig welfare compared to only 27% in the UK. More broadly, 76% of Danes reported themselves, in a survey on food-related risks, to be worried about animal welfare (Eurobarometer354, 2010), the second highest proportion amongst all EU countries (behind only Luxembourg).

However, this societal concern does need to be placed in the context of competing concerns regarding food security, efficiency of production and environmental considerations. Pig production like other areas of agriculture is subject to a number of different societal concerns beyond animal welfare. The predicted increase in world population and the associated requirements for food mean that for individual countries food security is increasingly an issue. Similarly concerns relating to climate change and the impact that livestock production has on the production of greenhouse gases are also highly prominent in the public agenda. Toma and others (2008) found that increasing litter size through altering sow diets during lactation and before oestrus had significant benefits on air and groundwater pollution. This emphasises that piglet mortality, whether prenatal or postnatal, is not only a significant source of lost profit for a farm, but that the wastage has significant implications for the environmental efficiency of pig production. Overall, the concept of sustainability is important. Sustainable agriculture has been defined as "agriculture that is ecologically sound, economically viable and socially just (Appleby, 2005)". Maintaining a sensible balance between these three competing priorities, in the face of the growing challenges facing agriculture, will be the central problem facing the livestock industry in the coming decades. Finally, it is also worth noting that although the heavy selection for large litter size in Denmark has given rise to a number of welfare and ethical concerns, overall welfare standards for pigs are comparatively high in Denmark. Denmark is prominent, along with Sweden, the UK, the Netherlands, in lists of European countries that have introduced higher welfare standards than required under EU legislation (Mul et al., 2010). From this perspective it could be considered that the overall welfare experienced by a Danish piglet is as good as or better than that in many other countries, irrespective of issues relating to litter size.

Acknowledgements

Funding for this report was provided by the Pig Research Centre, Copenhagen. We gratefully acknowledge the help of Agnieszka Futro who provided assistance with referencing the document. We also thank Cathy Dwyer for helpful comments on earlier drafts of this report.

References

Abáigar T 1990. Caracteristicas biológicas y ecológicas de una población de jabalies (Sus scrofa L.) en el SE Ibérico. PhD thesis, Universidad de Navarra.

Abáigar T 1992. Paramètres de la reproduction chez le sanglier (Sus scrofa) dans le sud-est de la Péninsule Ibérique. Mammali 56, 245-250

Abiven N, Seegers H, Beaudeau F, Laval A and Fourichon C 1998. Risk factors for high sow mortality in French swine herds. Preventive Veterinary Medicine 33, 109-119.

Adams R, Garry FB, Holland MD and Odde KG 1995. Clinicopathological measurements in newborn beef calves experiencing mild to moderate degrees of dystocia. Agri-Practice 16, 5-11.

Ahlstrom S, Jarvis S and Lawrence AB 2002. Savaging gilts are more restless and more responsive to piglets during the expulsive phase of parturition. Applied Animal Behaviour Science 76, 83-91.

Ahmad E, Brooks JE, Hussain I and Khan MH 1995. Reproduction in Eurasian wild boar in central Punjab, Pakistan. Acta Theriologica 40, 163-173

Ahrens M 1984. A study on wild boar reproduction. Beiträge Zur Jagd Und Wildforschung 13, 231–243.

Algers B 1984. Early weaning and cage rearing of piglets; influence on behaviour. Zentralblatt für Veterinärmedizin Reihe A 31, 14–24.

Alonso-Spilsbury M, Mota-Rojas D, Villanueva-Garcia D, Martinez-Burnes J, Orozco H, Ramirez-Necoechea R, LópezMayagoitia A and Trujillo ME 2005. Perinatal asphyxia pathophysiology in pig and human: a review. Animal Reproduction Science 90, 1-30.

Amarilyo G, Oren A, Mimouni FB, Ochshorn Y, Deutsch V and Mandel D 2011. Increased cord serum inflammatory markers in small-for-gestational-age neonates. Journal of Perinatology 31, 30-32

Andersen IL, Berg S and Boe KE 2005. Crushing of piglets by the mother sow (Sus scrofa) - purely accidental or a poor mother? Applied Animal Behaviour Science 93, 229-243.

Andersen IL, Berg S, Boe KE & Edwards S 2006. Positive handling in late pregnancy and the consequences for maternal behaviour and production in sows. Applied Animal Behaviour Science 99, 64-76.

Andersen IL, Haukvik IA and Boe KE 2009. Drying and warming immediately after birth may reduce piglet mortality in loose-housed sows. Animal 3, 592-597.

Andersen IL, Naevdal E, and Boe KE 2011. Maternal investment, sibling competition, and offspring survival with increasing litter size and parity in pigs (Sus scrofa). Behavioral Ecology and Sociobiology 65, 1159-1167.

Andersen IL, Tajet GM, Haukvik IA, Kongsrud S and Boe KE 2007. Relationship between postnatal piglet mortality, environmental factors and management around farrowing in herds with loose-housed, lactating sows. Acta Agriculturae Scandinavica Section A-Animal Science 57, 38-45.

Anderson LL 1978. Growth, protein content and distribution of early pig embryos. Anatomical Record 190, 143–154.

Anil SS, Anil L and Deen J 2008. Analysis of periparturient risk factors affecting sow longevity in breeding herds. Canadian Journal *of* Animal Science 88, 381-389.

Antipatis C, Finch AM and Ashworth CJ 2008. Effect of controlled alterations in maternal dietary retinol on foetal and neonatal retinol status and pregnancy outcome in pigs. Livestock Science 118, 247-254.

Appelius M 1995. Einflüsse auf die Populationsdynamik von weiblichen Schwarzwild-Frischlingen aus dem nördlichen Regierungsbezirk Braunschweig und dem Forstamt Saupark. Thesis, Tierärztliche Hochschule Hannover

Appleby MC 2005. Sustainable agriculture is humane, humane agriculture is sustainable. Journal of Agricultural and Environmental Ethics 18, 293-303.

Appleby MC, Weary DM, Taylor AA and Illmann G.1999. Vocal communication in pigs: Who are nursing piglets screaming at? Ethology 105, 881-892.

Arango J, Misztal I, Tsuruta S, Culbertson M, Holl JW, Herring W 2006. Genetic study of individual preweaning mortality and birth weight in Large White piglets using threshold-linear models. Livestock Science 101, 208-218.

Arey DS and Sancha ES 1996. Behaviour and productivity of sows and piglets in a family system and in farrowing crates. Applied Animal Behaviour Science 50, 135-145.

Ashworth CJ, Finch AM, Page KR, Nwagwu MO and McArdle HJ 2001. Causes and consequences of fetal growth retardation in pigs. Reproduction Suppl 58, 233–246.

Ashworth CJ, Toma LM and Hunter MG 2009. Nutritional effects on oocyte and embryo development in mammals: implications for reproductive efficiency and environmental sustainability. Philosophical Transactions of the Royal Society B. 364, 3351-3361.

Aumaitre A, Morvan C, Quéré JP, Peiniau J and Vallet G 1982. Productivité potentielle et reproduction hivernale chez la laie (Sus scrofa scrofa) en milieu sauvage. Journées Rech Porcine en France 14:109–124

Aumaître A, Quéré JP and Peiniau J 1984. Influence du milieu sur la reproduction hivernale et la prolificité de la laie. In Symposium International sur le Sanglier (eds F Spitz and D Pépin) pp. 69-78. Les Colloques de l'INRA 22.

Bandrick M, Pieters M, Pijoan C, Molitor TW and Baidoo SK 2011. Effect of cross-fostering on transfer of maternal immunity to Mycoplasma hyopneumoniae to piglets. Veterinary Record 168, 100 doi:10.1136/vr.c6163

Barker DJP, Godfrey KM, Gluckman PD, Harding JE, Owens JA and Robinson JS 1993. Fetal nutrition and cardiovascular disease in adult life. The Lancet 341, 938-941.

Barrier AC and Haskell MJ Submitted. Future calving performance and fertility of the dairy cow after a difficult calving. Journal of Dairy Science

Bate LA, Hurnik D and Crossley JG 1991. Benefits of using a photo-electric alert system for farrowing operations. Canadian Journal *of* Animal Science 71, 909-911.

Bateson P, Barker D, Clutton-Brock T, Deb D, D'Udine B, Foley RA, Gluckman P, Godfrey K, Kirkwood T, Lahr MM, McNamara J, Metcalfe NB 2004. Developmental plasticity and human health. Nature 430, 419-421.

Bauer R, Gedrange T, Bauer K, Walter B 2006. Intrauterine growth restriction induces increased capillary density and accelerated type I fiber maturation in newborn pig skeletal muscles. Journal of Perinatal Medicine 34, 235-242.

Bauer R, Walter B, Bauer K, Klupsch R, Patt S, Zwiener U 2002. Intrauterine growth restriction reduces nephron number and renal excretory function in newborn piglets. Acta Physiologica Scandinavica 176, 83-90.

Bauer R, Walter B, Hoppe A, Gaser E, Lampe V, Kauf E, Zwiener U 1998. Body weight distribution and organ size in newborn swine (Sus scrofa domestica) - a study describing an animal model for asymmetrical intrauterine growth retardation. Experimental Toxicology and Pathology 50, 59–65.

Baxter EM, Jarvis S, D'Eath RB, Ross DW, Robson SK, Farish M, Nevison IM, Lawrence AB, Edwards SA 2008. Investigating the behavioural and physiological indicators of neonatal survival in pigs. Theriogenology 69, 773-783.

Baxter EM, Jarvis S, Edwards SA. The Weaker Sex? The propensity for male-biased piglet mortality. *In prep.*

Baxter EM, Jarvis S, Sherwood L, Farish M, Roehe R, Lawrence AB & Edwards SA 2011. Genetic and environmental effects of piglet survival and maternal behaviourof the farrowing sow. Applied Animal Behaviour Science 130, 28-41.

Baxter EM, Jarvis S, Sherwood L, Robson SK, Ormandy E, Farish M, Smurthwaite KM, Roehe R, Lawrence AB and Edwards SA 2009. Indicators of piglet survival in an outdoor farrowing system. Livestock Science 124, 266-276.

Baxter SH 1984. Intensive pig production: environmental management and design. London, Granada.

Bazer FW, Ford JJ and Kensinger RS 2001. Reproductive physiology. In Biology of the Domestic Pig (ed. WG Pond and HJ Mersmann), pp. 150-224. Cornell University Press, New York.

Beattie VE, Breuer K, O'Connell NE, Sneddon IA, Mercer JT, Rance KA, Sutcliffe MEM and Edwards SA 2005. Factors identifying pigs predisposed to tail biting. Animal Science 80, 307-312.

Beattie VE, Walker N, Sneddon IA 1995. Effect of rearing environment and change of environment on the behaviour of gilts. Applied Animal Behaviour Science 46, 57-65.

Bellieni CV and Buonocore G 2008. Neonatal pain treatment: ethical to be effective. Journal of Perinatology 28, 87-88.

Bellows RA and Lammoglia MA 2000. Effects of severity of dystocia on cold tolerance and serum concentrations of glucose and cortisol in neonatal beef calves. Theriogenology 53, 803-813.

Bentham J 1789. The Principles of Morals and Legislation. New York: Hafner, 1948.

Berkley K.J., Robbins A. and Sato Y. (1993). Functional differences between afferent fibres in the hypogastric and pelvic nerves innervating female reproductive organs in the rat. J. Neuroendocrinol. 69, 533-544.

Bessei W 2006. Welfare of broilers: a review. World's Poultry Science Journal 62, 455-466.

Bieber C and Ruf T 2005. Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. Journal of Applied Ecology 42, 1203-1213.

Biensen NJ, Wilson ME, Ford SP 1998. The impact of either a Meishan or Yorkshire uterus on Meishan or Yorkshire fetal and placental development to days 70, 90, and 110 of gestation. Journal Of Animal Science 76, 2169-2176.

Bilkei G and Biro O. 1999. Der Einfluß des Geburtsgewichtes auf Absetzgewicht, Saugferkelverluste und Saugferkelerkrankungen. Tierärztliche Umschau 54, 372-377.

Blasco A, Bidanel JP and Haley CS 1995. Genetics and neonatal survival. In The Neonatal Pig: Development and Survival (ed. MA Varley), pp. 17-38. CABI, Wallingford, UK.

Bøe K 1993. The effect of age at weaning and post-weaning environment on the behavior of pigs. Acta Agriculturae Scandinavica Section A- Animal Science 43, 173-180.

Boissy A, Manteuffel G, Jensen MB, Moe RO, Spruijt B, Keeling LJ, Winckler, C, Forkman B, Dimitrov I, Langbein J, Bakken M, Veissier I, and Aubert A 2007. Assessment of positive emotions in animals to improve their welfare. Physiology and Behavior 92, 375-397.

Boitani L, Trapanese P, Mattei L and Nonis D 1995. Demography of a wild boar (Sus scrofa L.) population in Tuscany, Italy. Gibier Faune Sauvage 12,109–132

Bonde M 2008. Prevalence of decubital shoulder lesions in Danish sow herds (In Danish). Internal Report 12, University of Aarhus, Faculty of Agricultural Sciences, 8pp.

Bonica JJ 1986. Pain of Parturition. Clinics in Anaesthesiology 4, 1-31.

Borge KS, Tønnessen R, Nødtvedt A and Indrebø A 2011. Litter size at birth in purebred dogs – a retrospective study of 224 breeds. Theriogenology 75, 911-919.

Bostedt H, Maier G, Herfen K and Hospen R 1998. Clinical examinations on gilts with puerperal septicaemia and toxaemia. Tierärztliche Praxis 26, 332-338.

Brambell, F.W.R. 1965. Report of the Technical Committee to Enquire into the Welfare of Animal Kept under Intensive Livestock Husbandry Systems. Command Paper 2836. Her Majesty's Stationery Office, London.

Briedermann L 1971. Zur Reproduktion des Schwarzwildes in der Deutschen Demokratischen Republik. Tag Ber dt Akad Berlin 113,169–186

Broom DM 1986. Indicators of poor welfare. British Veterinary Journal 142, 524-526.

Broom DM 1998. Welfare, stress, and the evolution of feelings. Advances in the Study of Behavior 27, 371-403.

Broome J 1993. Goodness is reducible to betterness: the evil of death is the value of life. In P. Koslowski, & Y. Shionoya, The Good and the Economical: Ethical Choices in Economics and Management (pp. 70-84). Springer-Verlag.

Broome J 2004. Weighing Lives. Oxford: Oxford University Press.

Brown JME, Edwards SA, Smith WJ, Thompson E, Duncan J 1996. Welfare and production implications of teeth clipping and iron injection of piglets in outdoor systems in Scotland. Preventive Veterinary Medicine 27, 95-105.

Brownridge P 1991. Treatment Options for Relief of Pain During Childbirth. Drugs 41, 69-80.

Bruckner C 1986. Epidemiological observation on piglet rearing in Bavaria, with reference to the consequences of tooth clipping. Thesis, Tierarztliche Fakultat Ladwig-Maximilians-Universitat, Munchen, Deutschland.

