Trade-offs between litter size and offspring fitness in domestic pigs subjected to different genetic selection pressures

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Abstract

Artificial selection of the domestic pig (*Sus scrofa domesticus*) offers a useful model for investigating changes in behaviour associated with reproductive trade-offs between litter size and fitness of offspring. The aim of this study was to evaluate effects of litter size on teat stimulation, sibling competition, and pre-weaning survival and growth in three populations of domestic pigs subjected to different selection pressures (a maternal line selected for high reproductive investment, a paternal line selected for meat production traits, and a crossbred line). We predicted that, with increasing litter size, piglets would spend more time in udder massage, be less likely to gain access to a teat during milk letdown and, if surviving to weaning, have lower, more variable body weights. We also predicted that maternal line sows would wean more piglets of higher weight, despite larger litter sizes, than paternal line sows. Sows (maternal line, n=12, paternal line, n=12, crossbred line, n=14) were loose-housed with their litters in individual farrowing pens. We collected data on piglet behaviour during nursings at 1 day of age, when sibling competition was expected to be most intense. Piglets were weaned at 35 days of age, when they were weighed and cumulative mortality was calculated. As predicted, piglets in larger litters spent more time in pre- and post-letdown udder massage ($P = 0.050$ and $P < 0.001$, respectively). In larger litters, more piglets survived to weaning ($P = 0.002$), but at a cost of a lower proportion of nursings with letdown ($P < 0.001$), longer nursing intervals on average ($P = 0.018$), more piglets without a functional teat at letdown ($P < 0.001$), an increased risk of mortality due to starvation ($P < 0.001$) and crushing ($P = 0.002$), and lower ($P = 0.039$), more variable ($P = 0.002$) body weights at weaning. In the maternal line, nursing intervals lengthened with increasing litter size (litter size × breed: $P < 0.001$) despite more post-letdown udder massage ($P < 0.001$), and mortality due to crushing rose with increasing litter size ($P < 0.001$), without differential increments in number, weight or weight uniformity of weaned piglets with increasing litter size between breeds (litter size × breed: $P > 0.1$). Our results suggest that further artificial selection for larger litters in maternal lines will be unsustainable because increments in the number of piglets weaned have increasing costs (e.g. sibling competition, mortality, uneven growth) that compromise piglet welfare and fitness.

Keywords: Reproductive strategy; Artificial selection; Maternal investment; Brood reduction; Suckling behaviour; Offspring survival

1. Introduction

Overproduction of young is an insurance policy that increases parental fitness when access to resources is variable (e.g. Smith and Fretwell, 1974; Williams, 1966). A constraint on such reproductive “bet hedging” is that offspring often have lower weights and slower physical development in larger broods (e.g. Mendl, 1988; Nilsson and Gårdmark, 2001). This trade-off between number and fitness of offspring (Clutton-Brock and Godfrey, 1991; Lessells, 1991) may be particularly evident in artificial selection of the domestic pig (*Sus scrofa domesticus*) to capitalize on the pig’s capacity for overproduction. In pig breeding, selection pressure for litter size varies between breeds, offering a useful model for investigating trade-offs between reproductive strategies.

Selection indices for “maternal” pig lines (e.g. Norsvin Landrace) incorporate multiple traits including growth, feed efficiency, meat and carcass quality, reproduction and health but with the main emphasis on litter size (total born and born alive) and indirect measures of maternal capacity (lower piglet mortality to 21 days, litter weight at 21 days, total number of teats, and number of functional teats; Norsvin annual report, 2014). For example, the Norsvin Landrace selection index has placed a 25% weight on litter size at birth and a 16% weight on number of piglets surviving to 21 days (Martinsen, 2016). In contrast, “paternal” (i.e. “terminal sire”) lines such as the Norsvin Duroc are selected most heavily for meat production traits such as growth, carcass quality and health (receiving 89 % weight in the Norsvin Duroc selection index; Martinsen, 2016), consequently producing smaller litters with piglets growing at less uniform rates than those of maternal lines. Selection pressures on “multipurpose” breeds (e.g. Swedish Yorkshire) are more balanced between litter size and other maternal traits on the one hand and meat yield, carcass qualities, and health characteristics on the other hand. When lines are crossed, heterosis is expected to optimize the selected characteristics of both parents. Therefore, boars of paternal lines are often crossed with sows expressing stronger maternal traits to produce crossbred piglets destined for slaughter. It is unclear how these differing breeding strategies affect piglet behaviour towards the sow (i.e. signalling of need for milk) and siblings (i.e. competition for milk) and their impact on sow behaviour (e.g. milk provisioning versus crushing of piglets; Andersen et al., 2011).

