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# The effect of immunization against GnRF on nutrient requirements of male pigs: a review

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*In most countries, male pigs are physically castrated soon after birth to reduce the risk of boar taint and to avoid behaviours such as fighting and mounting. However, entire male pigs are more feed efficient and deposit less fat than barrows. In addition, many animal welfare organizations are lobbying for a cessation of castration, with a likelihood that this could lead to inferior pork unless an alternative method is used to control boar taint. An alternative to physical castration is immunization against gonadotrophin releasing factor (GnRF) which allows producers to capitalize on the superior feed efficiency and carcass characteristics of boars without the risk of boar taint. From a physiological perspective, immunized pigs are entire males until shortly after the second dose, typically given 4 to 6 weeks before slaughter. Following full immunization, there is a temporary suppression of testicular function and a hormonal status that resembles that of a barrow. Nutrient requirements will be different in these two phases, before and after full immunization. Given that there have been few published studies comparing the lysine requirements of entire males and barrows in contemporary genotypes, it is useful to use gilt requirements as a benchmark. A series of meta-analyses comparing anti-GnRF immunized boars and physical castrates and use of nutritional models suggest that the lysine requirement of entire males before the second immunization is 5% higher than for gilts, from 25 to 50 kg BW, and by 8% from 50 to 95 kg. Given that the penalty in growth performance for having inadequate dietary lysine is greater in males than in gilts or barrows, it is important to ensure that lysine requirements are met to obtain the maximum benefits of entire male production during this phase. After the second immunization, the lysine requirement of immunized males decreases and may become more like that of barrows. In addition, a consistent effect of full immunization is a marked increase in voluntary feed intake from about 10 days after the second dose. Putting these together, the estimated lysine requirement, expressed in terms of diet composition, falls to 94% of the gilt level. Although general principles can be described now, further research is needed to fully define the lysine requirements of immunized boars. It is important that the temporal pattern of tissue deposition rates and feed intake be explored to be incorporated into models to predict nutrient requirements over the period of rapidly changing metabolism.*

**Keywords:** finishing pigs, growth, boars, nutritional requirements, immunological castration.

## Implications

Male pigs immunized against gonadotrophin releasing factor are physiologically entire males for most of their life and as such they should be fed as entire males at least up until the second immunization. Shortly after that time, testicular

function is suppressed and the hormonal and metabolic status rapidly adjusts to resemble that of a physical castrate. As a consequence, feed intake and tissue deposition change and after the second immunization the lysine requirement could be up to 1.5 g/kg lower than boars. The existence of these two metabolic phases creates additional flexibility for dietary manipulation to help producers meet specific production targets.

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## Introduction

In pigs, as in many other domestic species, entire males are generally more muscular, less fat and more metabolically efficient than females or physical castrates (barrows; Campbell and Taverner, 1988; Dunshea *et al.*, 1993). Despite these advantages, however, the traditional practice in most countries is to physically castrate male piglets early in life. The major reason for doing this is to control boar taint, which is an offensive smell present in the meat of many sexually mature entire male pigs. The presence of boar taint can greatly reduce the acceptability of pork to consumers. A second reason is to control aggression and sexual behaviour in entire male pigs as they approach slaughter weight. Although boar taint and entire male behaviour are only problems in the older pig, for practical reasons, the physical act of castration is performed in the young piglet. The potential benefit of the higher entire male performance is thus lost for the entire growing period.

Driven by both the potential for productivity gains and, in some countries, animal welfare concerns, effort has been devoted to looking for alternative ways to control boar taint and remove the necessity for physical castration (EFSA, 2004). One method is immunization against gonadotrophin releasing factor (GnRF), also referred to as immunological castration (Dunshea *et al.*, 2001). The world's first, and only, commercial anti-GnRF vaccine is now freely available in many countries under several trade names (Improvac, Improvest, Vivax, Innosure; Zoetis Madison, NJ, USA). By using the immunization approach, physical castration early in life is replaced by a temporary immunological suppression of testicular function relatively near slaughter. Immunized animals temporarily become like castrates, with similar lack of boar taint and entire male behaviour. However, the difference in timing means that male pigs reared using an immunization regimen are allowed to grow as entire males for most of the growing–finishing period, benefiting from the naturally better feed conversion efficiency and improved carcass composition of entire males (Dunshea *et al.*, 2001; Millet *et al.*, 2011).

From a physiological perspective, the life of a male pig reared using an anti-GnRF immunization protocol can be divided into two phases – the first phase is before full immunization (two doses); the second phase from full immunization until slaughter. The immunization regimen requires two doses at a minimum interval of 4 weeks apart. The first 'priming' dose is generally given at any time after 10 weeks of age. The second dose is typically given 4 to 6 weeks before slaughter, although in some markets the timing of the second dose may be from 3 to 10 weeks before slaughter. Irrespective of the timing, until shortly after the second dose, the pig is a normal entire male. Following the second dose, testicular function is suppressed and hormonal status rapidly adjusts to resemble that of a barrow (Dunshea *et al.*, 2001). As a consequence, feed intake and tissue deposition characteristics also change, but initially these reflect the unique characteristics of an animal

transitioning from one metabolic state to another and are not identical to those of a long-term physical castrate. The goal of this review is to provide some guidance for the energy and lysine requirements of entire male pigs reared using immunization against GnRF as the method to control boar taint. This will reflect the two distinct physiological phases in the lives of such animals, initially being those of entire males where there is a significant body of existing knowledge, and secondly after full immunization when the physiology and metabolism of the immunized boar becomes more castrate-like. To understand the nutritional requirements of immunized boars, a series of meta-analyses and some modelling of recent published data was undertaken.

## Material and methods

Meta-analysis is a robust technique that utilizes the magnitude of, and the error around, the difference between treatments (in this case sex) to quantify the expected effect and the degree of uncertainty around this estimated effect. Meta-analyses are particularly valuable where a reasonable body of published data exists and especially where there may be some equivocal findings or small differences (Glass, 1976).

### Study inclusion

In this review, we report on a series of meta-analyses on data from up to 32 data sets from recent peer reviewed published reports and articles with improved genotypes. Non-peer reviewed papers, such as many conference proceedings, were excluded. Details of the references used for the meta-analyses are given in Supplementary Table S1.

Fourteen studies, post-2000, were used for the comparison between entire males and barrows (studies listed in supplementary Table S1); 19 published reports, post-2000, were used for the comparison between immunocastrated males and entire males (see supplementary Table S1); and 21 post-2000 reports for the final comparison between barrows and immunocastrated males (see supplementary Table 1 for the details of studies included). Some studies reported the performance of entire males, castrates and immunocastrated males. Only studies performed with group housed pigs were used, any studies that used individual housing were excluded. For the comparisons incorporating anti-GnRF immunized males only studies that were performed with the commercial anti-GnRF vaccine, from Zoetis, and that utilized a 4 to 6 week post-second immunization period were used. Studies that used an experimental, non-commercially available anti-GnRF vaccine or that were purported to require a single immunization strategy were excluded. Only studies that reported a measure of variation from which a standard error of the difference could be derived were used. Where studies included treatments with ractopamine or somatotropin only, the data for the non-ractopamine/somatotropin controls were used. In addition, only studies that reported separate data from second immunization to slaughter as opposed to the entire growing/finishing period were included. Any studies that did

not meet these criteria were excluded from the analyses and are listed in supplementary Table S2.