Bulfin LJ, Clarke MA, Buller KM and Spencer SJ In Press. Anxiety and hypothalamic-pituitary-adrenal axis responses to psychological stress are attenuated in male rats made lean by large litter rearing. Psychoneuroendocrinology (In Press).

Burger A 1983. Consequences of clipping incisors in piglets. Thesis, Tierarztliche Fakultat Ladwig-Maximilians-Universitat, Munchen, Deutschland.

Bywater KA, Apollonio M, Cappai N, Stephens PA 2010. Litter size and latitude in a large mammal: the wild boar *Sus scrofa*. Mammalian Review 40, 212-220.

Callaway TR, Morrow JL, Edrington TS, Genovese KJ, Dowd S, Carroll J, Dailey JW, Harvey RB, Poole TL, Anderson RC and Nisbet DJ 2006. Social stress increases fecal shedding of Salmonella typhimurium by early weaned piglets. Current Issues in Intestinal Microbiology 7, 65-71.

Campbell D 2001. A review of maternal complications of multiple pregnancy. Twin Research 4, 146-149.

Canario L, Cantoni E, Le Bihan E, Caritez JC, Billon Y, Bidanel JP and Foulley JL 2006a. Between-breed variability of stillbirth and its relationship with sow and piglet characteristics. Journal of Animal Science 84, 3185-3196.

Canario L, Roy N, Gruand J and Bidanel JP 2006b. Genetic variation of farrowing kinetics traits and their relationship with litter size and perinatal mortality in French Large White sows. Journal of Animal Science 84, 1053-1058

Carlin A and Neilson JP 2006. Twin clinics: a model for antenatal care in multiple gestations. In Multiple Pregnancy (eds M Kilby, P Baker, H Crtchley and D Field), RCOG Press, London.

Carranza J 1996. Sexual selection for male body mass and the evolution of litter size in mammals. American Naturalist 148, 81-100.

Carroll JA, Berg EL, Strauch TA, Roberts MP and Kattesh HG 2006. Hormonal profiles, behavioural responses, and short-term growth performance after castration of pigs at three, six, nine or twelve days of age. Journal of Animal Science 84, 1271-1278.

Carroll JA, Daniel JA, Keisler DH and Matteri RL 2000. Postnatal function of the somatotrophic axis in pigs born naturally or by caesarean section. Domestic Animal Endocrinology 19, 39-52.

Cassar G, Amezcua R and Friendship RM. 2010. Periparturient analgesia: does it improve neonatal survival and growth? Proceedings of the 21st IPVS Congress, Vancouver, Canada July 18-21, pp251

Cecchinato A, Bonfatti V, Gallo L and Carnier P 2008. Survival analysis of preweaning piglet survival in a dry-cured ham-producing crossbred line. Journal of Animal Science 86, 2486-2495.

Cellina S 2008. Effects of supplemental feeding on the body condition and reproductive state of wild boar Sus scrofa in Luxembourg. Unpublished PhD thesis, University of Sussex, UK.

Chaloupkova H, Illmann G, Bartos L, Spinka M 2007. The effect of pre-weaning housing on the play and agonistic behaviour of domestic pigs. Applied Animal Behaviour Science 103, 25-34.

Champagne FA and Curley JP 2009. Epigenetic mechanisms mediating the long-term effects of maternal care on development. Neuroscience and Biobehavioral Reviews 33, 593-600.

Chen C, Gilbert CL, Yang G, Guo Y, Segonds-Pichon A, Ma J, Evans G, Brenig B, Sargent C, Affara N and Huang L 2008. Maternal infanticide in sows: incidence and behavioural comparisons between savaging and non-savaging sows at parturition. Applied Animal Behaviour Science 109, 238-248.

Chorpita BF and Barlow DH 1998. The development of anxiety: the role of control in the early environment. Psychological Bulletin 124, 3-21

Christensen G 2001. Decubital ulcers in the shoulder region in sows. Internal note. Skuldersår hos søer, Interntnotat, The Danish Bacon and Meat Council, 11 pp. (in Danish).

Christison GI, Wenger II and Follensbee ME 1997. Teat seeking success of newborn piglets after drying or warming. Canadian Journal of Animal Science 77, 317-319.

Clayton NS, Russell J and Dickinson A 2009. Are animals stuck in time or are they chronesthetic creatures? Topics in Cognitive Science 1, 59-71.

Close WH and Mullan BP 1996. Nutrition and feeding of breeding stock. In Pig Production (eds MR Taverner and AC Dunkin), pp 169-202. Elsevier, New York.

Cogan R and Spinatto JA 1986. Pain and discomfort thresholds in late pregnancy. Pain 27, 63-68.

Coleman GJ, Hemsworth PH, Hay M and Cox M 2000. Modifying stockperson attitudes and behaviour towards pigs at a large commercial farm. Applied Animal Behaviour Science 66, 11-20.

Coombs TM, McIlvaney KM and Dwyer CM 2010 Effects of breed, nutrition and litter size on fetal lamb behaviour. Proceedings of the 44th International Congress of the International Society for Applied Ethology, 3-7 August 2010, Uppsala, Sweden

Corino C, Pastorelli G, Rosi F, Bontempo V, Rossi R 2009. Effect of dietary conjugated linoleic acid supplementation in sows on performance and immunoglobulin concentration in piglets. Journal Of Animal Science 87, 2299-2305.

Corli O, Grossi E, Roma G, Battagliarin G 1986. Correlation Between Subjective Labor Pain and Uterine Contractions – a Clinic Study. Pain 26, 53-60.

Couret D, Jamin A, Kuntz-Simon G, Prunier A and Merlot E 2009a. Maternal stress during late gestation has moderate but long-lasting effects on the immune system of the piglets. Veterinary Immunology and Immunopathology 131, 17-24.

Couret D, Prunier A, Mounier AM, Thomas F, Oswald IP and Merlot E 2009b. Comparative effects of a prenatal stress occurring during early or late gestation on pig immune response. Physiology & Behavior 98, 498-504.

Cranwell PD 1995. Development of the neonatal gut and enzyme systems. In The neonatal pig, development and survival (ed MA Varley), pp. CABI, Wallingford, Oxon, UK.

Cromi A, Ghezzi F, Raffaelli R, Bergamini V, Siesto G and Bolis P 2009. Ultrasonographic measurement of thymus size in IUGR fetuses: a marker of the fetal immunoendocrine response to malnutrition. Ultrasound in Obstetrics and Gynecology 33, 421-426.

Cronin GM, Leeson E, Cronin JG and Barnett JL 2001. The effect of broadcasting sow suckling grunts in the lactation shed on piglet growth. Asian-Australasian Journal of Animal Sciences 7, 1019-1023.

Cronin GM, Simpson GJ and Hemsworth PH 1996. The effects of the gestation and farrowing environments on sow and piglet behaviour and piglet survival and growth in early lactation. Applied Animal Behaviour Science 46, 175- 192.

D'Amato FR, Rizzi R and Moles A 2006. Aggression and anxiety in pregnant mice are modulated by offspring characteristics. Animal Behaviour 72, 773-780.

D'Inca R, Gras-Le Guen C, Che L, Sangild PT and Le Huërou-Luron I 2011. Intrauterine growth restriction delays feeding-induced gut adaptation in term newborn pigs. Neonatology 99, 208-216.

Da Silva-Buttkus P, van den Hurk R, te Velde ER, Taverne MA 2003. Ovarian development in intrauterine growth-retarded and normally developed piglets originating from the same litter. Reproduction 126, 249-258.

Dalayeun JF, Nores JM, Bergal S 1993. Physiology of beta-endorphins – a close-up view and a review of the literature. Biomedicine and Pharmacotherapy 47, 311-320.

Damgaard LH, Rydhmer L, Lovendahl P, Grandinson K 2003. Genetic parameters for within-litter variation in piglet birth weight and change in within-litter variation during suckling. Journal of Animal Science 81(3), pp. 604-610.

Damm BI, Friggens NC, Nielsen J, Ingvartsen KL, Pedersen LJ 2002. Factors affecting the transfer of porcine parvovirus antibodies from sow to piglets. Journal Of Veterinary Medicine Series A-Physiology Pathology Clinical Medicine 49, 487-495.

Daniel JA, Carroll JA, Keisler DH and Kojima CJ 2008. Evaluation of immune system function in neonatal pigs born vaginally or by Cesarean section. Domestic Animal Endocrinology 35, 81-87.

Daniel JA, Keisler DH, Sterle JA, Matteri RL and Carroll JA 1999. Birth by caesarean section alters postnatal function of the hypothalamic-pituitary-adrenal axis in young pigs. Journal of Animal Science 77, 742-749.

Dantzer R 2009. Cytokine, Sickness Behavior, and Depression. Immunology and Allergy Clinics of North America 29, 247-264.

Dardaillon M 1988. Wild boar social groupings and their seasonal changes in the Camargue, southern France. Z Säugetierkunde 53, 22–30.

Dawkins MS 1983. Cage size and flooring preferences in litter-reared and cage-reared hens. British Poultry Science 24, 177-182.

Dawkins MS 1990. From an animal's point of view: Motivation, Fitness, and Animal Welfare. Behavioral and Brain Sciences 13, 1-61.

Dawkins MS 1998. Evolution and Animal Welfare. The Quarterly Review of Biology 73, 305-328.

Dawkins MS 2003. Behaviour as a tool in the assessment of animal welfare. Zoology 106, 383–387.

De Kruif JM and Welling AA 1988. Incidence of chronic inflammations in gilts and castrated boars. Tijdschrift voor Diergeneeskunde 113, 415-417.

De Passille AMB and Robert S 1989. Behaviour of lactating sows: influence of stage of lactation and husbandry practices at weaning. Applied Animal Behaviour Science 23, 315-329.

De Passillé AMB and Rushen J 1989. Suckling and teat disputes by neonatal piglets. Applied Animal Behaviour Science 22, 23-38.

De Passillé AMB, Rushen J and Hartsock TG 1988. Ontogeny of teat fidelity in pigs and its relation to competition at suckling. Canadian Journal of Animal Science 68, 325-338.

D'Eath RB 2005. Socialising piglets before weaning improves social hierarchy formation when pigs are mixed post-weaning. Applied Animal Behaviour Science 93, 199-211.

D'Eath RB and Burn CC 2002. Individual differences in behaviour: A test of 'coping style' does not predict resident-intruder aggressiveness in pigs. Behaviour 139, 1175-1194.

D'Eath RB and Lawrence AB 2004. Early life predictors of the development of aggressive behaviour in the domestic pig. Animal Behaviour 67, 501-509.

D'Eath RB, Conington J, Lawrence AB, Olsson IAS and Sandøe P 2010. Breeding for behavioural change in farm animals: practical, economic and ethical considerations. Animal Welfare. 19(Suppl. 1), 17-27.

D'Eath RB, Tolkamp BJ, Kyriazakis I and Lawrence AB 2009. 'Freedom from hunger' and preventing obesity: The animal welfare implications of reducing food quantity or quality. Animal Behaviour 77, 275-288.

Deen MGH and Bilkei G 2004. Cross fostering of low-birthweight piglets. Livestock Production Science, 90, 279-284.

Dekkers JCM, Mathur PK and Knol EF 2011. Genetic improvement of the pig. In The Genetic of the Pig (ed. MF Rothschild and A Ruvinksy), pp. 390-425. CABI, Wallingford, UK.

Derbyshire SWG 2010. Foetal pain? Best Practice and Research Clinical Obstetrics and Gynaecology 24, 647-655.

Devillers N, Farmer C, Le Dividich J, Prunier A 2007. Variability of colostrum yield and colostrum intake in pigs. Animal 1, 1033-1041.

Diesch TJ, Mellor DJ, Johnson CB and Lentle RG 2010. Developmental changes in the electroencephalogram and responses to a noxious stimulus in anaesthetized tammar wallaby joeys (Macropus eugenii eugenii). Laboratory Animals 44, 79-87.

Dimitsantos E, Escorihuela RM, Fuentes S, Armario A and Nadal R 2007. Litter size affects emotionality in adult male rats. Physiology and Behavior 92, 708-716.

Ding N, Guo Y, Knorr C, Ma J, Mao H, Lan L, Xiao S, Ai H, Haley CS, Brenig B and Huang L 2009. Genome-wide QTL mapping for three traits related to teat number in a White Duroc x Erhualian pig resource population. BMC Genetics 10: 6.

Dowd SE, Callaway TR and Morrow-Tesch J 2007. Handling may cause increased shedding of *Escherichia coli* and total coliforms in pigs. Foodborne Pathogens and Disease 4, 99-102.

Drake A, Fraser D and Weary DM 2008. Parent-offspring resource allocation in domestic pigs. Behavioral Ecology and Sociobiology 62, 309-319.

Drickamer LC, Arthur RD and Rosenthal TL 1999a. Predictors of social dominance and aggression in gilts. Applied Animal Behaviour Science 63, 121-129.

Drickamer LC, Arthur RD and Rosenthal TL 1999b. Factors affecting the number of teats in pigs. Journal of Reproduction and Fertility 115, 97-100.

Dubost G, Charron F, Courcoul A and Rodier A 2011. The Chinese water deer, *Hydropotes inermis* – A fast-growing and productive ruminant. Mammalian Biology 76, 190-195.

Duckitt K and Harrington D 2005. Risk factors for pre-eclampsia at antenatal booking: systematic review of controlled studies. British Medical Journal, 330, 565-567.

Duncan IJ 1996. Animal welfare defined in terms of feelings. Acta Agriculturæ Scandinavica. Section A – Animal Science Supplement 27, 29 -35

Duncan IJ and Petherick JC 1991. The implications of cognitive processes for animal welfare. Journal of Animal Science 69, 5017-5022.

Duncan JR, Cock ML, Loeliger M, Louey S, Harding R and Rees SM 2004. Effects of exposure to chronic placental insufficiency on the postnatal brain and retina in sheep. Journal of Neuropathology and Experimental Neurology 63, 1131-1143.

Dwyer CM 2003. Behavioural development in the neonatal lamb: effect of maternal and birth-related factors. Theriogenology 59, 1027-1050.

Dwyer CM 2008. The welfare of the neonatal lamb. Small Ruminant Research 76, 31-41.

Dwyer CM and Lawrence AB 2005. A review of the behavioural and physiological adaptations of hill and lowland breeds of sheep that favour lamb survival. Applied Animal Behaviour Science 92, 235-260.

Dwyer, C.M., Moinard, C., McIlvaney, K.M., Ormandy, E., Morgan, C.A. & Bűnger, L 2007. Behavioural development is delayed in mice pups following maternal undernutrition in pregnancy. Proceedings of the 41st International Congress of the International Society for Applied Ethology, 30 July-3 August, Merida, Mexico.

Dzieciolowski RM 1991. Ecological niches of five big ungulate in a forest tract. Folia For Pol 33, 56–70

Dziuk PJ 1985. Effects of migration, distribution and spacing of pig embryos on pregnancy and fetal survival. Journal of Reproduction and Fertility. Supplement 33, 57–63.

Eder K, Ramanau A and Kluge H 2001. Effect of L-carnitine supplementation on performance parameters in gilts and sows. Journal of Animal Physiology and Animal Nutrition 85, 73-80.

Edwards SA 2002. Perinatal mortality in the pig: environmental or physiological solutions? Livestock Production Science 78, 3-12.