In the pig, nursing occurs in organized bouts, with each bout comprising an initial period of around 1 to 3 min of udder massage by the piglets (pre-massage), a brief milk ejection (letdown) period lasting approximately 15 s when piglets rapidly drink the milk, and a concluding period of udder massage (post-massage) of varying duration (Algers et al., 1990; Algers and Uvnäs-Moberg, 2007). If there is insufficient pre-massage (e.g. due to too few piglets at the udder, too many teat disputes, or too few accessible teats), the nursing is terminated without milk letdown (unsuccessful nursing; Illmann and Madlfousek, 1995). Following a successful nursing, the duration of post-massage of the udder appears to be positively correlated with future milk production (Algers and Jensen, 1991; Gill and Thomson, 1956; although not confirmed at the teat level, Špinka et al., 1995). The effort invested in post-massage might, thus, be considered investment for the future. If udder stimulation by the litter is high, sows may respond with more frequent successful nursings, thereby increasing daily milk provisioning (Algers and Jensen, 1991). However, there is likely to be an upper limit to the sows' flexibility to respond to increasing piglet demand with increasing litter size. Therefore, we can explore the impact of different breeding strategies by evaluating how much effort piglets invest in pre- and post-massage, and how sows respond to this signalling of the piglets' need for nourishment.

The aim of the present project was to investigate effects of litter size on sibling competition in breeding lines subjected to different genetic selection pressures. We hypothesized that increased litter size would lead to greater sibling competition. Consequently, we predicted that, with increased litter size, piglets would: 1) spend more time in pre- and post-massage of the udder, 2) be less likely to gain access to a functional teat during milk letdown, 3) have less opportunity to monopolize more than one teat, 4) receive a lower proportion of successful nursings, 5) be at greater risk of mortality from starvation and crushing, and 6) if surviving to weaning, have lower, more variable body weights.

Furthermore, we predicted that, by investing more resources in the current litter compared to sows of a paternal line, sows of a maternal line would be able to wean more piglets with higher body weights despite greater litter sizes. We predicted that a crossbred line would show intermediate results.

2. Material and methods

2.1 Animals

We studied sows (n = 38) with their offspring from two purebred lines (n = 12 Norsvin Landrace (NL) sows (a maternal line) inseminated with NL boar semen; n = 12 Norsvin Duroc (ND) sows (a paternal line) inseminated with ND boar semen), and from a four-way crossbred (CB) line (n = 14 NL × Swedish Yorkshire sows inseminated with NL×ND boar semen). The inclusion criteria were that the sows were healthy, at least 6 sows per line were primiparous, and all sows within one batch (n = 3) had similar expected farrowing dates. The sows of each breeding line (NL, ND, CB) were in their first (n = 6, 6, 8), second (n = 0, 5, 1), third (n = 4, 0, 0), fourth (n = 0, 1, 3), fifth (n = 1, 0, 2), and sixth parity (n = 1, 0, 0), respectively.