#### *Meta-analysis methodology*

Data were subjected to meta-analyses (Genstat Version 13) utilizing the response to immunization against GnRF as the effect and standard error of the difference of this effect as the measure of variation. Since the Genstat default measure of heterogeneity of Cochrane's Q has low power when the number of studies is small, as in these analyses, heterogeneity was assessed using the  $I^2$  statistic (Higgins *et al.*, 2003). There was no evidence of heterogeneity in the responses, so a fixed effect model was used for the meta-analyses. The exception was for carcass weight in the GnRF-immunized males *v.* entire males where there was indication of heterogeneity ( $P = 0.05$ ) and, in this case, a random effects model was used. All effects were visually appraised using Forest and Radial plots (Whitehead and Whitehead, 1991) but, for ease of presentation, the responses are presented as mean fixed effects (random effect for carcass weight) with 95% confidence intervals. Similar principles were applied to the meta-analyses reported later in this paper.

#### *InraPorc modelling methodology*

The InraPorc model was used to characterize the nutritional requirement of pigs (van Milgen *et al.*, 2008). On the basis of average feed intake and BW observed at different ages in entire males, castrated males and gilts by Quiniou *et al.* (2010), relationships between BW and age and between feed intake and BW were fitted to data using a Broyden–Fletcher–Goldfarb–Shanno optimization method. In the InraPorc model, a Gompertz function is used to describe protein deposition and thus BW gain. An exponential function ( $a \cdot (1 - e^{-b \cdot BW})$ ) was used to express the relationship between feed intake and BW. Then, the relationship between dietary lysine requirement and BW was simulated for each type of pigs.

## **Results and discussion**

#### *Impact of physical castration on growth performance and carcass characteristics*

The potential lean tissue growth and efficiency of weight and lean tissue gain are greater in entire males than in barrows prompting the cessation of castration 30 years ago in a few markets, particularly those that are focused on lean meat production. Some of these differences in tissue nutrient partitioning rates were demonstrated in a recent study designed to investigate the interactions between housing and gender in contemporary genotypes (Suster *et al.*, 2006). These authors found that under group-housed conditions, there was very little difference between entire males and barrows in daily gain and lean tissue content until 122 days of age (ca. 77 kg BW). Beyond 17 weeks of age, the barrows ate more feed and grew faster than the entire males but deposited less lean tissue and more fat. Thus, at 150 days of

age, the entire males weighed 5 kg less than the barrows but contained 3 kg more lean tissue and almost 6 kg less fat. In pigs raised in individual pens, the differences in body composition were even more profound in favour of entire males while the live weights were similar (73.1 *v.* 66.8 kg lean tissue and 20.6 *v.* 27.1 kg fat for entire males *v.* barrows, respectively). Over the finisher phase, the feed conversion ratio (FCR; kg feed/kg gain) was 13% higher in barrows than in entire males. These data for efficiency and P2 back fat were very similar to those observed elsewhere (Noblet *et al.*, 1994; Dunshea *et al.*, 2001; Quiniou *et al.*, 2010; Millet *et al.*, 2011).

The outcomes of the current meta-analysis of up to 14 studies conducted with group-housed contemporary pigs (data since 2000) shows that compared with entire male pigs physical castration significantly ( $P < 0.001$ ) increases feed intake ( $+420 \pm 35.5$  g/day), FCR ( $+0.47 \pm 0.03$ ), back fat ( $+4.6 \pm 0.32$  mm) and carcass weight ( $+2.6 \pm 0.59$  kg) with no effect on growth rate ( $+2.4 \pm 12.9$  g/day,  $P = 0.85$ ) over the last 4 to 6 weeks of the finisher phase. These outcomes in group housed pigs of the modern improved genotype are fully in agreement with the recent paper by Lovatto *et al.* (2010) who performed a meta-analysis on data from 22 studies conducted over the last 38 years with both individual- and group-housed pigs and found that physical castration increases feed intake, FCR, back fat, carcass weight (at a given BW because of the extra yield), carcass length and dressing percentage, and decreases daily gain and lean meat percentage. Although the differences in FCR have been extensively chronicled during the finishing phase, where they are most pronounced because of the decline in lean tissue deposition in the barrows, entire males are actually more feed efficient and leaner than barrows throughout the entire post-weaning growth phase (Campbell and Taverner, 1988).

Although it is accepted that boars are leaner and more efficient than barrows, the growth performance of entire males housed in groups is generally less than that of individually housed entire males (McCauley *et al.*, 2000; Suster *et al.*, 2006), suggesting that the putative benefits may not be as marked as assumed when pigs are housed under commercial conditions. Furthermore, during the late finishing phase, group-housed entire males often grow at a similar or slower rate than barrows (Dunshea *et al.*, 2001; Suster *et al.*, 2006; Quiniou *et al.*, 2010). This could be because of increased sexual and aggressive activities between entire males. From the peri-pubertal period onwards (as early as 16 to 17 weeks of age), boars exhibit negative aggressive and sexual behaviours that can detract from feeding (Cronin *et al.*, 2003; Rydhmer *et al.*, 2010). Similarly, these negative behaviours that occur with mixing of boars around slaughter cause carcass damage and reduced meat quality (Dunshea *et al.*, 2011; Lealiifano *et al.*, 2011).

#### *Impact of immunization against GnRF on growth performance, carcass characteristics and metabolism*

*Growth performance and carcass characteristics.* Immunization against GnRF is an alternative method of inhibiting sexual

**Table 1** Average fixed effects of immunization against GnRF compared with either entire males (immunized males – entire males) or physical castrates (immunized males – physical castrates) from meta-analyses of data from peer reviewed studies ( $n = 19$  data sets for entire male comparison and  $n = 21$  data sets for comparison with castrates) with group-housed pigs<sup>a,b,c</sup>

Trait	Immunized males v. Entire males					Immunized males v. Physical castrates				
	Effect	s.e.d.	95% confidence interval	P value	No. of studies	Effect	s.e.d.	95% confidence interval	P value	No. of studies
ADG (g/day)	119	8.9	(102, 136)	<0.001	17	163	11.6	(140, 185)	<0.001	14
ADFI (g/day)	429	26.8	(376, 482)	<0.001	12	95	37.8	(20, 169)	0.011	10
FCR	0.11	0.02	(0.07, 0.15)	<0.001	14	−0.35	0.03	(−0.41, −0.29)	<0.001	10
Live weight (kg)	2.96	0.43	(2.12, 3.80)	<0.001	16	3.16	0.36	(2.46, 3.87)	<0.001	19
Carcass weight (kg) <sup>d</sup>	2.09	0.35	(1.38, 2.94)	<0.001	17	0.07	0.31	(−0.67, 0.54)	0.83	11
Dressing percentage	−0.29	0.12	(−0.51, −0.07)	<0.001	11	−2.71	0.06	(−2.83, −2.58)	<0.001	14
Back fat (mm)	1.53	0.18	(1.16, 1.89)	<0.001	14	−2.64	0.10	(−2.84, −2.44)	<0.001	15

ADG = average daily gain; ADFI = average daily feed intake; FCR = feed conversion ratio.

<sup>a</sup>Analyses only included data from studies with animals slaughtered between 4 and 6 weeks after the second immunization (mean final live weight 107 to 110 kg).

<sup>b</sup>Differences were determined over the period between the second immunization and slaughter or equivalent time in barrows.