Edwards SA 2005. Enhancing sow performance and welfare by choice of dietary energy substrates. Biotechnology in Animal Husbandry 21, 149-154.

Edwards SA, Smith WJ, Fordyce C and MacMenemy F 1994. An analysis of the causes of piglet mortality in a breeding herd kept outdoors. Veterinary Record 135, 324-327.

Edwards-Jones G 2006. Modeling farmer decision-making: concepts, progress and challenges. Animal Science 82, 783-790.

EFSA 2007. Scientific Opinion of the Panel on Animal Health and Welfare on a request from the Commission on Animal health and welfare aspects of different housing and husbandry systems for adult breeding boars, pregnant, farrowing sows and unweaned piglets. The EFSA Journal (2007) 572, 1-13.

Eisenach JC, Pan PH, Smiley R, Lavand'homme P, Landau R and Houle TT 2008. Severity of acute pain after childbirth, but not type of delivery, predicts persistent pain and postpartum depression. Pain 140, 87-94.

Elsley FWH 1971. Nutrition and lactation in sows. In Lactation (ed. IR Faulkner), pp. 393-411. Butterworths, London, UK.

Engblom L, Lundeheim N, Dalin AM, Andersson K 2007. Sow removal in Swedish commercial herds. Livestock Science 106, 76-86.

English PR and Smith WJ 1975. Some causes of death in neonatal piglets. Veterinary Annals 15, 95-104.

English PR, Smith WJ, MacLean A 1977. The Sow – improving her efficiency. Farming Press Limited, Ipswich.

Eurobarometer229 2005. Attitudes of consumers towards the welfare of farmed animals. European Food Safety Authority. http://ec.europa.eu/food/animal/welfare/euro_barometer25_en.pdf

Eurobarometer354 2010. Food related risks. European Food Safety Authority. http://www.efsa.europa.eu/en/factsheet/docs/reporten.pdf

Farmer C and Quesnel H 2009. Nutritional, hormonal, and environmental effects on colostrum in sows. Journal of Animal Science 87, 56-64.

Farmer C, Knight C, Flint D 2007. Mammary gland involution and endocrine status in sows: Effects of weaning age and lactation heat stress. Canadian Journal of Animal Science 87, 35-43.

Farmer C, Robert S, Matte JJ, Girard CL and Martineau GP 1995. Endocrine and peripartum behavioural responses of sows fed high-fiber diets during gestation. Canadian Journal of Animal Science 75, 531-536.

FAWC 2004. FAWC Report on the welfare implications of animal breeding and breeding technologies in commercial agriculture. Farm Animal Welfare Council, Page Street, London.

FAWC 2009. Farm animal welfare in Great Britain: Past, present and future. Farm Animal Welfare Council, Page St., London.

Ferguson EM, Slevin J, Edwards SA, Hunter MG and Ashworth CJ 2006. Effect of alterations in the quantity and composition of the pre-mating diet on embryo survival and foetal growth in the pig. Animal Reproduction Science 96, 89-103.

Ferguson EM, Slevin J, Hunter MG, Edwards SA and Ashworth CJ 2007. Beneficial effects of a high fibre diet on oocyte maturity and embryo survival in gilts. Reproduction 133, 433-439.

Fernández-Llario P and Carranza J 2000. Reproductive performance of the wild boar in a Mediterranean ecosystem under drought conditions. Ethology Ecology & Evolution 12, 335–343.

Fernández-Llario P and Mateos-Quesada P 2005. Influence of rainfall on the breeding biology of wild boar (Sus scrofa) in a Mediterranean ecosystem. Folia Zoologica 54, 240–248.

Fernández-llario P, Carranza J and Mateos-quesada P 1999. Sex allocation in a polygenous mammal with large litters: the wild boar. Animal Behaviour 58, 1079-1084.

Fisker BN 1994. Loosehoused groupfed sows. Report no. 278. Løsgående gruppefodrede søer. Landsudvalget for Svin og Den rullende Afprøvning. Meddelelse nr. 278. 1994. http://danishpigproduction.org/Publikationer/Kilder/lu_medd/medd/278.aspx

Fitzgerald M 2005. The development of nociceptive circuits. Nature Reviews Neuroscience 6, 507-520.

Fix JS, Cassady JP, Holl JW, Herring WO, Culbertson MS and See MT 2010. Effect of piglet birth weight on survival and quality of commercial market swine. Livestock Science 132, 98-106.

Focardi S, Gaillard JM, Ronchi F and Rossi S 2008. Survival of wild boars in a variable environment : unexpected life-history variation in an unusual ungulate. Journal of Mammalogy 89, 1113-1123.

Fonseca C, daSilva AA, Alves J, Vingada J and Soares AMVM. 2011. Reproductive performance of wild boar females in Portugal. European Journal of Wildlife Research 57, 363-371.

Fonseca C, Santos P, Monzón A, Bento P, Alves da Silva A, Alves J Silvério A, Soares AMVM and Petrucci-Fonseca F 2004 Reproduction in the wild boar (Sus scrofa, Linnaeus, 1758) populations of Portugal. Galemys 16, 53–65.

Fowden AL, Giussani DA, and Forhead AJ 2006 Intrauterine Programming of Physiological Systems: Causes and Consequences. Physiology 21, 29–37

Fowden AL, Giussani DA, and Forhead AJ 2005 Endocrine and metabolic programming during intrauterine development. Early Human Development 81, 723–734.

Fowler, T., 2009. *2008 Pig cost of prod. in selected countries*. Milton Keynes, BPEX.

Foxcroft GR, Dixon WT, Novak S, Putman CT, Town SC and Vinsky MDA 2006. The biological basis for prenatal programming of postnatal performance in pigs. Journal of Animal Science 84, E105-E112.

Francis D, Diorio J, Liu D and Meaney MJ 1999. Nongenomic transmission across generations of maternal behavior and stress responses in the rat. Science 286, 1155-1158.

Fraser D 1975. The 'teat order' of suckling pigs II. Fighting during suckling and the effects of clipping the eye teeth. Journal of Agricultural Science 84, 393-399.

Fraser D 1978. Observations on the behavioural development of suckling and early-weaned piglets during the first six weeks after birth. Animal Behaviour 26, 22-30.

Fraser D 1980. A review of the behavioural mechanism of milk ejection of the domestic pig. Applied Animal Ethology 6, 247-255.

Fraser D 1990. Behavioural perspectives on piglet survival. Journal of Reproduction and Fertility. Supplement 40, 355-370.

Fraser D and Phillips PA 1989. Lethargy and low water intake by sows during early lactation: a cause of low piglet weight gains and survival. Applied Animal Behaviour Science 24, 13-22.

Fraser D and Rushen J 1992. Colostrum Intake By Newborn Piglets. Canadian Journal Of Animal Science 72, 1-13.

Fraser D and Thompson BK 1991. Armed sibling rivalry among suckling piglets. Behavioral Ecology and Sociobiology 29, 9-15.

Fraser D, Kramer DL, Pajor EA and Weary DM 1995. Conflict and cooperation: sociobiological principles and the behaviour of pigs. Applied Animal Behaviour Science 44, 139-157.

Fraser D, Weary DM, Pajor EA and Milligan BN 1997. A scientific conception of animal welfare that reflects ethical concerns. Animal Welfare 6, 187-205.

Friendship RM, Wilson MR and McMillan I 1986. Management and housing factors associated with piglet preweaning mortality. Canadian Veterinary Journal 27, 307-311

Fruzinski B 1995. Situation of wild boar populations in Western Poland. Ibex, Journal of Mountain Ecology 3, 186–187.

Futterkamp VM. 2011. Mutterlose Aufzucht im Rescue-Deck. SUS Online: http://www.susonline.de/versuchsberichte/1-versuchsberichte/109-1/2011/view-category.php

Gamallo A, Trancho GJ, Alario P 1988. Behavioral and physiologic effects of early nutrition and social factors in the rat. Physiology and Behavior 44, 307– 311.

Gamborg C, Olsson A and Sandøe P 2005. Guide for Implementation. D Ethics Report: Farm animal breeding related ethical concerns and tools for implementation. CODE EFABAR. http://www.effab.org/LinkClick.aspx?fileticket=zBchODgneBA%3dandtabid=162andmid=508

Gardner DS, Buttery PJ, Daniel Z and Symonds ME 2007. Factors affecting birth weight in sheep: maternal environment. Reproduction 133, 297-307.

Gardner IA, Hird DW and Franti CE 1989. Neonatal survival in swine: Effects of low birth weight and clinical disease. American Journal of Veterinary Research 50, 792-797.

Garreau H, Bolet G, Larzul C, Robert-Granié C, Saleil G, SanCristobal M and Bodin L. 2008. Results of four generations of a canalising selection for rabbit birth weight. Livestock Science 119, 55-62

Garzón-Heydt P 1991. Biology and ecology of wild boar (Sus scrofa L., 1758) in Monfragüe Natural Park. PhD Thesis, Universidad Autonoma de Madrid

Gaskin HR and Kelly KW 1995. Immunology and neonatal mortality. In The Neonatal Pig. Development and Survival (ed. MA Varley), pp. 39–56.CABI, Wallingford, UK.

Geisert RD and Schmitt RAM 2002. Early embryonic survival in the pig: Can it be improved? Journal of Animal Science 80, E54-E65.

Geisert RD, Morgan GL, Zavy MT, Blair RM, Gries LK, Cox A and Yellin T 1991. Effect of asynchronous transfer and oestrogen administration on survival and development of porcine embryos. Journal of Reproduction and Fertility 93, 475–481.

Gerjets I and Kemper N 2009. Coliform mastitis in sows: a review. Journal of Swine Health and Production 17, 97-105.

Gethöffer F, Sodeikat G and Pohlmeyer K 2007. Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. European Journal of Wildlife Research 53, 287-297.

Gill MA 2002. Perinatal and late neonatal mortality in the dog. In PhD thesis University of Sydney.

Gintzler AR 1980. Endorphin – Mediated Increases in Pain Threshold During Pregnancy. Science 210, 193-195.

Gintzler AR, Peters LC and Komisaruk BR 1983. Attenuation of pregnancy-induced analgesia by hypogastric neurectomy in rats. Brain Research 277, 186-188.

Gluckman PD, Hanson MA, Spencer HG 2005. Predictive adaptive responses and human evolution. Trends in Ecology and Evolutions 20, 527-533.

Gonyou HW, Beltranena E, Whittington DL and Patience JF 1998. The behaviour of pigs weaned at 12 and 21 days of age from weaning to market. Canadian Journal of Animal Science 78, 517-523.

Górecki MT 2003. Sex ratio in litters of domestic pigs (Sus scrofa f. domestica Linnaeus, 1758). Biology Letters 40, 111-118.

Gourdine JL, de Greef KH and Rydhmer L 2010. Breeding for welfare in outdoor pig production: a simulation study. Livestock Science 132, 26-34.

Grandinson K, Lund MS, Rydhmer L and Strandberg E 2002. Genetic parameters for the piglet mortality traits crushing, stillbirth and total mortality and their relation to birth weight. Acta Scandinavia, A. Animal Science 52, 167-173.

Grandinson, K. 2003. Genetic aspects of maternal ability in sows. Doctoral dissertation. Swedish University of Agricultural Sciences

Grandinson K, Rydhmer L, Strandberg E and Solanes FX 2005. Genetic analysis of body condition in the sow during lactation, and its relation to piglet survival and growth. Animal Science 80**,** 33-40.

Grantham – McGregor S 1995. A Review of Studies of the Effect of Severe Malnutrition on Mental-Development. Journal of Nutrition 125, S2233-S2238.

Graves HB 1984. Behavior and Ecology of Wild and Feral Swine (*Sus Scrofa*). Journal of Animal Science 58**,** 482-492.

Griffin J 1986. Well-Being. Its Meaning, Measurement and Moral Importance. Oxford: Clarendon Press.

Grota LJ and Ader R 1969. Effects of litter size on emotionality, adrenocortical reactivity, and susceptibility to gastric erosions in the rat. Psychological reports 24, 547– 549.

Grunau RE, Holsti L and Peters JWB 2006. Long-term consequences of pain in human neonates. Seminars in Fetal and Neonatal Medicine 11, 268-275.

Gunvaldsen SE, Waldner C and Harding JC 2007. Effects of farrowing induction on suckling piglet performance. Journal of Swine Health and Production 15, 84-91

Gustafsson B. 1983. Effects of sow housing systems in practical pig production. Transactions of the ASABE 26, 1181-1185.

Hammond J 1914. On some factors controlling fertility in domestic animals. Journal Of Agricultural Science 6, 263-277.

Hanayama R and Nagata S 2005. Impaired involution of mammary glands in the absence of milk fat globule EGF factor 8. Proceedings of the National Academy of the United States of America 102, 16886-16891.

Handel SE and Stickland NC 1987. The effects of low-birth-weight on the ultrastructural development of 2 myofiber types in the pig. Journal of Anatomy 150, 129-143.

Hansen, L. U., Vinther, J. & Lahrmann, H. P. 2009. DRÆGTIGE SØERS BRUG AF FODERSTATIONER (ESF) OG SAMMENHÆNG MELLEM SØERNES AFVIGENDE ÆDEAD-FÆRD OG BRUNST/SYGDOM. Meddelelse Nr. 841 Videncenter for Svineproduktion.

Hare E and Leighton EA 2006. Estimation of heritability of litter size in Labrador retrievers and German shepherd dogs. Journal of Veterinary Behaviour 1, 62-66

Hartsock TG and Graves HB 1976. Neonatal behavior and nutrition-related mortality in domestic swine. Journal of Animal Science 42, 235-241.

Haussmann MF, Carroll JA, Weesner GD, Daniels MJ, Matteri RL, Lay DC Jr 2000. Administration of ACTH to restrained, pregnant sows alters their pigs hypothalamic-pituitary-adrenal (HPA) axis. Journal of Animal Science 78, 2399-2411.

Haussmann MF, Lay DC Jr, Buchanan HS and Hopper JG 1999. Butorphanol tartrate acts to decrease sow activity, which could lead to reduced pig crushing. Journal of Animal Science 77, 2054-2059.

Hay M, Rue J, Sansac C, Brunel G and Prunier A 2004. Long-term detrimental effects of tooth clipping or grinding in piglets: a histological approach. Animal Welfare 13, 27-32

Hayashi M, Ingram DL and Dauncey MJ 1987. Heat production and respiratory enzymes in normal and runt newborn piglets. Biology of the Neonate 51, 324–331.

Held SDE and Špinka M 2011. Animal play and animal welfare. Animal Behaviour 81, 891-899.

Hellbrugge B, Tolle KH, Bennewitz J, Henze C, Presuhn U and Krieter J 2008. Genetic aspects regarding piglet losses and the maternal behaviour of sows. Part 1. Genetic analysis of piglet mortality and fertility traits in pigs. Animal 2, 1273-1280.

Hemsworth PH, Barnett JL, Coleman GJ and Hansen C 1989. A study of the relationship between the attitudinal and behavioural profiles of stockpersons and the level of fear of humans and reproductive performance of commercial pigs. Applied Animal Behaviour Science 23, 301-314.