2.2 Animal environment and husbandry

The research was conducted at the Pig Research Unit of the Norwegian University of Life Sciences, in accordance with Norwegian legislation governing the use of live animals in research and the care of farmed pigs (www.lovdata.no). One week before the expected parturition of the first sow in each batch (n = 3), sows were moved to a lactation room where they were loose-housed in individuals pens (8.9 m^2). Sows could move freely in a sow area, which had a solid concrete floor section covered with sawdust (3.3 m^2), and a slatted floor section (3.7 m^2). The sow area was equipped with two farrowing rails to prevent the sow from crushing piglets along the pen wall. An enclosed piglet creep area (1.9 m^2) was located in a front corner, which had a solid concrete floor covered with a thick layer of sawdust and was heated with an infrared heat lamp (providing a temperature of 34 °C for newborn piglets, and gradually lowered temperature until weaning). Ambient temperature in the lactation room was kept between 17 ºC and 20 ºC. In addition to natural light from the windows, artificial light was provided between 0700 and 1500 h.

Except for farrowing assistance (if sows were restless for more than 3-4 h and had contractions for more than 1-2 h without any births) and cross-fostering, the sow was responsible for piglet rearing and human intervention was kept to a minimum. Cross-fostering was performed if litter size exceeded the number of functional teats, by transferring randomly-selected excess newborn piglets to another litter of the same breeding line born on the same day. Routine husbandry comprised feeding, provision of nest-building material (i.e. straw in a hayrack) two days before expected birth of the piglets, cleaning the pen, and providing new sawdust as bedding material twice a day as well as peat as environmental enrichment on a daily basis. Iron was given orally to each newborn piglet, and male piglets were surgically castrated at 10 to 14 days of age. After parturition, sows were fed a standard concentrated lactation diet according to a standard feeding regimen, and the piglets received ad libitum access to creep feed from 21 days of age. Both sows and piglets had free access to water from nipple drinkers in the pen. The piglets were weaned at 35 days of age.

2.3 Data collection

Each sow and litter was video recorded starting one day postpartum with a camera (Foscam FI9821W, 1280×720P, ShenZhen Foscam Intelligent Technology Co., Ltd., Shenzhen, China) mounted above each pen. We focused observations on one-day-old piglets because sibling competition is most intense in early lactation when litter size is greatest (i.e., prior to any piglet mortality consequent to this competition). Continuous observations were made until six successful nursings per sow (i.e. with milk ejection) were documented, with durations of different behaviours recorded to the nearest second. We defined a nursing as a period when at least 50% of the piglets were actively engaged in teat stimulation at the udder. Nursing success (%) was calculated as the proportion of initiated nursings that resulted in milk ejection (i.e. six successful nursings multiplied by 100 and divided by the sum of successful and unsuccessful nursings). Based on udder massage during successful nursings, we defined the duration of pre-massage as encompassing the period from the beginning of the nursing to milk ejection, and the post-massage duration as covering the period from the end of milk ejection to the end of the nursing. The nursing interval was the duration from one milk ejection to the next milk ejection (i.e. the time between successful nursings). We counted the number of functional teats (i.e. teats that produced milk) when stimulated by hand shortly after completion of parturition. Also recorded were the proportion of piglets present at the udder that did not get access to a teat during each milk letdown (i.e. indicative of sibling competition), as well as the proportion of piglets monopolizing two teats (i.e. acquiring milk from two teats during successful nursings). It was not possible to record data blind because litter size and sow breed were evident from the video recordings.

Litter size was defined as the number of the sow’s own live-born piglets plus the number of piglets fostered into the litter or minus the number of piglets fostered out of the litter (i.e. number of piglets present when observations were made). We defined the number of surviving piglets as the number still present when the litter was weaned at 35 days of age, and mortality was calculated as the percentage of the observed piglets dying prior to weaning. All piglets dying before weaning were examined at the Norwegian Veterinary Institute, Pathology Section, to establish whether they had starved to death (empty stomach, small liver, no other findings) or were crushed by the sow (physical signs of crushing). We weighed surviving piglets individually to the nearest g at weaning, and the coefficient of variation in piglet weight at weaning was calculated as the standard deviation of piglet weights divided by mean piglet weight and multiplied by 100.