<sup>c</sup>Studies included were: McCauley *et al.* (2003 and 2004), Dunshea *et al.* (2001 and 2011), Oliver *et al.* (2003), Zamaratskaia *et al.* (2008), Hémonic *et al.* (2009), Fuchs *et al.* (2009), Pauly *et al.* (2009), Rikard-Bell *et al.* (2009), Schmoll *et al.* (2009), Fàbrega *et al.* (2010), Boler *et al.* (2011 and 2012), Font i Furnols *et al.* (2012), Lealiifano *et al.* (2011), Moore *et al.* (2011), Andersson *et al.* (2012), Schmidt *et al.* (2011), Skrlep *et al.* (2012), Yuan *et al.* (2012), Akit (2013) and Lanferdini *et al.* (2013). Some references reported more than one data set.

<sup>d</sup>Since there was evidence of heterogeneity ( $P = 0.05$ ) in the immunized males v. entire males comparison a random effects model was used.

development and aggressive behaviours in the late finisher phase and reducing the accumulation of boar taint compounds in carcass fat. This results in a reduction in plasma gonadotrophins and testosterone (Bonneau *et al.*, 1994; Dunshea *et al.*, 2001; McCauley *et al.*, 2003; Oliver *et al.*, 2003). The reduction in testosterone as a result of immunization against GnRF has a profound effect upon behaviour (Rydmer *et al.*, 2010). Cronin *et al.* (2003) found that there was a reduction in both aggressive and sexual activities in immunized boars who exhibited similar activities as barrows. As a consequence, the immunized pigs increased the amount of time they spent eating and feed intake rose. Further details of the metabolic and hormonal changes following the second immunization are discussed later in this review.

In comparison with individually housed contemporary boars the growth performance of the group-housed boars, during the finisher phase, was well below their growth potential (Pauly *et al.*, 2009). Immunization against GnRF provided a means of ameliorating the reduction in performance in group housed boars (Dunshea *et al.*, 2000). The growth rate of group-housed immunized boars and individually housed entire boars were identical over the 5-week period after the second immunization (1090 v. 1099 g/day), being ~20% and 15% higher than the group-housed entire boars and barrows, respectively. The variation in growth performance was also less which makes nutritional and sales management easier (Dunshea *et al.*, 2011).

There are now a number of studies conducted with anti-GnRF immunization across the globe and these have been incorporated into a series of meta-analyses. These analyses of 19 studies look only at the period between second immunization and slaughter and show that, compared with non-immunized boars, immunization against GnRF significantly ( $P < 0.001$ ) increases feed intake (+429 g/day) and

average daily gain (ADG; +119 g/day), with increase in FCR (+0.11). Final carcass weight is significantly increased (+2.1 kg) over that of entire males, as is P2 back fat (+1.5 mm; Table 1). Carcass dressing percentage is significantly decreased in immunized pigs (−0.3 percentage point). The decrease in dressing percent in immunized boars compared with non-immunized boars could possibly be because of increased gut size and fill as a consequence of the increased feed intake following the second immunization. The small increases in FCR appear to occur in smaller group sizes (4 to 8 pigs/pen) where negative activities, such as aggression and sexual activity, in the entire male controls may not be as great as in larger groups.

There are now sufficient data comparing the growth performance and carcass characteristics of immunized boars with those of barrows to conduct comparative meta-analyses as outlined previously. These analyses of up to 21 studies are looking only at the period post-second immunization. They show that, during this phase, immunization against GnRF significantly ( $P < 0.05$ ) increases feed intake (+95 g/day) and ADG (+163 g/day) and decreases FCR (−0.35,  $P < 0.001$ ), compared with contemporary barrows (Table 1). Final slaughter measurements show a significantly ( $P < 0.001$ ) increased live weight (+3.2 kg), decreased P2 back fat (−2.7 mm) and decreased dressing percentage (−2.7 percentage point), with no effect on carcass weight (+0.07 kg,  $P = 0.83$ ). The decreased dressing percentage in immunized boars compared with castrates is presumably mainly because of the presence of testes and other sex organs and also to the effect of increased feed intake and hence increased gut size and fill. However, these slaughter measurements reflect the combined effect of growth both before (boar phase) and after second immunization. These measurements could be strongly influenced by

the duration between the second immunization and slaughter. The analysis was performed on studies where this interval was 4 to 6 weeks.

The findings reported above are in complete alignment with the magnitude and direction of the growth responses reported in a recent meta-analysis from up to 30 studies (Batorek *et al.*, 2012). The meta-analysis by Batorek included studies conducted with experimental vaccines as well as with the commercially available anti-GnRF vaccine, Improvac. In markets where physical castration is not practiced, the increased growth rate and carcass weight of males immunized against GnRF, combined with assurances of better quality pork free of boar taint, provide real incentives. In the majority of markets, where physical castration is currently the norm, using immunization against GnRF when the technology is permitted, would allow producers to capture the production advantages of entire males. Compared with physical castrates, performance improvements are evident in both the boar and post-immunization phases. In order to maximize the returns, however, it is necessary to know the nutrient requirements and constraints to growth both before and after immunization. It is also important to understand the temporal nature of the metabolic and hormonal responses to immunization against GnRF.

*Metabolic and hormonal responses.* Antibody titres to GnRF peak a week after the second dose and gradually decline over the next 8 weeks or longer (Claus *et al.*, 2007; Dunshea *et al.*, 2008; Bauer *et al.*, 2009). The intensive studies of Claus *et al.* (2007) and Bauer *et al.* (2009) show that plasma androstenedione, testosterone and LH had all reached a nadir 6 to 10 days after the second immunization. Similarly, plasma urea nitrogen (PUN), an accurate proxy for excess amino acid catabolism, was found to be increased at 14 and 28 days after immunization against GnRF (McCauley *et al.*, 2003). This is a result of either increased protein intake, decreased lean tissue deposition or both. The temporal studies of Claus *et al.* (2007) and Bauer *et al.* (2009) indicate that PUN begins to increase within the first few days after immunization, before any increase in feed intake. This suggests that changes in protein metabolism occur very quickly. Indeed, when feed intake was restricted to either 2 or 3 kg/day, there was a rapid increase in PUN between 8 and 10 days after the second immunization (Bauer *et al.*, 2009). This increase in PUN is associated with the timing of the decrease in testicular activity as measured by plasma testosterone. Plasma IGF-I, which has been shown to be positively related to previous growth rate, decreased more gradually in immunized pigs and did not reach a plateau until beyond 14 days after the second immunization (Metz and Claus, 2003; Claus *et al.*, 2007; Bauer *et al.*, 2009). Plasma leptin concentration was increased at 14 and 28 days after immunization against GnRF (McCauley *et al.*, 2003), possibly in response to increased feed intake and fat deposition that occurs around this time. However, there are no data investigating the temporal pattern of plasma leptin in the immediate period after immunization.

The above data suggest that boars immunized against GnRF have reduced steroidogenic capacity soon after the second dose with the accompanying effects on muscle and fat metabolism, as well as feed intake occurring very soon after. The effects on steroidogenic capacity seem to be still present at least 8 weeks after the second dose even though antibody titres are decreasing (Dunshea *et al.*, 2008).