Hemsworth PH, Brand A and Willems P 1981. The behavioural response of sows to the presence of human beings and its relationship to productivity. Livestock Production Science 8, 67-74.

Hemsworth PH, Coleman GJ and Barnett JL 1994. Improving the attitude and behaviour of stockpersons towards pigs and the consequences on the behaviour and reproductive performance of commercial pigs. Applied Animal Behaviour Science 39, 349-362.

Hemsworth PH, Coleman GJ, Cronin GM and Spicer EM 1995. Human care and the neonatal pig. In The Neonatal pig: development and survival (ed. MA Varley), pp. 313-331. CABI, Wallingford, UK.

Hemsworth PH, Pedersen V, Cox M, Cronin GM and Coleman GJ 1999. A note on the relationship between the behavioural response of lactating sows to humans and survival of piglets. Applied Animal Behaviour Science 65, 43-52.

Herpin P, Damon M and LeDividich J 2002. Development of thermoregulation and neonatal survival in pigs. Livestock Production Science 78, 25-45.

Herpin P, Hulin JC, LeDividich J and Fillaut M 2001. Effect of oxygen inhalation at birth on the reduction of early postnatal mortality in pigs. Journal of Animal Science 79, 5-10.

Herpin P, Le Dividich J and Amaral N 1993. Effect of selection for lean tissue growth on body composition and physiological state of the pig at birth. Journal of Animal Science 71, 2645–2653.

Herpin P, LeDividich J, Hulin JC, Fillaut M, DeMarco F and Bertin R 1996. Effects of the level of asphyxia during delivery on viability at birth and early postnatal vitality of newborn pigs. Journal of Animal Science 74, 2067-2075.

Herrero J, García-Serrano A and García-González R 2008. Reproductive and demographic parametres in two Iberian wild boar populations. Acta Theriologica 53, 355–364.

Herskin MS, Bonde MK, Jørgensen E and Jensen KH 2011. Decubital shoulder ulcers in sows: a review of classification, pain and welfare consequences. Animal 5, 757-766.

Hickson RE, Lopez-Villalobos N, Kenyon PR and Morris ST 2008. Duration of parturition and frequency of abdominal contractions in primiparous, 2-year-old Angus heifers and the relevance of body dimensions of calves to dystocia. Australian Journal of Experimental Agriculture 48, 935-939.

Hinz G, Hecht K, Rohde W, Dorner G 1983. Long-term effects of early postnatal nutrition on subsequently body weight gain, emotionally and learning behaviour in male rats. Experimental and Clinical Endocrinology 82, 73–77.

Hirooka H, de Koning, DJ, Harlizius B, van Arendonk JA, Rattink AP, Groenen MA, Brascamp EW and Bovenhuis H 2001. A whole-genome scan for quantitative trait loci affecting teat number in pigs. Journal of Animal Science 79, 2320-2326.

Hirsch AC, Philipp H and Kleemann R 2003. Investigation on the efficacy of meloxicam in sows with mastitis-metritis-agalactia syndrome. Journal of Veterinary Pharmacology and Therapeutics 26, 355-360.

Hoge MD and Bates RO 2011. Developmental factors that influence sow longevity. Journal of Animal Science 89, 1238-1245.

Hohenshell LM, Cunnick JE, Ford SP, Kattesh HG, Zimmerman DR, Wilson ME, Matteri RL, Carroll JA and Lay DC 2000. Few differences found between early- and late-weaned pigs raised in the same environment. Journal of Animal Science 78, 38-49.

Holl JW and Johnson RK 2005. Incidence of splayleg pigs in Nebraska litter size selection lines. Journal of Animal Science 83, 34-40.

Holtug N 2010. Persons, Interests, and Justice. Cambridge: Cambridge University Press.

Holyoake PK, Dial GD, Trigg T and King VL 1995. Reducing pig mortality through supervision during the perinatal period. Journal of Animal Science 73, 3543-3551.

Horrell I and Bennett J 1981. Disruption of teat preferences and retardation of growth following cross-fostering of 1-week-old pigs. Animal Prodution 33, 99-106.

Horrell I and Hodgson J 1992a. The bases of sow–piglet identification: 1. The identification by sows of their own piglets and the presence of intruders. Applied Animal Behaviour Science 33, 319–327.

Horrell I and Hodgson J 1992b. The Bases Of Sow-Piglet Identification.2. Cues Used By Piglets To Identify Their Dam And Home Pen. Applied Animal Behaviour Science 33, 329-343.

Horrell RI 1982. Immediate behavioural consequences of fostering 1-week-old piglets. Journal of Agricultural Science 99, 329-336.

Hoshino Y, Sasaki Y and Koketsu YA 2009. High percentage of pigs born dead in litters in high-, intermediate- and low-performing herds. Journal of Veterinary Medical Science 71, 1579-1583.

Humphrey T 2006. Are happy chickens safer chickens? Poultry welfare and disease susceptibility. British Poultry Science 47, 379-391.

Hurka T 1993. Perfectionism. Oxford: Oxford University Press.

Hurley WL 1989. Mammary-Gland Function During Involution. Journal of Dairy Science 72, 1637-1646.

Hutter S, Heinritzi K, Reich E and Ehret W 1993. The effect of different methods of tooth resection in piglets, Tierärztliche Praxis 21, 417–428.

Huxley R, Neil A and Collins R 2002. Unravelling the fetal origins hypothesis: is there really an inverse association between birthweight and subsequent blood pressure? The Lancet 360, 659-665.

IASP Subcommittee on Taxonomy 1979. Pain terms: a list with definitions and notes on usage. Pain 6, 249-252.

IFOAM. 2005. Principles of Organic Agriculture. Bonn: IFOAM.

Isaacson RE, Firkins LD, Weigel RM, Zuckermann FA and DiPetro JA 1999. Effect of transportation and feed withdrawal on shedding on salmoenall typhimurium among experimentally infected pigs. American Journal of Veterinary Research 60, 1155-1158.

Jackson JR, Hurley WL, Easter RA, Jansen AH and Odle J 1995. Effects of induced or delayed parturition and supplemental dietary fat on colostrum and milk composition in sows. Journal of Animal Science 73, 1906–1913.

Janczak AM, Braastad BO and Bakken M 2000. Fear-related behaviour in two mouse strains differing in litter size. Animal Welfare 9, 25-38.

Janczak AM, Pedersen LJ, Rydhmer L and Bakken M 2003. Relation between early fear and anxiety-related behaviour and maternal ability in sows. Applied Animal Behaviour Science 82, 121-135.

Jarvis S, D'Eath RB, Robson SK and Lawrence AB 2006a. The effect of confinement during lactation on the hypothalamic-pituitary-adrenal axis and behaviour of primiparous sows. Physiology and Behavior 87, 345-352.

Jarvis S, McLean KA, Chirnside J, Deans LA, Calvert SK, Molony V and Lawrence AB 1997. Opioid-mediated changes in nociceptive threshold during pregnancy and parturition in the sow. Pain 72, 153-159.

Jarvis S, Moinard C, Robson SK, Baxter E, Ormandy E, Douglas AJ, Seckl JR, Russell JA, Lawrence AB 2006b. Programming the offspring of the pig by prenatal social stress: neuroendocrine activity and behaviour. Hormones and Behavior 49, 68-80.

Jean KB and Chiang SH 1999. Increased survival of neonatal pigs by supplementing medium-chain triglycerides in late-gestating sow diets. Animal Feed Science And Technology 76, 241-250.

Jensen P 1994. Fighting Between Unacquainted Pigs - Effects Of Age And Of Individual Reaction Pattern. Applied Animal Behaviour Science 41, 37-52.

Jensen P and Recén B 1989. When to wean – Observations from free-ranging domestic pigs. Applied Animal Behaviour Science 23, 49-60.

Johnson RK, Nielsen MK, Casey DS 1999. Responses in ovulation rate, embryonal survival, and litter traits in swine to 14 generations of selection to increase litter size. Journal of Animal Science 77, 541-557.

Jones PH, Roe JM and Miller BG 2001. Effects of stressors on immune parameters and on faecal shedding of enterotoxigenic *Escherichia coli* in piglets following experimental inoculation. Research in Veterinary Science 70, 9-17.

Kadarmideen HN and Janss LLG 2007. Population and systems analysis of cortisol in pigs divergently selected for stress. Phyiological Genomics 29, 57-65

Kahneman D, Fredrickson BL, Schreiber CA and Redelmeier DA 1993. When more pain is preferred to less: adding a better end. Psychological Science 4, 401-405.

Kajantie E, Phillips DIW, Andersson S, Barker DJP, Dunkel L, Forsén T, Osmond C, Tuominen J, Wood PJ and Eriksson J 2002. Size at birth, gestational age and cortisol secretion in adult life: foetal programming of both hyper- and hypocortisolism. Clinical Endocrinology 57, 635-641.

Kanis E, DeGreef KH, Hiemstra A and van Arendonk JAM 2005. Breeding for societally important traits in pigs. Journal of Animal Science 83, 948-957.

Kanitz E, Otten W, Tuchscherer M, Manteuffel G 2003. Effects of prenatal stress on corticosteroid receptors and monoamine concentrations in limbic areas of suckling piglets (Sus scrofa) at different ages. Journal Of Veterinary Medicine Series A-Physiology Pathology Clinical Medicine 50, 132-139.

Kanzaki N 1991. Timing of puberty of Japanese wild boar in Western Honsyu. In: Csanyi S, Ernhaft J (eds) Transactions of the XXth IUGB Congress Part II. University of Agricultural Sciences, Godöllö, pp 576–581

Kapell DNRG, Ashworth CJ, Knap PW and Roehe R 2011. Genetic parameters for piglet survival, litter size and birth weight or its variation within litter in sire and dam lines using Bayesian analysis. Livestock Science 135, 215-224.

Kapell, DNRG, Ashworth CJ, Walling GA, Lawrence AB, Edwards SA, Roehe R 2009. Estimation of genetic associations between reproduction and production traits based on a sire and dam line with common ancestry. Animal 3, 1354-1362

Kerr JC and Cameron ND 1995. Reproductive performance of pigs selected for components of efficient lean growth. Animal Science 60, 281–290.

Kikusui T, Isaka Y and Mori Y 30-7-2005. Early weaning deprives mouse pups of maternal care and decreases their maternal behavior in adulthood. Behavioural Brain Research 162, 200-206.

Kiley-Worthington M 1989. Ecological, ethological and ethically sound environments for animals: toward symbiosis. Journal of Agricultural Ethics 2, 323-347.

Kim SW and Easter RA 2001. Nutrient mobilization from body tissues as influenced by litter size in lactating sows. Journal of Animal Science 79, 2179-2186.

Kim SW, Easter RA and Hurley WL 2001. The regression of unsuckled mammary glands during lactation in sows: the influence of lactation stage, dietary nutrients, and litter size. Journal of Animal Science 79**,** 2659-2668.

Kirkden R D and Pajor E A 2006. Motivation for group housing in gestating sows. Animal Welfare 15, 119-130

Kirkden R D and Pajor EA 2006. Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. Applied Animal Behaviour Science 100, 29-47.

Kirkwood RN, Zak LJ and Goonewardene LA 1998. Influence of cross fostering on piglet growth and survival. In: *Proc. of 15th IPVS Congress, Birmingham, England, 5–9 July. Int. Pig Vet. Soc*, p. 403.

Klemcke HG, Lunstra DD, Brown-Borg HM, Borg KE, Christenson RK 1993. Association between low birth weight and increased adrenocortical function in neonatal pigs. Journal of Animal Science 71, 1010-1018.

Knap PW 2005. Breeding robust pigs. Australian Journal of Experimental Agriculture 45, 763-773.

Knap PW and Bishop SC 2000. Relationships between genetic change and infectious disease in domestic livestock. In: The Challenge of Genetic Change in Animal Production, pp65-80, WG Hill, SC Bishop, B McGuirk, JC McKay, G Simm and AJ Webb (eds), An Occational Publication of the British Society of Animal Science, British Society of Animal Science, Edinburgh, UK.

Knol EF, Ducro BJ, Van Arendonk JAM and van der Lende T 2002a. Direct, maternal and nurse sow genetic effects on farrowing, pre-weaning and total piglet survival. Livestock Production Science 73, 153–164.

Knol EF, Leenhouwers JI and Van der Lende T 2002b. Genetic aspects of piglet survival. Livestock Production Science 78, 47-55.

Kolmodin R and Bijma P 2004. Response to mass selection when the genotype by environment interaction is modelled as a linear reaction norm. Genetics Selection Evolution 36, 435-454.

Kongsted AG 2006. Relation between reproduction performance and indicators of feed intake, fear and social stress in commercial herds with group-housed non-lactating sows. Livestock Science 101, 46-56.

Korte SM, Olivier B and Koolhaas JM 2007. A new animal welfare concept based on allostasis. Physiology & Behavior 92, 422-428.

Koskela E, Juutistenaho P, Mappes T and Oksanen T 2000. Offspring defence in relation to litter size and age: experiment in the banl vole Clethrionomys glareolus. Evolutionary Ecology 14, 99-109.

Koslo P 1970. Faktoren die Populationdsdynamik des Widschweins im Urwald vom Belowesh bestimmten. Zoologische Journal 49, 422–430.

Krackow S 1997. Further evaluation of the developmental asynchrony hypothesis of sex ratio variation. Applied Animal Behaviour Science 51, 243-250.

Kranendonk G, Hopster H, Fillerup M, Ekkel ED, Mulder EJ, Wiegant VM, Taverne MA 2006. Lower birth weight and attenuated adrenocortical response to ACTH in offspring from sows that orally received cortisol during gestation. Domestic Animal Endocrinology 30, 218-238.

Kuller WI 2008. Consequences of intermittent suckling for performance in the pig. PhD Thesis, Utrecht University, The Netherlands.

Kuller WI, Soede NM, van Beers-Schreurs HMG, Langendijk P, Taverne MAM, Kemp B and Verheijden JHM 2007. Effects of intermittent suckling and creep feed intake on pig performance from birth to slaughter. Journal of Animal Science 85, 1295-1301.

La Barba RC, White JL. 1971. Litter size variations and emotional reactivity in BALB-c mice. Journal of Comparative and Physiological Psychology 75, 254–257.

La Prairie JL and Murphy AZ 2010. Long-term impact of neonatal injury in male and female rats: sex differences, mechanisms and clinical implications. Frontiers in Neuroendocrinology 31, 193-202.

Larson G, Cucchi T and Dobney K 2011. Genetic aspects of pig domestication. In The Genetic of the Pig (ed. MF Rothschild and A Ruvinksy), pp. 14-37. CABI, Wallingford, UK.

Lassen J, Sandøe P and Forkman B 2006. Happy pigs are dirty! - Conflicting perspectives on animal welfare. Livestock Science 103, 221-230.

Lauterbach MD, Raz S, Sander CJ 2001. Neonatal hypoxic risk in preterm birth infants: The influence of sex and severity of respiratory distress on cognitive recovery. Neuropsychology 15, 411-420.

Law CM and Shiell AW 1996. Is blood pressure inversely related to birth weight? The strength of evidence from a systematic review of the literature. Journal of Hypertension 14, 935-941.