2.4 Statistical analysis

We performed statistical analyses using the SAS 9.4 statistical software program (SAS Institute Inc., Cary, NC). Litters were the source of variation in all models, with analyses based on a single mean per litter for each variable for which multiple measures were taken. The effect of breed (ND, NL, CB) on the number of functional teats per piglet was analyzed in a generalized linear model (GENMOD procedure) with a Gamma response distribution. The effects of litter size (as a continuous variable), breed (NL, ND, CB) as a class variable, and their interaction on nursing success, pre-massage duration, proportion of piglets missing milk letdown, proportion of piglets monopolizing two teats, piglet weight at weaning, and the coefficient of variation in piglet weight at weaning were analyzed using a general linear model (GLM procedure). Because residuals were not normally distributed, the effects of litter size, breed and their interaction on post-massage duration and nursing interval duration were analyzed in a generalized linear model (GENMOD procedure) with Poisson response distribution. We also used this model to analyze the number of surviving piglets, mortality, and proportions of piglets dying from starvation and crushing. Statistical significance was set at $P = 0.05$.

3. Results

3.1 Nursing success and udder massage

Nursing success decreased with increasing litter size ($P < 0.001$; Table 1). There was no significant additional effect of breed ($P = 0.245$; Table 1-2) or interaction between litter size and breed ($P = 0.351$; Table 1, Fig. 1) on nursing success (overall mean ± SE, 92.5 ± 1.6 %). Time spent in udder pre-massaging was greater in larger litters ($P = 0.050$; Table 1) but unaffected by breed ($P = 0.955$, Table 1-2, Fig. 1) or the interaction between litter size and breed ($P = 0.961$; Table 1, Fig. 1; overall mean ± SE, 152.8 ± 9.3 s). Time piglets spent post-massaging the udder was also greater in larger litters ($P < 0.001$; Table 1), and was lower in the ND than the NL breed, with the CB intermediate ($P = 0.002$; Table 1-2). There was an interaction between litter size and breed, with the increase in post-massage duration with litter size being greater in the NL line compared to the CB and ND lines ($P < 0.001$; Table 1, Fig. 1). Overall, the nursing interval increased with increasing litter size ($P = 0.018$; Table 1) and was shorter in the NL than the CB line, with ND intermediate ($P < 0.001$; Table 1-2). The nursing interval declined with increasing litter size in the ND breed whereas it increased in the NL and CB lines ($P < 0.001$; Table 1, Fig. 1).

3.2 Sibling competition and teat monopolization

The number of functional teats per piglet was greater in the ND than in the other two breeding lines (GENMOD, $\chi^2_{2, n = 38} = 13.9$, *P* < 0.001; Table 2). The proportion of piglets failing to get access to a teat during milk letdown increased with increasing litter size (*P* < 0.001; Table 1) but was lower in the ND breed than in the other two breeds (*P* = 0.034; Table 1-2), increasing strongly with litter size only in the NL and CB piglets (*P* = 0.021; Table 1, Fig. 1). The proportion of piglets that monopolized two teats decreased with increasing litter size overall (*P* < 0.001; Table 1) and was higher in the ND breed than in the others two breeds (*P* < 0.001; Table 1-2), with a strong decline with increasing litter size occurring only in the ND breed (*P* < 0.001; Table 1, Fig. 1).

3.3 Piglet survival and growth

The number of piglets surviving to weaning increased with increasing litter size (*P* = 0.002; Table 1) but was not further affected by breed (*P* = 0.442; Table 1-2) or the interaction between litter size and breed (*P* = 0.538; Table 1, Fig. 2; overall mean ± SE, 10.9 ± 1.3 piglets). Mean mortality was 12.3 ± 2.3 %, with 26 % of the deaths due to starvation, 36 % due to maternal crushing, and the remaining 38 % due to other causes. Overall, mortality increased with increasing litter size (*P* < 0.001; Table 1) and was higher in the ND breed than in the other two breeds (*P* < 0.001; Table 1-2), but the rise with increasing litter size was most pronounced in the NL breed (*P* < 0.001; Table 1, Fig. 2). The percentage of piglets that died from starvation increased with increasing litter size (*P* < 0.001; Table 1) but was not further affected by breed (*P* = 0.653; Table 1-2) or the interaction between litter size and breed (*P* = 0.109; Table 1, Fig. 2; overall mean ± SE, 3.2 ± 1.3 %). The percentage of piglets crushed by the sow increased with increasing litter size overall (*P* = 0.002; Table 1), and was highest in the ND breed and lowest in the CB line (*P* < 0.001; Table 1-2). There was an interaction between litter size and breed, as crushing increased with increasing litter size in the NL breed, declined in the ND breed, and showed little change in the CB (*P* < 0.001; Table 1, Fig. 2).