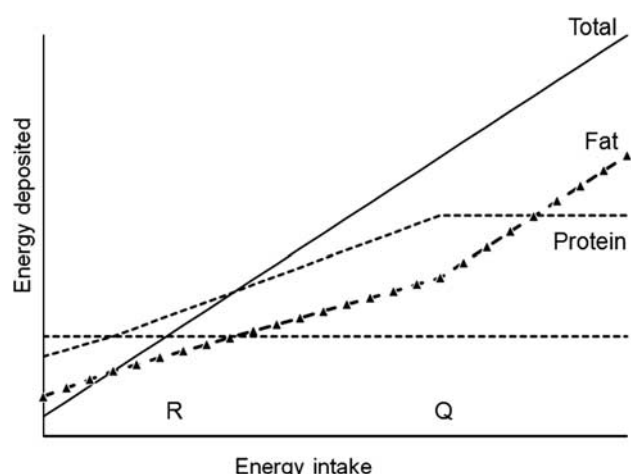
#### *Nutritional constraints to growth*

For the past three decades, a major driver of improved productive efficiency in the pig industry has been the efficient deposition of lean tissue. The major determinant of lean tissue deposition is protein deposition. Most management practices, therefore, are now aimed at maximizing protein deposition while minimizing or controlling fat deposition. As a consequence, we now have an excellent understanding of many of the nutritional constraints to protein deposition. Numerous factors such as genotype, gender, age and environment can impact lean tissue growth and development (Standing Committee on Agriculture (SCA), 1987; Quiniou *et al.*, 1999; de Lange *et al.*, 2001; National Research Committee (NRC), 2012). In order to optimize the response to dietary protein (or lysine) in males immunized against GnRF, it is important to understand the relationship between protein deposition and protein intake and how this relationship is altered by energy intake, genotype and age.

A theoretical response to dietary protein intake in an individual pig is shown in the supplementary Figure S1 which depicts the two distinct phases of protein deposition. The first phase is an initial protein-dependent phase where protein deposition increases linearly with protein intake regardless of energy intake, whereas the second phase is an energy-dependent phase in which protein deposition will only increase if additional energy is provided. These theoretical relationships have been confirmed for a very homogeneous group of pigs (see SCA 1987; Moehn *et al.*, 2000).

Knowledge of the relationship between protein deposition and energy intake is crucial to determining optimum feeding strategies for different classes of pigs, including those immunized against GnRF. These relationships are outlined in models proposed by the SCA (1987), van Milgen *et al.* (2008), Brossard *et al.* (2009) and NRC (2012) and are illustrated in Figure 1. The potential impact of energy intake upon body composition is closely related to what intake, if any, for a particular pig corresponds to a point 'Q' because beyond this level of intake, there is a sharp linear increase in the ratio of fat to protein in BW gain. Therefore, whether protein deposition continues to respond linearly up to the limit of appetite or reaches a plateau at an intermediate energy intake can have profound effects upon the composition of weight gain, body composition and FCR (SCA, 1987; NRC, 2012).

*Effect of gender on protein and lysine requirements.* There are very few published data comparing the protein or lysine requirements of contemporary entire males and barrows. Given that the lysine requirements of gilts are generally considered to be similar to, or slightly higher than, that of



**Figure 1** Effect of energy intake on total energy (solid line) and energy deposited as protein (dashed line) or fat (dashed line with triangles) (from SCA, 1987). Energy retained as protein increases linearly up to a maximum at an energy intake of Q, beyond which further energy has no effect on protein deposition. After Q, an increase in the rate of fat deposition occurs. At zero, energy balance (R), protein gain is still marginally positive, whereas fat deposition is negative (energy level indicated by horizontal dashed line).

barrows (Quiniou *et al.*, 2010; NRC, 2012), and that there have been a number of studies comparing the lysine requirement of entire males and gilts, it is pragmatic to use the gilt requirements as a reference point.

During the early 1980s, a number of studies were conducted that suggested that the protein deposition potential (g/day) and the estimated lysine requirement of entire grower males (up to 60 kg) was slightly higher than those of gilts (Batterham *et al.*, 1985; Giles *et al.*, 1986). However, studies from the early 2000s suggested that, although the daily protein deposition and growth potential of entire males was greater than that of gilts, there was little difference in the lysine (g/kg feed) requirement of grower and finisher entire males and gilts (King *et al.*, 2000; O'Connell *et al.*, 2005 and 2006).

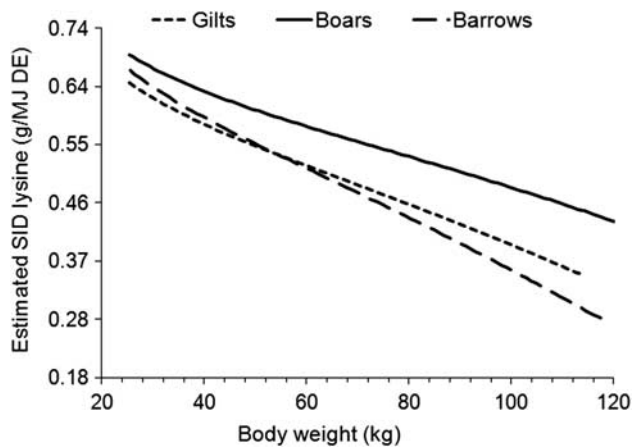
King *et al.* (2000) found that there was no difference in the lysine requirement to maximize protein deposition and minimize FCR in heavy (80 to 120 kg BW) finisher entire males and gilts. O'Connell *et al.* (2005) found that, in three studies in grower entire males and gilts (20 to 68 kg BW), there were no differences in the lysine requirements (g/kg) to maximize growth and minimize FCR. In heavier pigs (60 to 100 kg BW), these authors found the lysine requirement (g/kg) was slightly higher in entire males than in gilts in one study but not in two others (O'Connell *et al.*, 2006). However, in the most recent studies conducted with high-performing grower pigs, it was found that the lysine requirement of entire males was higher than that of gilts (Quiniou *et al.*, 2010; Moore *et al.*, 2012; Rikard-Bell *et al.*, 2012).

The studies that have shown no difference in lysine requirement have often been conducted with individually penned pigs where the full feed intake potential can be expressed and sometimes, in these cases, entire males may

consume more feed than gilts (Dunshea *et al.*, 1998; King *et al.*, 2004). However, in commercial conditions, the *ad libitum* feed intake of entire males is well below that seen when entire males are penned in individual pens and slightly less than gilts (Dunshea, 2005). This may be where the differences in lysine requirement between entire males and gilts may be exhibited. It is likely that, as a result of both a greater protein deposition potential and a lower feed intake under commercial conditions, entire males have higher dietary lysine requirements than gilts and barrows. In addition, many of the studies have used different means of defining lysine requirements and there is a need to harmonize the way in which lysine requirements are expressed (Stein *et al.*, 2007).

In an effort to clarify the situation, the published data in which lysine requirements of entire males and gilts have simultaneously been determined ( $n = 13$ ) were subject to a meta-analysis using a fixed effects model (since there was no evidence of heterogeneity) as outlined previously. Values were converted to standardized ileal digestible (SID) lysine (Stein *et al.*, 2007) using collated values for ingredients (NRC, 2012) and expressed on an energy basis (i.e. per MJ digestible energy (DE)). The studies used in these analyses included those reported by Batterham *et al.* (1985), Giles *et al.* (1986 and 1987), Campbell *et al.* (1988), Hansen and Lewis (1993), King *et al.* (2000), O'Connell *et al.* (2005 and 2006), Moore *et al.* (2012) and Rikard-Bell *et al.* (2012) with some publications containing more than one study. The meta-analysis indicated that entire males have a higher dietary lysine requirement than gilts (0.600 v. 0.549 g SID lysine/MJ DE,  $P = 0.009$ ) over the finisher stage. As these studies were conducted across a wide range of live weights and period of time, these factors may have an impact on lysine requirements; these data were also subjected to multi-regression analyses. For these analyses, estimated lysine requirements were regressed against average live weight, sex and year of publication using the Generalized Linear Models procedure in Genstat 13. The regression analysis indicates that lysine requirements decrease with live weight ( $-0.0043 \pm 0.00058$  g SID lysine/MJ DE per kg BW  $P < 0.001$ ), and are greater for entire males than for gilts ( $+0.051 \pm 0.0233$  g SID lysine/MJ DE  $P = 0.039$ ) and have increased over time ( $+0.0093 \pm 0.00139$  g SID lysine/MJ DE per year  $P < 0.001$ ). Since the slope of the protein dose response curve is greater in entire males than in gilts, the penalty in growth performance for having inadequate dietary lysine will be greater in the former (Hansen and Lewis, 1993).