Lawlor PG and Lynch PB 2005. Management interventions to help keep piglets alive in large litters. Irish Veterinary Journal 58, 640-645.

Lawrence AB, Petherick JC, McLean K, et al. 1992. Naloxone Prevents Interruption of Parturition and Increases Plasma Oxytocin Following Environmental Disturbance in Parturient Sows. Physiology and Behavior 52, 917-923.

Laws J, Litten JC, Laws A, Lean IJ, Dodds PF and Clarke L 2009. Effect of type and timing of oil supplements to sows during pregnancy on the growth performance and endocrine profile of low and normal birth weight offspring. British Journal of Nutrition 101, 240-249.

Lay DC, Matteri RL, Carroll JA, Fangman TJ and Safranski TJ 2002. Preweaning survival in swine. Journal of Animal Science 80 (E. Suppl. 1), E74-E86.

Lay DCJ, Friend TH, Randel RD, Bowers CL, Grisson KK, Neuendorff DA and Jenkins OC 1998. Effects of restricted nursing on physiological and behavioral reactions of Brahman calves to subsequent restraint and weaning. Applied Animal Behaviour Science 56, 109-119.

Le Dividich J, Morméde P, Catheline M and Caritez JC 1991. Body composition and cold resistance of the neonatal pig from European (Large White) and Chinese (Meishan) breeds. Biology of the Neonate 59, 268–274.

Le Dividich J, Rooke JA and Herpin P 2005. Nutritional and immunological importance of colostrum for the new-born pig. Journal of Agricultural Science 143, 469-485.

Leach KA, Whay HR, Maggs CM, Barker ZE, Paul ES, Bell AK and Main DCJ 2010a. Working towards a reduction in cattle lameness: 1. Understanding barriers to lameness control on dairy farms. Research in Veterinary Science 89, 311-317.

Leach KA, Whay HR, Maggs CM, Barker ZE, Paul ES, Bell AK and Main DCJ 2010b. Working towards a reduction in cattle lameness: 2. Understanding dairy farmers' motivations. Research in Veterinary Science 89, 318-323.

Leenhouwers JI, de Almeida CA, Knol EF, van der Lende T 2001.Progress of farrowing and early postnatal pig behavior in relation to genetic merit for pig survival. Journal of Animal Science 79, 1416-1422.

Leenhouwers JI, van der Lende T, Knol EF 1999. Analysis of stillbirth in different lines of pig. Livestock Production Science 57, 243-253.

Leibbrandt VD, Ewan RC, Speer VC and Zimmerman DR 1975. Effect of Weaning and Age at Weaning on Baby Pig Performance. Journal of Animal Science 40, 1077-1080.

Leitner Y, Heldman D, Harel S and Pick CG 2005. Deficits in spatial orientation of children with intrauterine growth retardation. Brain Research Bulletin 67, 13-18.

Lensink BJ, Leruste H, LeRouxT, Bizeray-Filoche D 2009. Relationship between the behaviour of sows at 6 months old and the behaviour and performance at farrowing. Animal 3, 128-134.

Levitsky DA and Barnes RH 1970. Effect of early malnutrition on the reaction of adult rats to aversive stimuli. Nature 225, 468-469.

Levitsky DA and Barnes RH 1972. Nutritional and environmental interactions in the behavioral development of the rat: Long-term effects. Science 176, 68-71.

Liggins G. 1994. The role of cortisol in preparing the fetus for birth. Reproduction, Fertility and Development 6, 141-150.

Linde-Forsberg C and Persson G 2007. A survey of dystocia in the Boxer breed. Acta Veterinaria Scandinavica 49, 8.

Litten JC, Drury PC, Corson AM, Lean IJ and Clarke L 2003. The influence of piglet birth weight on physical and behavioural development in early life. Biology of the Neonate 84, 311-318.

Liu D, Diorio J, Tannenbaum B, Caldji C, Francis D, Freedman A, Sharma S, Pearson D, Plotsky PM and Meaney MJ 1997. Maternal care, hippocampal glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress. Science 277, 1659-1662.

Lombard JE, Garry FB, Tomlinson SM and Garber LP 2007. Impacts of dystocia on health and survival of dairy calves. Journal of Dairy Science 90, 1751-1760.

Long HF, Ju WS, Piao LG and Kim YY 2010. Effect of dietary energy levels of gestating sows on physiological parameters and reproductive performance. Asian-Australasian Journal of Animal Science 23, 1080-1088.

Long PA and Oats JN 1987. Preeclampsia in twin pregnancy – severity and pathogenesis. Australian and New Zealand Journal of Obstetrics and Gynaecology 27, 1-5.

Louik C, Hernandez-Diaz S, Werler MM and Mitchell AA 2006. Nausea and vomiting in pregnancy: maternal characteristics and risk factors. Paediatric and Perinatal Epidemiology 20, 270-278.

Lund MS, Puonti M, Rydhmer L and Jensen J 2002. Relationship between litter size and perinatal and pre-weaning survival in pigs. Animal Science 74, 217-222.

Lund V and Röcklinsberg H 2001. Outlining a conception of animal welfare for organic farming systems. Journal of Agricultural and Environmental Ethics 14, 391-424.

Lyte M, Varcoe JJ and Bailey MT 1998. Anxiogenic effect of subclinical bacterial infection in mice in the absence of overt immune activation. Physiology and Behavior 65, 63-68.

MacPhail EM 1998. The Evolution of Consciousness. Oxford University Press, New York.

Maestripieri D and Alleva E 1990. Maternal aggression and litter size in female house mouse. Ethology 84, 27-34

Mainau E, Dalmau A, Ruiz-de-la-Torre JL and Manteca X 2010. A behavioural scale to measure ease of farrowing in sows. Theriogenology 74, 1279-1287.

Malmkvist J, Pedersen LJ, Damgaard BM, Thodberg K, Jørgensen E and Labouriau R 2006. Does floor heating around parturition affect the vitality of piglets born to loose housed sows? Applied Animal Behaviour Science 99, 88-105.

Manteca, X. 2009. Behavioural modifications associated with calving in dairy cows and with farrowing in sows. 2nd Boehringer Ingelheim Expert Forum on Farm Animal well-being, pp27-29.

Marchant-Forde JN 2002. Piglet- and stockperson-directed sow aggression after farrowing and the relationship with a pre-farrowing, human approach test. Applied Animal Behaviour Science 75, 115-132.

Marchant-Forde JN 2009. Welfare of Dry Sows. In The Welfare of Pigs (ed. JN Marchant-Forde), pp. 95-139. Springer.

Marchant-Forde JN, Lay, DC, McMunn, KA, Cheng HW, Pajor EA and Marchant-Forde RM 2009. Postnatal piglet husbandry practices and well-being: the effects of alternative techniques delivered separately. Journal of Animal Science 87, 1479-1492

Mark T and Sandøe P 2010. Genomic dairy cattle breeding: risks and opportunities for cow welfare. Animal Welfare 19, 113-121.

Markina FA, Sáez-Royuela C and De Garnica R 2003. Reproductive phenology of wild boar (Sus scrofa L.) in the cantabric mountains (Álava, North Spain). Galemys 15,145–155

Martys M 1982. Observations on parturition and reproductive biology in captive European wild boars (Sus scrofa L.). Z Säug 47,100–113

Mason GJ, Cooper J and Clarebrough C 2001. Frustrations of fur-farmed mink. Nature 410, 35-36.

Massei G, Genov P, Staines B and Gorman M 1997. Mortality of wild boar, Sus scrofa, in a Mediterranean area in relation to sex and age. Journal of Zoology 242, 394-400.

Mauget R 1972. Observations on wild pig (Sus scrofa L.) reproduction. Annales De Biologie Animale Biochimie Biophysique 12, 195–202.

Mauget R 1972. Observations sur la reprodution du sanglier (Sus scrofa L.) a l`état sauvage. Ann Biol Anim Bioch Biophys 12, 195–202

Mauget R and Pépin D 1991. Energy intake, growth and timing of puberty in the European wild boar Sus scrofa L. In: Bobek B, Perzanowski K, Regelion W (eds) Global trends in wildlife management. Trans. 18th IUGB Congress 1987. Swiat, Krakow- Warszawa, pp 205–209

McBride G 1963. The "teat order" and communication in young pigs. Animal Behaviour 11, 53-56.

McDade TW, Beck MA, Kuzawa C and Adair LS 2001. Prenatal undernutrition, postnatal environments, and antibody response to vaccination in adolescence. American Journal of Clinical Nutrition 74, 543-545.

McGlone JJ, Nicholson RI, Hellman JM and Herzog DN 1993. The development of pain in young pigs associated with castration and attempts to prevent castration-induced behavioural changes. Journal of Animal Science 71, 1441-1446

McMahan J 2002. The Ethics of Killing. Problems at the Margins of Life. Oxford: Oxford University Press.

Mellor DJ 2010. Galloping colts, fetal feelings, and reassuring regulations: putting animal-welfare science into practice. Journal of Veterinary Medical Education 37, 94-100.

Mellor DJ and Diesch TJ 2006. Onset of sentience: the potential for suffering in fetal and newborn farm animals. Applied Animal Behaviour Science 100, 48-57.

Mellor DJ and Gregory NG 2003. Responsiveness, behavioural arousal and awareness in fetal and newborn lambs: experimental, practical and therapeutic implications. New Zealand Veterinary Journal 51, 2-13.

Mellor DJ and Stafford KJ 2004. Animal welfare implications of neonatal mortality and morbidity in farm animals. The Veterinary Journal 168, 118-133.

Mellor DJ, Diesch TJ, Gunn AJ and Bennet L 2005. The importance of 'awareness' for understanding fetal pain. Brain Research Reviews 49, 455-471.

Melzack R. (1992). Labour pain as a model of acute pain. Pain 53, 117-120.

Mendl M and Paul ES 2008. Do animals live in the present? Current evidence and implications for welfare. Applied Animal Behaviour Science 113, 357-382.

Mesa H, Safranski TJ, Cammack KM, Weaber RL and Lamberson WR 2006. Genetic and phenotypic relationships of farrowing and weaning survival to birth and placental weights in pigs. Journal of Animal Science 84, 32-40.

Mesa H, Safranski TJ, Fischer KA, Cammack KM and Lamberson WR 2005. Selection for placental efficiency in swine: Genetic parameters and trends. Journal of Animal Science 83, 983-991.

Metz JHM and Gonyou HW 1990. Effect of age and housing conditions on the behavioural and hemolytic reactions of piglets to weaning. Applied Animal Behaviour Science 27, 299-309.

Mgheni M and Christensen K 1985. Selection experiment on growth and litter size in rabbits III. Two-way selection response for litter size. Acta Agriculturæ Scandinavica 35, 287-294.

Milkovic K, Paunovic J, Joffe JM 1976. Effects of pre- and postnatal litter size reduction on development and behavior of rat offspring. Developmental psychobiology 9, 365–75.

Milligan BN, Fraser D and Kramer DL 2001a. Birth weight variation in the domestic pig: effects on offspring survival, weight gain and suckling behaviour. Applied Animal Behaviour Science 73, 171–191.

Milligan BN, Fraser D and Kramer DL 2002. Within-litter weight variation in the domestic pig and its relation to pre-weaning survival, weight gain, and variation in weaning weights. Livestock Production Science 76, 181-191.

Milligan, B. N., Fraser, D., Kramer, D. L. 2001b. The effect of littermate weight on survival, weight gain, and suckling behavior of low-birth-weight piglets in cross-fostered litters. J. Swine. Health Prod., 9, 161-166.

Milon A, Aumaitre A, Le Dividich J, Franz J and Metzger JJ 1983. Influence of birth prematurity on colostrum composition and subsequent immunity of piglets. Annales de Recherches Vétérinaires 14, 533–540.

Miquet J and Viana G 2010. Facilitation of nursing behavior in primiparous sows during colostrum phase improves piglet condition. Proceedings of the 21st IPVS Congress, Vancouver, Canada July 18-21, pp160

Mock DW and Forbes LS 1995. The Evolution of Parental Optimism. Trends in Ecology and Evolution 10, 130-134.

Mock DW and Parker GA 1998. Siblicide, family conflict and the evolutionary limits of selfishness. Animal Behaviour 56, 1-10.

Moinard C, Mendl M, Nicol CJ and Green LE 2003. A case control study of on-farm risk factors for tail biting in pigs. Applied Animal Behaviour Science 81, 333-355.

Mollard RC, Kohut J, Zhao JP and Weiler HA 2004. Proximal intestinal absorption of calcium is elevated in proportion to growth rate but not bone mass is small for gestational age piglets. Journal of Nutritional Biochemistry 15, 149-154.

Molony V 1997. Comments on Anand and Craig. Pain 67, 3-6.

Monks J, Geske FJ, Lehman L and Fadok VA 2002. Do inflammatory cells participate in mammary gland involution? Journal of Mammary Gland Biology and Neoplasia 7, 163-176.

Moore SE, Cole TJ, Collinson AC, Poskitt EME, McGregor IA and Prentice AM 1999. Prenatal or early postnatal events predict infectious deaths in young adulthood in rural Africa. International Journal of Epidemiology 28, 1088-1095.

Moretti M 1995. Birth distribution, structure and dynamics of a hunted mountain population of wild boars (Sus scrofa L.), Ticino, Switzerland. Ibex, Journal of Mountain Ecology 3, 192–196.

Morgane PJ, Austinlafrance R, Bronzino J, Tonkiss J, Diazcintra S, Cintra L, Kemper T and Galler JR 1993. Prenatal Malnutrition and Development of the Brain. Neuroscience and Biobehavioral Reviews 17, 91-128.

Morise A, Louveau I and Le Huërou-Luron I 2008. Growth and development of adipose tissue and gut and related endocrine status during early growth in the pig: impact of low birth weight. Animal 2, 73-83.

Mormède P, Foury A, Terenina E and Knap PW 2011. Breeding for robustness: the role of cortisol. Animal 5, 651-657.

Morrow-Tesch J and McGlone JJ 1990. Sources of maternal odors and the development of odor preferences in baby pigs. Journal of Animal Science 68, 3563–3571.

Mota-Rojas D, Martinez-Burnes J, Trujillo-Ortega ME, Alonso-Spilsbury M, Ramirez-Necoechea R and Lopez A 2002. Effect of oxytocin treatment in sows on umbilical cord morphology, meconium staining, and neonatal mortality of piglets. American Journal of Veterinary Research 63, 1571-1574.

Mota-Rojas D, Rosales AM, Trujillo ME, Orozco H, Ramirez R and onso-Spilsbury M 2005. The effects of vetrabutin chlorhydrate and oxytocin on stillbirth rate and asphyxia in swine. Theriogenology 64, 1889-1897.

Mota-Rojas D, Trujillo-Ortega ME, Villanueva-Garcia D, González-Lozano M, Orozco-Gregorio H, Ramirez-Necoechea R, Olmos-Hernández A and Alonso-Spilsbury M 2006. Can uterotonics reduce fetal and newborn piglet mortality by perinatal asphyxia and improve functional vitality? Journal of Medical Sciences 6, 884-893.