Mean piglet weight at weaning decreased (*P* = 0.039), and variation in weights increased (*P* = 0.002), with increasing litter size (Table 1). There was no significant additional effect of breed (*P* = 0.111; Table 1-2), or interaction of litter size and breed (*P* = 0.129; Table 1, Fig. 2), on mean piglet weight (overall mean ± SE, 11.1 ± 0.3 kg) or variation in weight at weaning (breed, *P* = 0.985; Table 1-2; litter size x breed, *P* = 0.441; Table 1, Fig. 2; overall mean ± SE, 14.9 ± 1.1 %).

4. Discussion

4.1 Litter size effects

As predicted, piglets in larger litters spent more time in pre- and post-massaging at the udder. In general, the hungrier the offspring, the more intense are their begging signals even if costly to perform (Hudson and Trillmich, 2008; Mock and Parker, 1997), resulting in the parents being likely to provide them with more food (Godfray, 1991, 1995; Harper, 1986). In pigs, massaging the udder consumes extra energy, given that piglets lose body weight five times faster when active at the udder than when resting (Klaver et al., 1981), providing support for udder massage as an honest signal of need in pigs (Jensen et al., 1998; Dostálková et al., 2002). Sows appear to have responded to signals of honest begging by providing more milk, as suggested by greater loss of sow body condition during lactation with increasing litter size (Ocepek et al., 2016b). However, whereas increased daily milk output has been associated with decreased intervals between nursings in sows (Auldist et al., 2000; Špinka et al., 1997) and other ungulates such as cows (*Bos taurus*; Poole, 1982) and goats (*Capra aegagrus*; Henderson et al., 1983), in the current study, sows bearing larger litters had longer nursing intervals on averages. Thus, our results suggest that, due to biological limitations, sows with the largest litters were unable to respond to signals of honest begging by providing even more milk.

As expected, the larger the litter, the more piglets failed to access a functional teat during milk letdown, and fewer had access to more than one teat. Additionally, in larger litters, more nursings were terminated without milk letdown (i.e. nursing success was lower), despite piglet investment in udder massage and teat defense during unsuccessful nursings (durations not measured). Some precocial species, such as the domestic pig (e.g. Andersen et al., 2011) and spotted hyena (*Crocuta crocuta*; Smale et al., 1999), exhibit intense sibling competition shortly after birth. Piglets are equipped with specialized weaponry (outward-projecting deciduous canine teeth) used to compete with siblings over teats (Andersen et al., 2011; Drake et al., 2008; Fraser and Thompson, 1991). During teat disputes, piglets can be damaged by these teeth, placing them at risk of missing milk ejection and thereby becoming weaker and less able to defend a teat against better-nourished rivals in future nursings (e.g. Fraser, 1975; Fraser and Thompson, 1991). Indeed, our results show that, in larger litters, fewer piglets were able to hold on to a teat during milk letdown. Furthermore, during intense fighting for access to teats, the piglets' canine teeth may have scratched the udder, causing discomfort to the sow when nursing. This could be one reason why sows with larger litters were more likely to terminate nursings without letdown (i.e. nursing success was lower). In larger litters, we also found that fewer piglets were able to monopolize more than one teat. Piglets monopolizing only one teat may gain weight more slowly (Hartsock and Graves, 1976; Illmann et al., 2007), reducing their chances for survival during early competition for teats.