Quiniou *et al.* (2010) characterized the growth performance and feed intake patterns of gilts, boars and barrows. According to simulations performed with the InraPorc software over the 25 to 116 kg BW range, the SID lysine requirement was on average 0.050 and 0.063 g SID lysine/MJ DE higher for entire males than for gilts and barrows (Figure 2). In the Quiniou simulation, the entire male and gilt lysine requirements decline over time and the relative (percentage) differences become greater at heavier live weights. Although the InraPorc model did not include anti-GnRF immunized pigs these simulations,



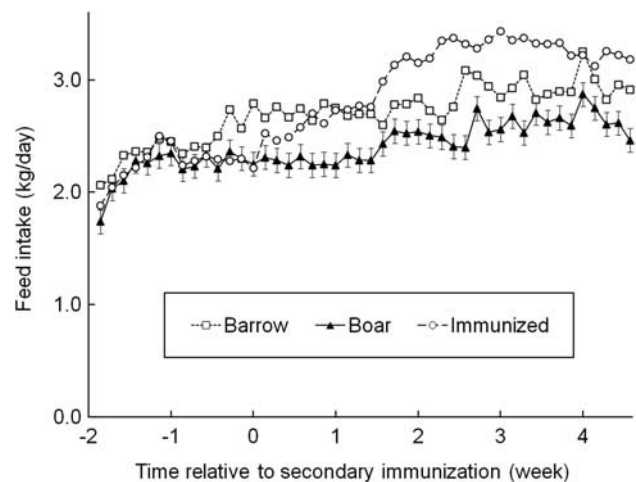
**Figure 2** Relationship between estimated standardized ileal digestible (SID) lysine content (g/MJ DE) and BW in boars (solid line), barrows (dashed line) and gilts (dotted line). Estimates were obtained from InraPorc (van Milgen *et al.*, 2008) simulations of performance data (after Quiniou *et al.*, 2010).

combined with the temporal pattern of tissue, hormone and metabolite responses to the secondary immunization can assist with estimation of likely requirements.

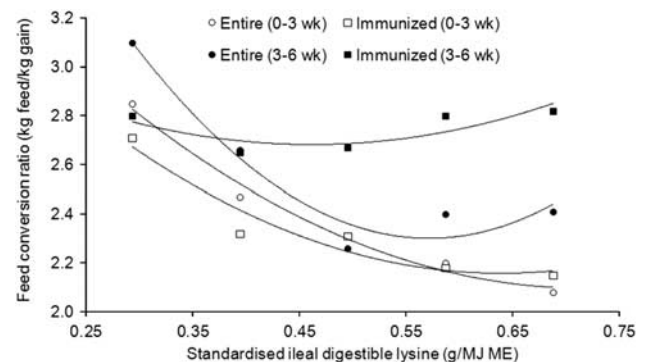
#### *Lysine requirements of immunocastrated pigs*

The rate of lean tissue deposition of immunized males appears to be maintained (Oliver *et al.*, 2003; Dunshea *et al.*, 2008; Moore *et al.*, 2009) or decreased slightly (McCauley *et al.*, 2003; Rikard-Bell *et al.*, 2009; Huber *et al.*, 2012) compared with that of entire males until approximately 4 weeks after the second immunization. Similarly, the rate of protein deposition, as measured continuously in respiration chambers, was maintained in the 4 weeks after the second immunization (J. Noblet, E. Gonzalo, E. Labussière, S. Dubois and J. van Milgen, unpublished data). This would suggest a similar daily requirement for lysine to entire males. However, it should be noted that feed intake is universally increased beyond 10 to 14 days after secondary immunization (Figure 3) and, therefore, the dietary SID lysine content of the diet could likely be reduced beyond this point since the daily requirement is either unchanged or decreased. In limit-fed immunized pigs, where the increase in feed intake is not allowed to occur, PUN increases after approximately 1 week after secondary immunization suggesting that there is excess protein (lysine) at this time (Claus *et al.*, 2007) and that lean tissue deposition is reduced relative to entire males at least in limit-fed animals. In contrast, in *ad libitum* fed pigs an increase in PUN could be, at least in part, because of the increase in feed intake rather than simply a reduction in lean tissue deposition.

Although there are no tissue deposition rate data beyond 4 weeks after secondary immunization, it is likely that the rate of lean tissue would decrease and fat deposition increase relative to entire males beyond 4 weeks. The reduction in ratio of lean to fat in BW gain would become more pronounced with increased time after secondary immunization. This is provided



**Figure 3** Effect of time relative to the second immunization against GnRF on feed intake in group-housed pigs (Dunshea *et al.*, 2011). Data are means with the standard error of the difference indicated on the entire males.



**Figure 4** Effect of standardized ileal digestible lysine (g/MJ DE) on feed conversion ratio in entire males and males immunized against GnRF. Data are shown for both the first 3-week period after the second immunization (open symbols) and for the second 3-week period after the second immunization (solid symbols; K.L. Moore, F.R. Dunshea and B.P. Mullan, unpublished data from Pork CRC project).

that energy intake is not limiting protein deposition before the secondary immunization. If this was the case, then high rates of protein deposition may be maintained. Research by King *et al.* (2004) showed that contemporary higher genotype boars did not reach a plateau in protein deposition at feed intakes up to 3.4 kg/day.

Recent data obtained using a dose titration approach suggests that, based on FCR, the SID lysine requirement of immunized pigs could be up to 0.084 g /MJ DE lower than entire males after the second immunization (Moore *et al.*, 2011). It should be noted that these requirements were determined over the entire 6 weeks after second immunization. Further interrogation of the data from Moore *et al.* (2011) shows that the lysine requirements of immunized boars are actually similar to entire boars during the first 2 to 3 weeks after the second immunization and then decrease (Figure 4; K.L. Moore, F.R. Dunshea and B.P. Mullan, unpublished data). Similar serial N-balance observations



**Table 2** Suggested dietary standardized ileal digestible SID lysine requirements (% of diet or g/unit of energy) in a three-phase feeding programme adapted to meet requirements for pigs from different genders<sup>a</sup> (levels are expressed relative to those for gilts, %)

	BW range (kg)		
	25 to 50	50 to 95	95 to 125 <sup>b,c</sup>
Gilts	100	100	100
Entire males	105	108	114
Immunized males	105	108	94
Barrows	100	94	94

<sup>a</sup>See Figures 3 and 4 for a guide to requirements.<sup>b</sup>Equivalent to 4 to 5 weeks between second injection and slaughter.<sup>c</sup>Where possible may commence the immunized male feeding programme 1 week after the second immunization.