Moustsen VA, Lahrmann HP and D'Eath RB 2011. Relationship between size and age of modern hyper-prolific crossbred sows. Livestock Science, doi:10.1016/j.livsci.2011.06.008

Mul M, Vermeij I, Hindle V and Spoolder H 2010. EU-Welfare legislation on pigs. Wageningen UR Livestock Research Report 273.

Mulder HA, Bijma P and Hill WG 2007. Breeding for uniformity by exploiting genetic differences in environmental variance with an application to carcass weight in pigs. EAAP, 26-29. august, Dublin, Ireland.

Mulder HA, Bijma P and Hill WG 2008. Selection for uniformity in livestock by exploiting genetic heterogeneity of residual variance. Genetics Selection Evolution 40, 37-59.

Müller K. 2011. 30 abgesetzte Ferkel –nur eine Frage der Genetik? Möglichkeiten die Aufzuchtleistung durch Ammen zu verbessern. Landwirtschaftskammer Schleswig-Holstein. http://www.znvg.de/cms_images/KMueller.pdf

Munsterhjelm C, Valros A, Heinonen M, Hälli O, Siljander-Rasi H and Peltoniemi OAT 2009. Environmental enrichment in early life affect cortisol patterns in growing pigs. Animal 4, 242-249.

Musse,S. L. 2007. Effect of manual assistance and of drying off newborn piglets. MSc thesis. University of Copenhagen

Musser RE, Goodband RD, Tokach MD, Owen KQ, Nelssen JL, Blum SA, Dritz SS and Civis CA 1999. Effects of L-carnitine fed during gestation and lactation on sow and litter performance. Journal of Animal Science 77, 3289-3295.

Nagy ZM and Porada KJ 1991. Effects of Undernutrition by Rearing in Large Litters on Acquisition and Memory of Active-Avoidance Learning in Mice. Bulletin of the Psychonomic Society 29, 351-354.

Náhlik A and Sándor G 2003. Birth rate and offspring survival in a freeranging wild boar Sus scrofa population. Wildlife Biology 9, 37–42

Neet CR 1995. Population dynamics and management of Sus scrofa in Western Switzerland: a statistical modelling approach. Ibex, Journal of Mountain Ecology 3, 188–191.

Newberry RC and Wood-Gush DGM 1985. The suckling behaviour of domestic pigs in a semi-natural environment. Behaviour 95, 11-25.

Newberry RC. and Swanson JC 2008. Implications of breaking mother-young social bonds. Applied Animal Behaviour Science 110, 3-23.

Niekamp SR, Sutherland MA, Dahl GE, Salak-Johnson JL. 2006. Photoperiod influences the immune status of multiparous pregnant sows and their piglets. Journal of Animal Science 84, 2072-2082.

Nielsen B and Berg P 2011. Faldende dødelighed i avl og opformeringer. Landbrugsavisen, Submitted.

Nielsen N-P 1995. Electronic sow feeding. Report no.312. Elektronisk sofodring. Landsudvalget for Svin og Den rullende Afprøvning. Meddelelse nr. 312. 1995. http://vsp.lf.dk/Publikationer/Kilder/lu_medd/medd/312.aspx

Nizard J and Arabin B 2005. Maternal cardiovascular adaptation. In Multiple pregnancy: epidemiology, gestation and perinatal outcome (ed. I Blickstein and LG Keith), pp. 436-443. Informa UK Ltd.

Norring M, Valros A, Munksgaard L, Puumala M, Kaustell KO and Saloniemi H 2006. The development of skin, claw and teat lesions in sows and piglets in farrowing crates with two concrete flooring materials. Acta Agriculturae Scandinavica Section A-Animal Science 56, 148-154.

Ødegård J, Meuwissen THE, Heringstad B and Madsen P 2010. A simple algorithm to estimate genetic variance in an animal threshold model using Bayesian inference. Genetics Selection Evolution 42, 29.

Oliviero C, Heinonen M, Pastell M, Heikkonen J, Valros A, Vainio O and Peltoniemi O 2007. Modern technology in supervision of parturition to prevent piglet mortality. Acta Veterinaria Scandinavica 49 (Suppl 1), S12.

Oliviero C, Heinonen M, Valros A and Peltoniemi O 2010. Environmental and sow-related factors affecting the duration of farrowing. Animal Reproduction Science 119, 85-91.

Oloff H 1951. Zur Biologie Und Ökologie Des Wildschweines. Dr. Paul Schöps Verlag, Frankfurt, Germany.

Olson GL, Robine L, Rosengren LB, Baker CD, Duggan M, Chirino M, Weber LP and Harding CS 2009. Parturition induction two days prior to term decreases birth weight and lactational growth, but not pigletmaturity, health or post-weaning growth. Canadian Journal of Animal Science 89, 219-228.

Olsson IAS, Gamborg C and Sandøe P 2006. Taking ethics into account in farm animal breeding: what can the breeding companies achieve? Journal of Agricultural and Environmental Ethics 19, 37-46.

Oltenacu PA and Broom DM 2010. The impact of genetic selection for increased milk yield on the welfare of dairy cows. Animal Welfare 19, 39-49.

Oostindjer M, Bolhuis JE, van den Brand H, Roura E and Kemp B 2010. Prenatal flavor exposure affects growth, health and behavior of newly weaned piglets. Physiology & Behavior 99, 579-586.

Otten W, Kanitz E, Tuchscherer M and Nurnberg G 2001. Effects of prenatal restraint stress on hypothalamic-pituitary-adrenocortical and sympatho-adrenomedullary axis in neonatal pigs. Animal Science 73, 279-287.

Otten W, Kanitz E, Tuchscherer M, Puppe B and Nurnberg G 2007. Repeated administrations of adrenocorticotropic hormone during gestation in gilts: Effects on growth, behaviour and immune responses of their piglets. Livestock Science 106, 261-270.

Pajor EA, Weary DM, Fraser D and Kramer DL 1999. Alternative housing for sows and litters - 1. Effects of sow-controlled housing on responses to weaning. Applied Animal Behaviour Science 65, 105-121.

Parfit D 1984. Reasons and persons. Oxford: Clarendon Press.

Partlow GD, Fisher KRS, Page PD, MacMillan K and Walker AF 1993. Prevalence and types of birth-defects in Ontario swine determined by mail survey. Canadian Journal of Veterinary Research 57, 67-73.

Patterson R, Connor ML, Krause DO and Nyachoti CM 2008. Response of piglets weaned from sows fed diets supplemented with conjugated linoleic acid (CLA) to an Escherichia coli K88(+) oral challenge. Animal 2, 1303-1311.

Pedersen LJ and Jensen T 2008. Effects of late introduction of sows to two farrowing environments on the progress of farrowing and maternal behavior. Journal of Animal Science 86, 2730-2737.

Pedersen LJ, Berg P, Jørgensen E, Bonde MK, Herskin MS, Møllegaard Knage-Rasmussen K, Kongsted AG, Lauridsen C, Oksbjerg N, Poulsen HD, Sorensen DA, Su G, Sørensen MT, Theil PK, Thodberg K and Jensen KH 2010. Pattegrisedødelighed i dk: Muligheder for reduktion af pattegrisedødeligheden i Danmark. DJF Rapport Husdyrbrug Nr. 86.

Pedersen LJ, Berg P, Jørgensen G and Andersen IL 2011. Neonatal traits of importance for survival in crates and indoor pens. Journal of Animal Science 89, 1207-1218.

Pedersen ML, Moustsen VA, Nielsen MBF and Kristensen AR 2011. Improved udder access prolongs duration of milk letdown and increases piglet weight gain. Livestock Science, In Press.

Pedone P, Mattioli L, Mattioli S, Siemoni N, Lovari C and Mazzarone V 1991. Body growth and fertility in wild boars of Tuscany, central Italy. In: Csanyi S, Ernhaft J (eds) Transactions of the XXth IUGB Congress Part II. University of Agricultural Sciences, Godöllö, pp 604–609

Peeters-Scholte C, Koster J, van den Tweel E, Blomgren K, Hamers N, Zhu C, van Buul-Offers S, Hagberg H, van Bel F, Heijnen C and Groenendaal F 2002. Effects of selective nitric oxide synthase inhibition on IGF-1, caspases and cytokines in a newborn piglet model of perinatal hypoxia-ischaemia. Developmental Neuroscience 24, 396-404.

Peeters-Scholte C, Koster J, Veldhuis W, van den Tweel E., Zhu C, Kops N, Blomgren K, Bar D, van Buul-Offers S, Hagberg H, Nicolay K, van Bel F and Groenendaal F 2002. Neuroprotection by selective nitric oxide synthase inhibition at 24h after perinatal hypoxia-ischemia. Stroke 33, 2304-2310.

Penny RCH and Hill FWG 1974. Observations of some conditions in pig at the abattoir with particular reference to tail biting. The Veterinary Record 94, 174-178.

Perry JS and Rowell JG 1969. Variations In Foetal Weight And Vascular Supply Along Uterine Horn of Pig. Journal of Reproduction and Fertility 19, 527-534.

Phillips DIW, Walker BR, Reynolds RM, Flanagan DEH, Wood PJ, Osmond C, Barker DJP and Whorwood CB 2000. Low birth weight predicts elevated plasma cortisol concentrations in adults from 3 populations. Hypertension 35, 1301-1306.

Piao LG, Ju WS, Long HF and Kim YY 2010. Effects of Various Feeding Methods for Gestating Gilts on Reproductive Performance and Growth of Their Progeny. Asian-Australasian Journal of Animal Sciences 23, 1354-1363.

Pittaway MJ and Brown PL. 1974. Early weaning and cage rearing. Pig Farming 22:26–29.

Pluske JR 1995. Nutrition of the neonatal pig. In *The neonatal pig development and survival* (ed. MA Varley), pp.187-235. CABI, Wallingford, UK.

Poore KR and Fowden AL 2003. The effect of birth weight on hypothalamic-pituitary-adrenal axis function in juvenile and adult pigs. Journal of Physiology 547, 107-116.

Poore KR, Forhead AJ, Gardner DS, Giussani DA and Fowden AL 2002. The effects of birth weight on basal cardiovascular function in pigs at 3 months of age. Journal of Physiology 15, 969-978.

Pope WF 1994. Embryonic mortality in swine. In: Geisert, RD and Zavy MT (eds.) Embryonic Mortality in Domestic Species. pp 53–78.Boca Raton: CRC Press.

Prager G, Stefanski V, Hudson R and Rödel H. 2010. Family matters: maternal and litter-size effects on immune parameters in young laboratory rats. Brain, Behavior and Immunity 24, 1371-1378.

Price EO, Hutson GD, Price MI and Borgwardt R 1994. Fostering in Swine As Affected by Age of Offspring. Journal of Animal Science 72, 1697-1701.

Prunier A and Quesnel H 2000. Nutritional influences on the hormonal control of reproduction in female pigs. Livestock Production Science 63, 1–16.

Prunier A, Bonneau M, vonBorell EH, Cinotti S, Gunn M, Fredriksen B, Giersing M, Morton DB, Tuyttens FAM and Velarde A 2006. A review of the welfare consequences of surgical castration in piglets and the evaluation of non-surgical methods. Animal Welfare 15, 277-289.

Prunier A, Heinonen M and Quesnel H 2010. High physiological demands in intensively raised pigs: impact on health and welfare. Animal 4, 886-898.

Prunier A, Mounier AM and Hay M 2005. Effects of castration, tooth resection, or tail docking on plasma metabolites and stress hormones in young pigs. Journal of Animal Science 83, 216-222.

Pumfrey RA, Johnson RK, Cunningham PJ and Zimmerman DR 1980. Inheritance of teat number and its relationship to maternal traits in swine. Journal of Animal Science 50, 1057-1060.

Puppe B and Tuchscherer A 1999. Developmental and territorial aspects of suckling behaviour in the domestic pig (Sus scrofa f. domestica). Journal of Zoology 249, 307-313.

Quesnel H 2009. Lactational and nutritional effects on follicular development in the sow. In Control of Pig Reproduction VIII (ed. H Rodriguez-Martinez, JL Vallet and AJ Ziecik), pp. 121–134. Nottingham University Press, Nottingham, UK.

Quesnel H 2011. Colostrum production by sows: variability of colostrum yield and immunoglobulin G concentrations. Animal, In Press.

Quesnel H and Prunier A 1995. Endocrine bases of lactational anoestrus in the sow. Reproduction Nutrition and Development 35, 395-414.

Quesnel H, Brossard L, Valancogne A and Quiniou N 2008. Influence of some sow characteristics on within-litter variation of piglet birth weight. Animal 2, 1842-1849.

Quiniou N, Dagorn J and Gaudre D 2002 Variation of piglets birth weight and consequences on subsequent performance. Livestock Production Science 78, 63-70

Quinton VM, Wilton JW, Robinson JA and Mathur PK 2006. Economic weights for sow productivity traits in nucleus pig populations. Livestock Science 99, 69-77.

Rajala PJ and Grohn YT 1998. Effects of dystocia, retained placenta, and metritis on milk yield in dairy cows. Journal of Dairy Science 82, 3172-3181.

Randall GCB 1972. Observations on parturition in the sow. I. Factors associated with the delivery of the piglets and their subsequent behaviour. Veterinary Record 90, 178–182.

Rantzer D, Svendsen J and Westrom B 1995. Weaning of Pigs Raised in Sow-Controlled and in Conventional Housing Systems .2. Behavior Studies and Cortisol-Levels. Swedish Journal of Agricultural Research 25, 61-71.

Rashwan AA and Marai IFM 2000. Mortality in young rabbits: a review. World Rabbit Science 8, 111-124.

Rauw WM 2009. Resource allocation theory applied to farm animal production. CAB International, Wallingford.

Reese D, Prosch A, Travnicek DA and Eskridge KM 2008. Dietary fiber in sow gestation diets – an updated review. Nebraska Swine Report 2008, 14-18.

Ridgeon B 1993. The Economics of Pig Production: Records and performance of pig production as monitored by the Cambridge pig management scheme. Farming Press, Ipswich.

Rigatto H, Moore M and Cates D 1986. Fetal Breathing and Behaviour Measured Through a Double-Wall Plexiglas Window in Sheep. Journal of Applied Physiology 61,160-164.

Robert S and Martineau GP 2001. Effects of repeated cross-fosterings on preweaning behavior and growth performance of piglets and on maternal behavior of sows. Journal of Animal Science 79, 88-93.

Robert S, Thompson BK, and Fraser D. 1995. Selective tooth clipping in the management of low-birth-weight piglets, Canadian Journal of Animal Science 75, 285–289.

Robinson E 1975. Effect of crowding and litter size on several behaviors of white rats. Psychological Reports 37, 599–606.

Rödel HG, Meyer S, Prager G, Stefanski V and Hudson R 2010. Litter size is negatively correlated with corticosterone levels in weanling and juvenile rats. Physiology and Behavior 99, 644-650.

Rödel HG, Starkloff A, Seltmann MW, Prager G and von Holst D 2009. Causes and consequences of nest mortality in a European rabbit population. Mammalian Biology 74, 198-209.

Roehe R 1999 Genetic determination of individual birthweight and its association with sows' productivity traits using Bayesian analysis. Journal of Animal Science 77, 330–343.