As predicted, piglets in larger litters were at greater risk of dying and, if they survived until weaning, had lower, more variable body weights (i.e. lower litter uniformity). Consistent with Andersen et al. (2011), the incidence of maternal infanticide (crushing) and sibling competition (starvation) increased with increasing litter size. Crushing as a consequence of overlying by the sow is the most common source of progeny loss in domestic sows (Andersen et al., 2011; Chen et al., 2008; Drake et al., 2008) as in farmed wild sows (e.g. Harris et al., 2001), and can be viewed as a form of maternal infanticide resulting in brood reduction (Andersen et al., 2005) given that infanticide implies not only physical abuse or direct infant killing but also neonatal rejection and maternal failure to protect offspring (Hrdy, 1979). Despite higher losses in larger litters, overall, sows bearing larger litters weaned more piglets.

Nevertheless, when the number of offspring in the current reproductive effort increases, this may be associated with reduced individual offspring fitness (Clutton-Brock and Godfrey, 1991; Lessells, 1991). This trend has been observed in several studies of domesticated mammals despite ample human provisioning of the mothers (Andersen et al., 2011; Guerra and de Nunes, 2001; Mendl, 1988; Milligan et al., 2002; Priestnall, 1972). In agreement, we found that piglets in larger litters had lower, more variable body weights at weaning. This lack of weight uniformity may persist beyond weaning because, in social groups, individual growth rates before and after weaning can be correlated (Klindt, 2003; Mahan, 1993; Quiniou et al., 2002). Even if smaller pigs exhibited some compensatory growth following weaning, such pigs may have a lower lean percentage and, thus, higher back fat thickness (Prevolnik et al., 2011). Pigs with relatively low body weights, high back fat thickness or low lean percentage at 150 days of age are generally slaughtered rather than being kept for reproduction, indicating a fitness cost associated with slower growth prior to weaning.

4.2 Breed differences

Because of greater selection emphasis on maternal traits, we expected that NL sows would be better able to mitigate sibling competition than ND piglets. However, we found that NL piglets were less likely to gain access to a functional teat during milk letdown compared to ND piglets. Although NL sows had more functional teats than ND sows, the ratio of functional teats to piglets was approximately 30% lower in the NL line compared to the ND line, and as much as 50% lower when compared to the wild boar (Fernandez-Llario and Mateos-Quesada, 2005). Moreover, the proportion of piglets missing milk letdown was more than four times higher in the NL than the ND line. These results indicate that the ratio of functional teats to piglets was suboptimal in the NL line even though it was positive (mean 1.2), and cross-fostering was practiced to smooth out differences in litter size within breed. Similarly, the CB line also showed evidence of suboptimal teat access.

Some studies indicate that piglets prefer more anterior teats (Fraser et al., 1979; Newberry and Wood-Gush, 1985; Skok and Gerken, 2016). Recently, Ocepek et al. (2016a) showed that competition for, and suckling of, the anterior teats was elevated because those teats were more accessible. That is, the distance between teats was lower in the anterior than the more posterior regions of the udder where the upper teat row of the laterally recumbent sow tended to be excessively high above ground and teats in the lower teat row tended to be poorly exposed (Ocepek et al., 2016a). These findings highlight the importance of surplus functional teat accessibility. Two decades ago, highly competitive piglets could sample approximately seven teats during one milk letdown in early lactation (de Passillé et al., 1988; de Passillé and Rushen, 1989). In the current study, the proportion of piglets using more than one teat was 70% lower in the NL than the ND line, suggesting that high sibling competition prompted NL piglets to develop early fidelity to a single teat and defend it fiercely.

Consistent with increased sibling competition, NL piglets invested more time and energy in the post-massage phase of the nursing bout, engaging in post-massage for an average of 2 min longer in successful nursing bouts than piglets of the ND line. NL sows responded by nursing their piglets more frequently, with nursing intervals that were for 8 min shorter than those of ND sows. However, despite the increased nursing rate of the NL sows, the percentage of nursings that were successful was similar between breeds after accounting for litter size. This might partly explain why, despite inclusion of body weight at 3 weeks in the NL selection index, mean body weight at weaning, and the coefficient of variation in weaning weight, did not differ significantly between breeds.