(Huber *et al.*, 2012) and data from trials in respiration chambers (J. Noblet *et al.*, unpublished data) also indicate that a sharp decrease in amino acid requirements of immunized boars (in addition to the usual decrease because of increased BW) occurs during the third week after the second immunization.

The temporal pattern of the hormonal, metabolic and feed intake responses after immunization would support the prolonged use of a boar diet for ~2 weeks after secondary immunization, before reducing the dietary lysine content. Taken together, the following estimates of lysine requirements for entire and immunized males have been developed as a starting point (Table 2). These estimates are highly consistent with factorially derived estimates of lysine requirements of immunized males according to the NRC (2012). They have been developed with the aim of maximizing lean tissue gain and minimizing FCR.

**Effect of gender on energy requirements.** The slope of the relationship between energy intake and protein deposition is steeper for entire males than for gilts or barrows (Campbell *et al.*, 1985; Quiniou *et al.*, 1996; Dunshea *et al.*, 1998; King *et al.*, 2004). Although older data suggest that, in finisher pigs, a plateau in protein deposition was achieved in all genders at an intake of around 33 to 42 MJ DE/day (Campbell *et al.*, 1985; Campbell and Taverner, 1988), studies conducted with genetically improved pigs suggest that the plateau occurs at higher feed intakes or, in the case of elite entire males, not at all (Rao and McCracken 1992; Dunshea *et al.*, 1998; King *et al.*, 2004).

The practical message from these studies is that in many lines of genetically improved entire male pigs, and many lines of genetically improved gilts and barrows, can often be fed *ad libitum* to maximize protein deposition without the pigs getting over fat. This is particularly so when it is realized that feed intake is generally lower under commercial conditions than it is in the individually housed pigs that have been used for many of these studies (Dunshea, 2005). One implication from these findings is that the growth performance and rate of lean tissue deposition of the improved

pig, regardless of gender, is vulnerable to any factors that reduce feed intake. The recommendations for feeding entire males are to maximize energy intake from weaning through until slaughter, and this will apply to pigs reared using immunization against GnRF, at least up until the second immunization.

After the second immunization, there is a dramatic increase in feed intake (Figure 3) with a resultant increase in daily gain, carcass weight and P2 back fat depth (see Table 1). However, according to a recent trial performed with different feeding levels after the second immunization, only ADG was reduced in restrictively fed immunized lean-type males when compared with *ad libitum* fed ones, whereas neither FCR nor carcass leanness were improved (Quiniou *et al.*, 2012). Such results seem to indicate that after the second immunization, the plateau in protein deposition is still not reached in lean-type pigs even under increased feed intake.

Where a producer is paid on carcass weight, then they may choose to continue to feed *ad libitum* to maximize the effect on weight gain. In many markets, the increase in fatness is not an issue and may really be desirable especially since it may be associated with an increase in intramuscular fat (D'Souza *et al.*, 2000). These markets will be also those that can make use of the increase in carcass weight. If local directions for use allow it, some may wish to extend the slaughter age out to 8 weeks after immunization to maximize carcass weight without compromising boar taint compounds (Dunshea *et al.*, 2008). There needs to be research aimed at investigating the way in which the additional energy consumed by immunized boars can be converted to carcass and/or carcass lean to maximize the profitability in various markets. These strategies will clearly not be the same in all markets.

## Conclusions

Recent data suggest that the dietary SID concentration that meets the requirement of entire males is higher (ca. 10%) than for gilts, and that the difference increases with BW, but it is important that this is verified and further quantified. Given that the penalty in growth performance for inadequate dietary lysine is greater in entire males than in gilts or barrows, it is important to ensure that dietary lysine requirements are met to obtain the maximum benefits of the entire male production phase in animals immunized against GnRF. It is also important that the temporal pattern of tissue deposition rates and feed intake be further explored to be incorporated into growth models to predict nutrient requirements over the second period of rapidly changing metabolism. Keeping in mind the increase in feed intake and decline in protein deposition, a substantial reduction in dietary lysine concentration should be possible over this period.

The existence of two metabolic phases potentially creates additional flexibility and opportunities for dietary manipulation to help producers meet specific production targets. A full understanding of nutritional requirements, and their interaction with management decisions on immunization

timing and target slaughter weights, will be important to ensure that the benefits of immunization against GnRF can be optimized in all the markets where it will be available.