Roehe R and Kalm E 2000. Estimation of genetic and environmental risk factors associated with pre-weaning mortality in piglets using generalized linear mixed models. Animal Science 70, 227-240.

Roehe R, Shrestha NP, Mekkawy W, Baxter EM, Knap PW, Smurthwaite KM, Jarvis S, Lawrence, AB, Edwards SA 2009. Genetic analyses of piglet survival and individual birth weight on first generation data of a selection experiment for piglet survival under outdoor conditions. Livestock Science 121, 173-181.

Roehe R, Shrestha NP, Mekkawy W, Baxter EM, Knap PW, Smurthwaite KM, Jarvis S, Lawrence AB and Edwards SA 2010. Genetic parameters of piglet survival and birth weight from a two-generation crossbreeding experiment under outdoor conditions designed to disentangle direct and maternal effects. Journal of Animal Science 88, 1276-1285.

Roehe R 1991. Development of optimal selection strategies when using an animal model in the nucleus of swine breeding programs. PhD thesis, University of Kiel, Germany.

Romano T, Wark JD, Owens JA and Wlodek ME 2009. Prenatal growth restriction and postnatal growth restriction followed by accelerated growth independently program reduced bone growth and strength. Bone 45, 132-141.

Rooke JA, Sinclair AG, Edwarcs SA, Cordoba R, Pkiyach S, Penny PC, Penny P, Finch AM and Horgan GW 2001. The effect of feeding salmon oil to sows throughout pregnancy on pre-weaning mortality of piglets. Animal Science 73, 489-500.

Rosell C 1998. Biology and Ecology of wild boar (Sus scrofa L.,1758) from two northeast Iberian populations: Management purposes. PhD. Thesis, Universitat de Barcelona

Rosendo A, Druet T, Gogué J, Canario L and Bidanel JP 2007. Correlated responses for litter traits to six generations of selection for ovulation rate or prenatal survival in French Large White pigs. Journal of Animal Science 85, 1615-1624.

Rosochacki SJ, Piekarzewska AB, Poloszynowicz J and Sakowski T 2000. The influence of restraint immobilization stress on the concentration of bioamines and cortisol in plasma of Pietrain and Duroc pige. Journal of Veterinary Medicine Series A-Physiology Pathology Clinical Medicine 47, 231-242.

Ross JW and Prather RS 2011. Transgenics and modern reproductive technologies. In The Genetic of the Pig (ed. MF Rothschild and A Ruvinksy), pp. 242-262. CABI, Wallingford, UK.

Royal College of Obstetricians and Gynaecologists 2010. Fetal Awareness: Review of Research and Recommendations for Practice, Report of a working party. http://www.rcog.org.uk/files/rcog-corp/RCOGFetalAwarenessWPR0610.pdf

Royston JP, Flecknell PA and Wootton R 1982. New evidence that the intra-uterine growth-retarded piglet is a member of a discrete subpopulation. Biology of the Neonate 42, 100–104.

Rushen J 2003. Changing concepts of farm animal welfare: bridging the gap between applied and basic research. Applied Animal Behaviour Science 81, 199-214.

Rutgers B and Heeger R 1999. Inherent Worth and Respect for Animal Integrity. In Recognizing the Intrinsic Value of Nature (ed. M Dol, MF van Vlissingen, S Kasanmoentalib, T Visser and H Zwart), pp. 41–53. Van Gorcum, Assen, The Netherlands.

Rutherford KMD, Robson SK, Donald RD, Jarvis S, Sandercock DA, Nolan AM, Lawrence AB 2009. Prenatal stress amplifies spontaneous behavioural responses to acute pain in the neonatal pig. Biology Letters 5, 452-454.

Rutherford KMD, Piastowska A, Donald RD, Robson SK, Ison SH, Brunton PJ, Russell JA and Lawrence AB Submitted. Prenatal stress creates anxiety prone females and impairs maternal behaviour in the domestic pig. Hormones and Behavior

Rutter N and Doyal L 1998. Neonatal care and management of pain: historical and ethical issues. Seminars in Neonatology 3, 297-302.

Ryan V, Wehmer F 1975. Effect of postnatal litter size on adult aggression in the laboratory mouse. Developmental Psychobiology 8, 363–70.

Rydhmer L, Lundeheim N and Canario L 2008. Genetic correlations between gestation length, piglet survival and early growth. Livestock Science 115, 287-293.

Saether BE and Gordon IJ 1994. The adaptive significance of reproductive strategies in ungulates. Proceedings of the Royal Society B: Biological Sciences 256, 263-268.

Sáez-Royuela C and Tellería JL 1987. Reproductive trends of the wild boar (Sus scrofa) in Spain. Folia Zoologica 36, 21–25

Salmon, H 2000 Mammary gland immunology and neonate protection in pigs. Homing of lymphocytes into the MG. Advances in Experimental Medicine and Biology 480, 279–286

Sander HW and Gintzler AR 1987. Spinal – Cord Mediation of the Opioid Analgesia of Pragnancy. Brain Research 408, 389-393.

Sangild PT, Hilsted L, Nexø E, Fowden AL and Silver M 1995. Vaginal birth versus elective caesarean section: effects on gastric function in the neonate. Experimental Physiology 80, 147-157.

Sargison ND, Scott PR, Penny CD and Pirie RS 1995. Effect of An Outbreak of Sheep Scab (Psoroptes Ovis Infestation) During Mid-Pregnancy on Ewe Body Condition and Lamb Birth-Weight. Veterinary Record 136, 287-289.

Scheel DE, Graves HB and Sherritt GW 1977. Nursing order, social dominance, and growth in swine. Journal of Animal Science 45, 219-229.

Schenck EL, Mcmunn KA, Rosenstein DS, Stroshine RL, Nielsen BD, Richert BT, Marchant-Forde JN and Lay DC 2008. Exercising stall-housed gestating gilts: Effects on lameness, the musculo-skeletal system, production, and behavior. Journal of Animal Science 86, 3166-3180.

Sellier P and Ollivier L 1982. A genetic study of splayleg in the new-born piglet. I. Multifactorial model with one threshold. Annales de Genetique et de Selection Animale 14, 77-92.

Sellier P, Dando E and Dando P 1999. Induction of parturition in the sow and incidence of splayleg syndrome in the newborn piglet. Annales de Zootechnie 48, 153-161

Sephton SE, Sapolsky RM, Kraemer HC and Spiegel D 2000. Diurnal cortisol rhythm as a predictor of breast cancer survival. Journal of the National Cancer Institute 92, 994-1000.

Serenius T and Stalder KJ 2006. Selection for sow longevity. Journal of Animal Science 84, E166

Serenius T and Stalder KJ 2007. Length of productive life of crossbred sows is affected by farm management, leg conformation, sow's own prolificacy, sow's origin parity and genetics. Animal 1, 745-750.

Servanty S, Gaillard JM, Allainé D, Brandt S and Baubet E 2007. Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. Behavioral Ecology 18, 427-432.

Smith-Levitin M and Vohra N 2005. Hypertension disorders. In Multiple pregnancy: epidemiology, gestation and perinatal outcome (ed. I Blickstein and LG Keith), pp. 444-450. Informa UK Ltd.

Smulders FJM 2009. A practical approach to assessing risks for animal welfare – methodological considerations. In: Welfare of production animals: assessment and management of risks, pp239-274, FJM Smulders & B Algers (eds), Food safety assurance and veterinary public health, Volume 5, Wageningen Academic Publishers, Wageningen.

Sommavilla R, Hötzel MJ and Dalla Costa OA 2011. Piglets' weaning behavioural response is influenced by quality of human-animal interactions during suckling. Animal (In Press).

Sorensen D, Vernersen A and Andersen S 2000. Bayesian analysis of response to selection: a case study using litter size in Danish Yorkshire pigs. Genetics 156, 283–295.

Spencer SJ and Tilbrook A 2009. Neonatal overfeeding alters adult anxiety and stress responsiveness. Psychoneuroendocrinology 34, 1133-1143.

Spinka M and Algers B 1995. Functional view on udder massage after milk let-down in pigs. Applied Animal Behaviour Science 43, 197-212.

Spötter A and Distl O 2006. Genetic approaches to the improvement of fertility traits in the pig. The Veterinary Journal 172, 234-247.

Stalder KJ, Knauer M, Baas TJ, Rothschild MF and Mabry JW. 2004. Sow longevity. Pig News Inf. 25, 53–74.

Star L, Ellen ED, Uitdehaag K and Brom FWA 2008. A please to implement robustness into a breeding goal: poultry as an example. Journal of Agricultural and Environmental Ethics 21, 109-125.

Steinman JL, Carlton SM, Willis WD 1992. The Segmental Distribution of Afferent – Fibers from the Vaginal Cervix and Hypogastric Nerve in Rats. Brain Research 575, 25-31.

Stewart TS and Diekman MA 1989. Effect of birth and fraternal litter size and cross-fostering on growth and reproduction in swine. Journal of Animal Science 67, 635-640.

Stott GH and Reinhard EJ 1978. Adrenal function and passive immunity in the dystocial calf. Journal of Dairy Science 61, 1457-1461.

Strange, T. 2011. Genetic parameters of piglet mortality traits in Danish crossbred pigs. Master Thesis, University of Copenhagen, Faculty of Life Sciences, Department of Basic Animal and Veterinary Sciences, Denmark, pp. 33.

Straw B, Bates R and May G 2008. Influence of method of administration of prostaglandin onfarrowing and relationship between gestation length and piglet performance. Journal of Swine Health and Production 16, 138-143.

Straw BE, Dewey CE and Bürgi EJ 1998. Patterns of crossfostering and piglet mortality on commercial U.S. and Canadian swine farms. Preventive Veterinary Medicine 33, 83-89.

Stubbe W and Stubbe M 1977. Vergleichende Beiträge zur Reproduktions und Geburtsbiologie von Wild und Hausschwein *Sus scrofa* L., 1758. Beiträge Zur Jagd Und Wildforschung 10, 153–179.

Su G, Lund MS and Sorensen D 2007. Selection for litter size at day five to improve litter size at weaning and piglet survival rate. Journal of Animal Science 85, 1385-1392.

Su G, Sorensen D and Lund MS 2008. Variance and covariance components for liability of piglet survival during different periods. Animal 2, 184-189.

Suddendorf T and Corballis MC 2007. The evolution of foresight: what is mental time travel, and is it unique to humans? Behavioral and Brain Science 30, 299-351.

Sumner BEH, D'Eath RB, Farnworth MJ, Robson S, Russell JA, Lawrence AB and Jarvis S 2008. Early weaning results in less active behaviour, accompanied by lower 5-HT1A and higher 5-HT2A receptor mRNA expression in specific brain regions of female pigs. Psychoneuroendocrinology 33, 1077-1092.

Sundrum A 2011. Epidemiological study concerning the characteristics of organic pig farming in selected European countries. CORE Organic project Nr 1904. http://orgprints.org/18428/1/18428.pdf

SVC. 1997 The welfare of intensively kept pigs. Report of the Scientific Veterinary Committee of the EU. http://ec.europa.eu/food/animal/welfare/farm/out17_en.pdf

Svendsen LS, Westrom B.R., Svendsen J, Olsson A.C. and Karlsson B.W. 1991. Blood serum characteristics of newborn pigs: comparison of unaffected pigs with pigs belonging to five mortality groups. Acta Vet Scand 32, 287-299.

Taddio A, Katz J, Ilersich AL and Koren G 1997. Effect of neonatal circumcision on pain response during subsequent routine vaccination. Lancet 349, 599-603.

Taylor NR, Main DCJ, Mendl M and Edwards SA 2010. Tail-biting: A new perspective. The Veterinary Journal 186, 137-147.

Taylor P 1986. Respect for Nature. Princeton: Princeton University Press.

Ten Napel J, Bianci F and Bestman M 2006. Utilising intrinsic robustness in agricultural production systems. Transforum Working Papers No. 1, Zoetermeer, pp. 32–52.

Tenhagen BA, Edinger D and Heuwieser W. 1999. Impact of dystocia in primiparous cows on lactational performance and survival. Tierarztliche Umschau 54, 617-623.

Theil PK, Sejrsen K, Hurley WL, Labouriau R, Thomsen B and Sorensen MT 2006 Role of suckling in regulating cell turnover and onset and maintenance of lactation in individual mammary glands of sows. Journal of Animal Science 84, 1691-1698

Thorup F 2006. Back fat level at farrowing affects the frequency of shoulder lesions. 19th congress of the International Pig Veterinary society. Copenhagen. No. P.33-07, p. 486.

Thorup F 2010b. Productivity in sows nursing large litters. 21st intn. Pig vet. Soc. Conf., Vancouver, 66

Thorup F and Musse SL 2010.Piglet Survival depends on relative birth weight. Proceedings 21st IPVS Congress, Vancouver, Canada, pp1184

Thorup F and Sorensen AK 2006. Moving the nurse sow. Report number 748. Dansk Svineproduktion

Thorup F and Sørensen AK 2006. Use of one step or two step nurse sows for surplus piglets. 19th congress of the International Pig Veterinary society. Copenhagen. No. O.13-02, p. 105.

Thorup F, 2007. Effect of a sow having functioned as a nurse sow. Report number 793. Dansk Svineproduktion

Thorup F, Eriksen L and Risum D 2004. Predicting piglets at birth with a high risk for mortality. 18th congress of the International Pig Veterinary society. Germany, 478

Tölle K-H and Meyer C 2008. Schweine aktuell: Umgang mit vielen Saugferkeln (Teil 2): Erfahrungen mit technischen Ammen im LVZ Futterkamp. Bauernblatt 15. 37-39

Toma L, Ashworth CJ and Stott A 2008. A partial equilibiurm model of the linkages between animal welfare, trade and the environment in Scotland. In Proc., 109th EAAE Seminar: The CAP after the Fischler reform: National Implementations, impact assessment and the agenda for future reforms, November 2008, Viterbo, Italy.

Torrey S and Widowski TM 2007. Relationship between growth and non-nutritive massage in suckling pigs. Applied Animal Behaviour Science 107, 32-44.

Torrey S, Devillers N, Lessard M, Farmer C and Widowski T 2009. Effect of age on the behavioural and physiological responses of piglets to tail docking and ear notching. Journal of Animal Science 87, 1778-1786.

Tse WY, Town SC, Murdock GK, Novak S, Dyck MK, Putman CT, Foxcroft GR and Dixon WT 2008. Uterine crowding in the sow affects litter sex ratio, placental development and embryonic myogenin expression in early gestation. Reproduction, Fertility and Development 20, 497-504.

Tuchscherer M, Kanitz E, Otten W and Tuchscherer A 2002. Effects of prenatal stress on cellular and humoral immune responses in neonatal pigs. Veterinary Immunology and Immunopathology 86, 195-203.

Tuchscherer M, Puppe B, Tuchscherer A and Tiemann U 2000. Early identification of neonates at risk: Traits of newborn piglets with respect to survival. Theriogenology 54, 371-388.

Turner SP, Farnworth MJ, White IMS, Brotherstone S, Mendl M, Knap P, Penny P and Lawrence A B 2006. The accumulation of skin lesions and their use as a predictor of individual aggressiveness in pigs. Applied Animal Behaviour Science 96, 245-259.

Uvnäs-Moberg K 1989. The Gastrointestinal-Tract in Growth and Reproduction. Scientific American 261, 78-83.

Vaillancourt JP, Marsh WE and Dial GD 1992. Internal consistency of preweaning mortality data collected by swine production. Preventive Veterinary Medicine 14, 115-128.

Vaillancourt JP, Stein TE, Marsh WE, Leman AD and Dial GD 1990. Validation of producer-recorded causes of preweaning mortality in swine. Preventive Veterinary Medicine 10, 119-130.

Vallet JL and Freking BA 2006. Changes in fetal organ weights during gestation after selection for ovulation rate and uterine capacity in swine. Journal of Animal Science 84, 2338-2345.

Valros A, Rundgren M, Spinka M, Saloniemi H, Rydhmer L, Hultén F, Uvnäs-Moberg K, Tománek M, Krejcí P and Algers B 2003. Metabolic state of the sow, nursing behaviour and milk production. Livestock Production Science 79**,** 155-167.

Van den Brand H, Soede NM and Kemp B 2006. Supplementation of dextrose to the diet during the weaning to estrus interval affects subsequent variation in within-litter piglet birth weight. Animal Reproduction Science 91, 353-358.

Van den Brand H, van Enckevort LCM, van der Hoeven EM and Kemp B 2009. Effects of dextrose plus lactose in the sows diet on subsequent reproductive performance and within litter birth weight variation. Reproduction in Domestic Animals 44, 884-888.

Van Der Heyd H, De Mets JP, Porreye L, Henderickx H, Calus A, Bekaert H and Buysse F 1989. Influence of Season Litter Size Parity Gestation Length Birth Weight Sex and Farrowing Pen on Frequency of Congenital Splayleg in Piglets. Livestock Production Science 21, 143-156.

Van der Lende T and deJager D 1991. Death risk and preweaning growth rate of piglets in relation to the within-litter weight distribution at birth. Livestock Production Science 28, 73-84.

Van der Lende T, Knol EF and Leenhouwers JI 2001. Prenatal development as a predisposing factor for perinatal losses in pigs. Journal Of Reproduction And Fertility, Supplements 58, 247-261.

Van Dijk AJ, Jonker FH and Taverne MAM 2008. The effect of administration of 2-iminobiotin at birth on growth rates, morbidity and mortality in piglets under farm conditions. Livestock Science 115, 129-136.

Van Dijk AJ, van Rens BTTM, van der Lende T and Taverne MAM 2005. Factors affecting duration of the expulsive stage of parturition and piglet birth intervals in sows with uncomplicated, spontaneous farrowings. Theriogenology 64, 1573-1590.

Van Erp-van der Kooij E, Kuijpers AH, van Eerdenburg FJCM and Tielen MJM 27-8-2001. A note on the influence of starting position, time of testing and test order on the backtest in pigs. Applied Animal Behaviour Science 73, 263-266.

Van Kempen T 2007. Sports supplements to facilitate parturition and reduce perinatal mortality. In Recent Advances in Animal Nutrition – 2007 (eds P Garnsworthy and J Wiseman) Nottingham University Press, Nottingham, UK.

Van Rens BTTM, De Koning G, Bergsma, R and Van Der Lende T 2005. Preweaning piglet mortality in relation to placental efficiency. Journal of Animal Science 83, 144-151.

Van Rens BTTM and van der Lende T 2004. Parturition in gilts: duration of farrowing, birth intervals and placenta expulsion in relation to maternal, piglet and placental traits. Theriogenology 62, 331-352

Vanderhaeghe C, Dewulf J, DeVliegher S, Papdopoulos GA, deKruif A and Maes D 2010a. Longitudinal field study to assess sow level risk factors associated with stillborn piglets. Animal Reproduction Science 120, 78-83.

Vanderhaeghe C, Dewulf J, Jourquin J, deKruif A and Maes D 2011. Incidence and prevention of early parturition in sows. Reprodution in Domestic Animals 46, 428-433.

Vanderhaeghe C, Dewulf J, Ribbens S, deKruif A and Maes D 2010b. A cross-sectional study to collect risk factors associated with stillbirths in pig herds. Animal Reproduction Science 118, 62-68.

Vannucci RC and Perlman JM 1997. Interventions for perinatal hypoxic-ischemic encephalopathy. Pediatrics 100, 1004-1114.

Veras MM, Damaceno-Rodrigues NR, Silva RMG, Scoriza JN, Saldiva PH, Caldini EG and Dolhnikoff M 2009. Chronic exposure to fine particulate matter emitted by traffic affects reproductive and fetal outcomes in mice. Environmental Research 109, 536-543

Vermorel M, Vernet J, Dardillat C, SAIDO, Demigne C and Davicco MJ 1989. Energy metabolism and thermoregulation in the newborn calf: Effect of calving conditions. Canadian Journal of Animal Science 69, 113-122.

Vinsky MD, Novak S, Dixon WT, Dyck MK and Foxcroft GR 2006. Nutritional restriction in lactating primiparous sows selectively affects female embryo survival and overall litter development. Reproduction Fertility and Development 18, 347-355.

Vogt DW, Gipson TA, Akremi B, Dover S and Ellersieck MR 1984. Associations of sire, breed, birth weight, and sex in pigs with congenital splayleg. American Journal of Veterinary Research 45, 2408-2409.

Waldner CL and Rosengren LB 2009. Factors associated with serum immunoglobulin levels in beef calves from Alberta and Saskatchewan and association between passive transfer and health outcomes. Canadian Veterinary Journal 50, 275-281.

Wang JJ, Chen LX, Li DF, Yin YL, Wang XQ, Li P, Dangott LJ, Hu WX and Wu GY 2008. Intrauterine growth restriction affects the proteomes of the small intestine, liver, and skeletal muscle in newborn pigs. Journal of Nutrition 138, 60-66.

Wang JS, Wu MC, Chang HL and Young MS 2007. Predicting parturition time through ultrasonic measurement of posture changing rate in crated Landrace sows. Asian-Australasian Journal of Animal Science 20, 682-692.

Wang T, Huo YJ, Shi F, Xu RJ and Hutz RJ 2005. Effects of intrauterine growth retardation on development of the gastrointestinal tract in neonatal pigs. Biology of the Neonate 88, 66-72.

Wassink GJ, King EM, Grogono-Thomas R, Brown JC, Moore LJ and Green LE 2010. A within farm clinical trial to compare two treatments (parenteral antibacterials and hoof trimming) for sheep lame with footrot. Preventive Veterinary Medicine 96, 93-103.

Watkins AJ, Wilkins A, Cunningham C, Perry VH, Seet MJ, Osmond C, Eckert JJ, Torrens C, Capampang FRA, Cleal J, Gray WP, Hanson MA and Fleming TP 2008. Low protein diet fed exclusively during mouse oocyte maturation leads to behavioural and cardiovascular abnormalities in offspring. Journal of Physiology 586, 2231-2244.

Weary DM and Fraser D 1995. Calling By Domestic Piglets - Reliable Signals Of Need. Animal Behaviour 50, 1047-1055.

Weary DM and Fraser D 1999. Partial tooth-clipping of suckling pigs: effects on neonatal competition and facial injuries. Applied Animal Behaviour Science 65, 21-27.

Weary DM, Appleby MC and Fraser D 1999. Responses of piglets to early separation from the sow. Applied Animal Behaviour Science 63,289-300.

Weary DM, Huzzey JM and von Keyserlingk MAG 2009. Using behavior to predict and identify ill health in animals. Journal of Animal Science 87, 770-777.

Weary DM, Jasper J and Hotzel MJ 2008. Understanding weaning distress. Applied Animal Behaviour Science 110, 24-41.

Weary DM, Pajor EA, Thompson BK and Fraser D 1996. Risky behaviour by piglets: a trade off between feeding and risk of mortality by maternal crushing? Animal Behaviour 51, 619-624.

Webb AJ 1998. Objectives and strategies in pig improvement: an applied perspective. Journal of Dairy Science 81, 36-46.

Webster AJF 1998. What use is science to animal welfare? Naturwissenschaften, 85, 262-269.

Weng RC, Edwards SA and Hsia LC 2009. Effect of individual, group or ESF housing in pregnancy and individual or group housing in lactation on the performance of sows and their piglets. Asian-Australian Journal of Animal Science 22, 1328-1333.

Whatson TS and Bertram JM 1982. Some observations on mother infant interactions in the pig (Sus scrofa). Applied Animal Ethology 9, 253-261.

Whay HR, Main, DCJ, Green LE and Webster AJF 2003. Assessment of the welfare of dairy cattle using animal-based measurements: direct observations and investigation of farm records. Veterinary Record 153, 197-202.

Whipple B, Josimovich JB and Komisaruk BR 1990. Sensory thresholds during the antepartum, intrapartum and postpartum periods. International Journal of Nursing Studies 27, 214-221.

White KR, Anderson DM and Bate LA 1996. Increasing piglet survival through an improved farrowing management protocol. Canadian Journal of Animal Science 76, 491-495.

White M 2008. NADIS Pig Health- September 2008. BPEX knowledge transfer, NADIS health bulletins.

Whittemore CT 1998. Influence of pregnancy feeding on lactation performance. In The lactating sow (ed. MWA Verstegen, PJ Moughan and JW Schrama), pp. 183-200. Wageningen Pers, Wageningen, The Netherlands.

Wilcox AJ 2001. On the importance – and the unimportance – of birthweight. International Journal of Epidemiology 30, 1233-1241.

Willgert K 2011. The economic and welfare impact of lameness in sows in England. BPEX Report.http://www.bpex.org.uk/downloads/301258/299207/The%20economic%20and%20welfare%20impact%20of%20lameness%20in%20sows%20in%20England.pdf

Wilson ME, Biensen NJ, Youngs CR and Ford SP 1998. Development of Meishan and Yorkshire littermate conceptuses in either a Meishan or Yorkshire uterine environment to day 90 of gestation and to term. Biology of Reproduction 58, 905-910.

Wiseman BS, Molitor TW, Dial GD, Morrison RB. 1995. Research Investment Report, National Pork Producers Council, Des Moines, IA.

Wolf J, Žáková E and Groeneveld E 2008. Within-litter variation of birth weight in hyperprolific Czech Large White sows and its relation to litter size traits, stillborn piglets and losses until weaning. Livestock Science 115, 195-205.

Wootton R, McFadyen IR and Cooper JE 1977. Measurement of placental blood-flow in pig and its relation to placental and fetal weight. Biology of the Neonate 31, 333-339.

Xu RJ, Mellor DJ, Birtles MJ, Reynolds GW and Simpson HV 1994. Impact of intrauterine growth retardation on the gastrointestinal tract and the pancreas in newborn pigs. Journal of Pediatric Gastroenterology and Nutrition 18, 231-240.

Yeates JW 2010. Death is a Welfare Issue. Journal of Agricultural and Environmental Ethics 23, 229-241.

Yeates JW and Main DCJ 2008. Assessment of positive welfare: a review. The Veterinary Journal 175, 293-300.

Yoshioka G, Imaeda N, Ohtani T and Hayashi K 2005. Effects of cortisol on muscle proteolysis and meat quality in piglets. Meat Science 71, 590-593.

Zaleski HM and Hacker RR 1993. Comparison of Viability Scoring and Blood-Gas Analysis As Measures of Piglet Viability. Canadian Journal of Animal Science 73, 649-653.

Zurbrigg K 2006. Sow shoulder lesions: Risk factors and treatment effects on an Ontario farm. Journal of Animal Science, 84, 2509-2514.

Appendix One: Priority for action classification based on combinations of welfare impact and certainty

		WELFARE IMPACT		
		LOW	MEDIUM	HIGH
CERTAINTY	HIGH	MEDIUM	MEDIUM/HIGH	HIGH
	MEDIUM	LOW	MEDIUM	HIGH
	LOW	LOW	LOW/MEDIUM	MEDIUM

Appendix Two: Severity scores of the adverse effects (pig welfare RA; from EFSA 2007) (Taken from Smulders 2009, Table 5)

Severity of the adverse effect	Description	Score
Critical	Fatal, death occurs either immediately or after some time	4
Severe	Involving explicit pain, malaise, frustration, fear or anxiety. Strong stress reaction, dramatic change in motor behaviour, vocalisation may occur.	3
Moderate	Some pain, malaise, frustration, fear or anxiety. Stress reaction, some change in motor behaviour, occasional vocalisation may occur	2
Limited	Minor pain, malaise, frustration, fear or anxiety. Physiological effects may be recorded as well as moderate behavioural change.	1
Negligible	No pain, malaise, frustration, fear or anxiety.	0

Appendix Three: Summary of Studies on Wild Boar Litter Size and pre- and post-natal mortality (Bywater et al 2010; Fonseca et al 2011; and other references).

Reference	Country	Mean Litter Size	Mean Prenatal mortality (%)	Mean Postnatal mortality (%)
Fonseca et al 2011	Portugal	4.1	9.7	6.3
Sáez-Royuela and Telleria 1987	Spain	4.3		
Abáigar 1990, 1992	Spain	4.1	31.0	31
Garzón-Heydt 1991	Spain	3.9		
Rosell 1998	Spain	3.6	24.5	
Fernández-Llario et al 1999	Spain	3.7		
Markina et al 2003	Spain	3.9		
Herrero et al 2008	Spain	Median = 4	Median =40.0	
Mauget 1972	France		14.0	
Aumaitre et al 1982	France		13.4	
Aumaitre et al 1984	France	4.6		
Dardaillon 1988	France	4.4		
Mauget and Pépin 1991	France			
Pedone et al 1991	Italy	4.9		
Boitani et al 1995	Italy	5.0		
Briedermann 1971	Germany	5.0		5 – 25
Appelius 1995	Germany	4.4	7.4 – 8.4	
Gethöffer et al 2007	Germany	5.2 – 7.6	8.0	
		4.6 – 6.7	6.0 – 18.0	
Martys 1982	Austria	5.8		17.0
Dzieciolowski 1991	Poland	5.2		
Náhlik and Sándor 2003	Hungary	6.7	12.0	55.1 – 60.9
Ahmad et al 1995	Pakistan		16.0	
Kanzaki 1991	Japan			
Servanty et al 2007				
Fernandez-Llario and Carranza 2000	Spain	3.05		
Fonseca et al 2004	Portugal	4.37		
Fernández-Llario et al 1999	Spain	3.69		
Fernández-Llario and Mateos-Quesada 2005	Spain	3.75		
Fonseca et al 2004	Portugal	3.94		
Fonseca et al 2004	Portugal	3.96		
Focardi et al 2008	Italy	4.2		
Massei et al 1997	Italy	3.88		
Cappai et al 2008	Italy	4.6		
Mauget 1972	France	4.62		
Moretti 1995	Switzerland	4.9		
Neet 1995	Switzerland	4.17		
Náhlik and Sandor 2003	Hungary	6.7		
Celina 208	Luxembourg	5.3		
Bieber and Ruf 2005	Germany / E. Poland	5.3		
Oloff 1951	Germany	6.5		
Stubbe and Stubbe 1977	Germany	5.3		
Fruzinkski 1995	Poland	4.83		
Koslo 1970	Belarus	6.12		
Ahrens 1984	Germany	5.49		