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## Supplementary materials

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S1751731113001407>

## References

- Akit H 2013. The influence of dietary lecithin on growth performance, dressing percentage, and intramuscular collagen in determining pork objective quality of finisher pigs of different sexes. PhD thesis, The University of Melbourne.
- Andersson K, Brunius C, Zamaratskaia G and Lundstrom K 2012. Early vaccination with Improvac: effects on performance and behaviour of male pigs. *Animal* 6, 87–95.
- Batorek N, Candek-Potokar M, Bonneau M and van Milgen J 2012. Meta-analysis of the effects of immunocastration on production performance, reproductive organs and boar taint compounds in pigs. *Animal* 6, 1330–1338.
- Batterham ES, Giles LR and Dettmann EB 1985. Amino acid and energy interactions in growing pigs. 1. Effects of food intake, sex and live weight on the responses of growing pigs to lysine concentration. *Animal Production* 40, 331–343.
- Bauer A, Lacorn M and Claus R 2009. Effects of two levels of feed allocation on IGF-I concentrations and metabolic parameters in GnRH-immunized boars. *Journal of Animal Physiology and Animal Nutrition* 93, 744–753.
- Boler DD, Killefer J, Meeuwse DM, King VL, McKeith FK and Dilger AC 2012. Effects of slaughter time post-second injection on carcass cutting yields and bacon characteristics of immunologically castrated male pigs. *Journal of Animal Science* 90, 334–344.
- Boler DD, Kutzler LW, Meeuwse DM, King VL, Campion DR, McKeith FK and Killefer J 2011. Effects of increasing lysine on carcass composition and cutting yields of immunologically castrated male pigs. *Journal of Animal Science* 89, 2189–2199.
- Bonneau M, Dufour R, Chouvet C, Roulet C, Meadus W and Squires E 1994. The effects of immunization against luteinizing hormone-releasing hormone on performance, sexual development, and levels of boar taint-related compounds in intact male pigs. *Journal of Animal Science* 72, 14–20.
- Brossard L, Dourmad JY, Rivest J and van Milgen J 2009. Modelling the variation in performance of a population of growing pig as affected by lysine supply and feeding strategy. *Animal* 3, 1114–1123.
- Campbell RG and Taverner MR 1988. Genotype and sex effects on the relationship between energy intake and protein deposition in growing pigs. *Journal of Animal Science* 66, 676–686.
- Campbell RG, Taverner MR and Curic DM 1985. Effects of sex and energy intake between 48 and 90 kg on protein deposition in growing pigs. *Animal Production* 40, 497–504.
- Campbell RG, Taverner MR and Curic DM 1988. The effects of sex and live weight on the growing pig's responses to dietary protein. *Animal Production* 46, 123–130.
- Claus R, Lacorn M, Danowski K, Pearce MC and Bauer A 2007. Short-term endocrine and metabolic reactions before and after second immunization against GnRH in boars. *Vaccine* 25, 4689–4696.
- Cronin GM, Dunshea FR, Butler KL, McCauley I, Barnett JL and Hemsworth PH 2003. The effects of immuno-castration and surgical-castration on the behaviour and consequently growth of group-housed, male finisher pigs. *Applied Animal Behavior Science* 81, 111–126.
- de Lange CFM, Birkett SH and Morel PCH 2001. Protein, fat and bone tissue growth in swine. In *Swine nutrition* (ed. AJ Lewis and LL Southern). 2nd edition, pp. 65–84. CRC Press, Boca Raton, USA.
- D'Souza DN, Hennessy DP, Danby M, McCauley I and Mullan BP 2000. The effect of Improvac on pork quality. *Journal of Animal Science* 78 (suppl. 1), 158.
- Dunshea FR 2005. Sex and porcine somatotropin impact on variation in growth performance and back fat thickness. *Australian Journal of Agricultural Research* 45, 677–682.
- Dunshea FR, King RH, Eason PJ and Campbell RG 1998. Interrelationships between dietary ractopamine, energy intake, and sex in pigs. *Australian Journal of Agricultural Research* 49, 565–574.
- Dunshea FR, King RH, Campbell RG, Sainz RD and Kim YS 1993. Interrelationships between sex and ractopamine on protein and lipid deposition in rapidly growing pigs. *Journal of Animal Science* 71, 2919–2930.
- Dunshea FR, McCauley I, Jackson P, Long KA, Nugent EA, Simons JA, Walker J and Hennessy DP 2008. An immunocastration vaccine decreases boar taint compounds for at least 8 weeks after the second vaccination. Proceedings of the 59th Annual Meeting of the European Association for Animal Production, 103pp.
- Dunshea FR, Colantoni C, Howard K, McCauley I, Jackson P, Long KA, Lopaticki S, Nugent EA, Simons JA, Walker J and Hennessy DP 2001. Vaccination of boars with a GnRH vaccine (Improvac) eliminates boar taint and increases growth performance. *Journal of Animal Science* 79, 2524–2535.
- Dunshea FR, Cronin GM, Barnett JL, Hemsworth PH, Hennessy DP, Campbell RG, Luxford B, Smits RJ, Tilbrook AJ, King RH and McCauley I 2011. Immunisation against gonadotrophin releasing hormone (GnRH) increases growth and reduces variability in group-housed boars. *Animal Production Science* 51, 695–701.
- Dunshea FR, McCauley I, Barnett JL, Cronin GM, Hemsworth PH, King RH, Campbell RH, Luxford B, Smits RJ, Hennessy DP, Butler KL and Tilbrook AJ 2000. Improving the performance/efficiency of entire male pigs under commercial conditions. Final Report for Project DV160/1344, to Pig Research and Development Corporation, Canberra, Australia.
- EFSA Scientific Panel 2004. Opinion of the scientific panel on animal health and welfare on a request from the commission related to welfare aspects of the castration of piglets. *The EFSA Journal* 91, 1–18.
- Fàbrega E, Cros J, Soler J, Velarde A, Gispert M and Suarez P 2010. Effect of immunisation against gonadotropin-releasing hormone, using Improvac on growth performance, body composition, behaviour and acute phase protein response. *Livestock Production Science* 132, 53–59.
- Font-i-Furnols M, Gispert M, Soler J, Diaz M, Garcia-Regueiro JA, Diaz I and Pearce MC 2012. Effects of vaccination against gonadotrophin-releasing factor on growth performance, carcass, meat and fat quality of male Duroc pigs cured for dry-ham production. *Meat Science* 91, 148–154.
- Fuchs T, Nathues H, Koehrmann A, Andrews S, Brock F, Sudhaus N, Klein G and Beilage EG 2009. A comparison of the carcass characteristics of pigs immunized with a 'gonadotrophin-releasing factor (GnRF)' vaccine against boar taint with physically castrated pigs. *Meat Science* 83, 702–705.
- Giles LR, Batterham ES and Dettmann EB 1986. Amino acid and energy interactions in growing pigs. 2 Effects of food intake, sex and live weight on responses to lysine concentration in barley-based diets. *Animal Production* 42, 133–144.
- Giles LR, Batterham ES, Dettmann EB and Lowe RF 1987. Amino acid and energy interactions in growing pigs. 3. Effects of sex and live weight and cereal on the responses to dietary lysine concentration when fed ad libitum or to a restricted food scale on diets based on wheat or barley. *Animal Production* 45, 493–502.
- Glass GV 1976. Primary, secondary, and meta-analysis of research. *Educational Researcher* 5, 3–8.
- Hansen BC and Lewis AJ 1993. Effects of dietary protein concentration (corn:soybean meal ratio) on the performance and carcass characteristics of growing boars, barrows, and gilts: mathematical descriptions. *Journal of Animal Science* 71, 2122–2132.
- Hémonic A, Courboulay V, Kuhn G, McClaughlin CL, Martin VA, Brock FC and Pearce MC 2009. Evaluation of the efficacy and production benefits of vaccination against boar taint in male pigs raised under commercial field conditions in France. *Revue de Médecine Vétérinaire* 160, 383–393.
- Higgins JPT, Thompson SG, Deeks JJ and Altman DG 2003. Measuring inconsistency in meta-analyses. *British Medical Journal* 327, 557–560.
- Huber L, Wey D and de Lange CFM 2012. Dynamics of nitrogen retention in entire male pigs immunized with Improvest. *Journal of Animal Science* 90 (suppl. 4), 422.

- King RH, Campbell RG, Smits RJ, Morley WC, Ronnfeldt K and Dunshea FR 2004. The influence of dietary energy intake on growth performance and protein deposition in pigs between 80 and 120 kg live weight. *Australian Journal of Agricultural Research* 55, 1271–1281.
- King RH, Campbell RG, Smits RJ, Morley WC, Ronnfeldt K, Butler K and Dunshea FR 2000. Interrelationships between dietary lysine, sex and porcine somatotropin administration on growth performance and protein deposition in pigs between 80 and 120 kg live weight. *Journal of Animal Science* 78, 2639–2851.
- Lanferdini E, Lovatto PA, Melchior R, Orlando UAD, Ceccantini M and Poleze E 2013. Feeding surgically castrated, entire male and immunocastrated pigs with different levels of amino acids and energy at constant protein to energy ratio with or without ractopamine. *Livestock Science* 151, 246–251.
- Lealiifano AK, Pluske JR, Nicholls RR, Dunshea FR, Campbell RG, Hennessy DP, Miller DW, Hansen CF and Mullan BP 2011. Reducing the length of time between harvest and the secondary GnRF immunization improves growth performance and clears boar taint compounds in male finishing pigs. *Journal of Animal Science* 89, 278–2792.
- Lovatto PA, Lehnen CR, Andretta I, Kipper M and Demori AB 2010. Nutrição de suínos machos inteiros. *Proceedings IV Congresso Latino Americano de Nutrição Animal* 205–214.
- McCauley I, Watt M, Suster D, Kerton DJ, Oliver WT, Harrell RJ and Dunshea FR 2003. A GnRF vaccine (Improvac®) and porcine somatotropin (Reporcin®) have synergistic effects upon growth performance in both boars and gilts. *Australian Journal of Agricultural Research* 54, 11–20.
- McCauley I, Cronin GM, Barnett JL, Butler KL, Hennessy DP, Campbell RG, Luxford B, Smits RJ, Tilbrook AJ and Dunshea FR 2000. An immunocastration vaccine (Improvac®) increases growth in individually and group-housed boars. *Journal of Animal Science* 78 (suppl. 1), 138.
- McCauley I, Cronin GM, King RH, Hemsworth PH, Barnett JL, Luxford B, Smits RJ, Hennessy DP, Campbell RG and Dunshea FR 2004. Dietary narcoleptics and immunocastration improve growth in group-housed boars. *Asia Pacific Journal of Clinical Nutrition* 13 (suppl.), S89.
- Metz C and Claus R 2003. Active immunization of boars against GnRH does not affect growth hormone but lowers IGF-I in plasma. *Livestock Production Science* 81, 129–137.
- Millet S, Gielkens K, De Brabander D and Janssens GPJ 2011. Considerations on the performance of immunocastrated male pigs. *Animal* 5, 1119–1123.
- Moehn S, Gilles AM, Moughan PJ and de Lange CFM 2000. Influence of lysine and energy intakes on body protein deposition and lysine utilization in the growing pig. *Journal of Animal Science* 78, 1510–1519.
- Moore KL, Dunshea FR and Mullan BP 2011. Available lysine:energy requirements for male pigs immunised against gonadotrophin releasing hormone. In *Manipulating pig production XIII* (ed. RJ van Barneveld), p. 73. Australasian Pig Science Association, Werribee, Australia.
- Moore KL, Mullan BP, Campbell RG and Kim J 2012. The response of entire male and female pigs from 20 to 100 kg live weight to dietary available lysine. *Animal Production Science* 53, 67–74.
- Moore KL, Dunshea FR, Mullan BP, Hennessy DP and D'Souza DN 2009. Ractopamine supplementation increases lean deposition in entire and immunocastrated male pigs. *Animal Production Science* 49, 1113–1119.
- National Research Committee (NRC) 2012. Nutrient requirements of swine, 11th edition. National Academy Press, Washington, DC.
- Noblet J, Karege C and Dubois S 1994. Prise en compte de la variabilité de la composition corporelle pour la prévision du besoin énergétique et de l'efficacité alimentaire chez le porc en croissance. *Journées de la Recherche Porcine en France* 26, 267–276.
- O'Connell MK, Lynch PB and O'Doherty JV 2005. Determination of the optimum dietary lysine concentration for growing pigs housed in pairs and in groups. *Animal Science* 81, 249–255.
- O'Connell MK, Lynch PB and O'Doherty JV 2006. Determination of the optimum dietary lysine concentration for boars and gilts penned in pairs and in groups in the weight range 60 to 100 kg. *Animal Science* 82, 65–73.
- Oliver WT, McCauley I, Harrell RJ, Suster D, Kerton DJ and Dunshea FR 2003. A gonadotropin-releasing factor vaccine (Improvac) and porcine somatotropin have synergistic and additive effects on growth performance in group-housed boars and gilts. *Journal of Animal Science* 81, 1959–1966.
- Pauly C, Spring P, O'Doherty JV, Ampuero Kragten S and Bee G 2009. Growth performance, carcass characteristics and meat quality of group-penned surgically castrated, immunocastrated (Improvac®) and entire male pigs and individually penned entire male pigs. *Animal* 3, 1057–1066.
- Quiniou N, Dourmad JY and Noblet J 1996. Effect of energy intake on the performance of different types of pigs from 45 to 100 kg body weight. 1. Protein and lipid deposition. *Animal Science* 63, 277–288.
- Quiniou N, Noblet J, Dourmad JY and van Milgen J 1999. Influence of energy supply on growth characteristics in pigs and consequences for growth modelling. *Livestock Production Science* 60, 317–328.
- Quiniou N, Courboulay V, Salaün Y and Chevillon P 2010. Conséquences de la non castration des porcs mâles sur les performances de croissance et le comportement : comparaison avec les mâles castrés et les femelles. *Journées de la Recherche Porcine* 42, 113–118.
- Quiniou N, Monziols M, Colin F, Goues T and Courboulay V 2012. Effect of feed restriction on the performance and behaviour of pigs immunologically castrated with Improvac®. *Animal* 6, 1420–1426.
- Rao DS and McRracken KJ 1992. Energy:protein interactions in growing boars of high genetic potential for lean growth. 2. Effects on chemical composition of gain and whole-body protein turn-over. *Animal Production* 54, 83–93.
- Rikard-Bell CV, Pluske JR, van Barneveld RJ, Mullan BP, Edwards AC, Gannon NJ, Henman DJ and Dunshea FR 2012. Dietary ractopamine promotes growth, feed efficiency and carcass responses over a wide range of available lysine levels in finisher boars and gilts. *Animal Production Science* 53, 8–17.
- Rikard-Bell C, Curtis MA, van Barneveld RJ, Mullan BP, Edwards AC, Gannon NJ, Henman DJ, Hughes PE and Dunshea FR 2009. Ractopamine hydrochloride improves growth performance and carcass composition in immunocastrated boars, intact boars, and gilts. *Journal of Animal Science* 87, 3536–3543.
- Rydmer L, Lundstrom K and Andersson K 2010. Immunocastration reduces aggressive and sexual behaviour in male pigs. *Animal* 4, 965–972.
- Schmidt T, Calabrese JM, Grodzky M, Paulick M, Pearce MC, Rau F and von Borell E 2011. Impact of single-sex and mixed-sex group housing of boars vaccinated against GnRF or physically castrated on body lesions, feeding behaviour and weight gain. *Applied Animal Behaviour Science* 130, 42–52.
- Schmoll F, Kauffold J, Pfutzner A and Baumgartner J 2009. Growth performance and carcass traits of boars raised in Germany and either surgically castrated or vaccinated against gonadotropin-releasing hormone. *Journal of Swine Health and Production* 17, 250–255.
- Škrlep M, Batorek N, Bonneau M, Prevolnik M, Kubale V and Čandek-Potokar M 2012. Effect of immunocastration in group-housed commercial fattening pigs on reproductive organs, malodorous compounds, carcass and meat quality. *Czech Journal of Animal Science* 57, 290–299.
- Standing Committee on Agriculture (SCA) 1987. Feeding standards for Australian livestock: Pigs. CSIRO, Melbourne, Australia.
- Stein HH, Sève B, Fuller MF, Moughan PJ and de Lange CF 2007. Invited review: amino acid bioavailability and digestibility in pig feed ingredients: terminology and application. *Journal of Animal Science* 85, 172–180.
- Suster D, Leury BJ, Kerton DJ, Borg MR, Butler KL and Dunshea FR 2006. Longitudinal DXA measurements demonstrate lifetime differences in lean and fat tissue deposition in individually penned and group-penned boars and barrows. *Australian Journal of Agricultural Research* 57, 1009–1015.
- van Milgen J, Valancogne A, Dubois S, Dourmad JY, Sève B and Noblet J 2008. InraPorc: a model and decision support tool for the nutrition of growing pigs. *Animal Feed Science and Technology* 143, 387–405.
- Whitehead A and Whitehead J 1991. A general parametric approach to the meta-analysis of randomized clinical trials. *Statistics in Medicine* 10, 1665–1677.
- Yuan YL, Li J, Zhang WH, Li C, Gao F and Zhou GH 2012. A comparison of slaughter performance and meat quality of pigs immunised with a gonadotropin-releasing factor vaccine against boar taint with physically castrated pigs. *Animal Production Science* 52, 911–916.
- Zamaratskaia G, Andersson HK, Chen G, Andersson K, Madej A and Lundstrom K 2008. Effect of a gonadotropin-releasing hormone vaccine (Improvac) on steroid hormones, boar taint compounds and performance in entire male pigs. *Reproduction in Domestic Animals* 43, 351–359.