Fewer piglets died due to crushing, and overall, in the NL compared to the ND line, consistent with selection of the NL line for lower mortality (16 % weight in the NL selection index; Martisen, 2016). The average number of piglets surviving to weaning was approximately one piglet higher in the CB line than that reported for CB piglets by Andersen et al. (2011) based on data collected about 10 years ago, and two piglets higher in the NL line. The NL line has experienced the strongest selection pressure for larger litters (mean 25 % of the weight in the NL selection index), and currently produces 30 % larger litters at birth compared to the ND line (Ocepek et al., 2016b). However, after accounting for differences due to litter size, breeding for maternal traits did not result in further gains in number of piglets weaned.

The CB results were either intermediate between those of the NL and ND lines as expected, or sometimes similar to the NL line. These results are logical given that the sows rearing the CB piglets were more similar to the NL than the ND line, and heterosis was expected due to crossbreeding.

4.3 Litter size by breed interactions

Further insights into trade-offs between litter size and piglet fitness can be found through examination of the litter size by breed interactions. A significant interaction was found for all variables exhibiting breed differences. Compared to the ND line, the NL piglets showed a relatively steeper increase in post-massage duration, proportion of piglets missing milk letdowns, and overall mortality with increasing litter size, as well as an increase rather than decrease in sow nursing interval duration and piglet crushing incidence. Piglet monopolization of two teats declined with increasing litter size in the ND line whereas it was already low and remained low with increasing litter size in the NL line. Results for the CB line were mostly intermediate between those for the NL and ND lines. These results suggest that it is still possible to stretch the sow reproductive capacity, but with decreasing benefits, and increasing costs in terms of animal welfare (piglet competition, mortality, variable growth) and, therefore, social sustainability.

Furthermore, the increased maternal investment of the NL sows was costly in terms of a higher prevalence of painful shoulder lesions and greater loss of body condition during lactation, especially in primiparous sows still needing resources for their own growth (Ocepek et al., 2016b). Sows in poor body condition tend to have a longer interval from weaning to oestrus (Engblom et al., 2007), placing them at risk of being culled from the breeding population and, thereby, reducing their reproductive success. Already, up to 30% of first parity sows are culled (Thingnes et al., 2015). Ongoing selection for litter size in maternal lines is likely to result in a further shift towards maternal investment early in life (i.e. r-selection as opposed to K-selection, Newberry and Swanson, 2008), with correspondingly greater costs to the sow from nourishing larger litters. It could be argued that human provisioning of neonatal piglets could compensate for the sow's inability to further increase her lactational output. This strategy has, however, met with limited success due to higher labour costs, poor immunity to diseases, and failure to thrive in piglets raised on sow milk substitutes (e.g. Gomez, 1997), although advances in automation (i.e. precision farming), piglet nutrition and health management may improve feasibility.

5. Conclusions

Sows have an evolved capacity to produce more young than they can usually rear under natural conditions, an "insurance policy" against unpredictable early mortality. Through human provisioning of sows and artificial selection for increased reproductive investment, we have been able to utilize this "overproduction" capacity of the sow to increase weaned piglet production, but at a cost of increased sibling rivalry. Irrespective of breed, increased litter size resulted in increased time spent by piglets in pre- and post-massage of the udder, longer nursing intervals, lower nursing success, an increased proportion of piglets missing milk letdowns, fewer piglets able to monopolize more than one teat, and increased piglet mortality due to starvation and maternal crushing. In larger litters, more piglets survived until weaning, but with lower, more variable body weights. In the maternal NL line, which already produces the largest litters, it appears unlikely that continued selection for even larger litters will be socially sustainable. We arrive at this conclusion because the increase in post-massage duration (i.e. honest begging) with increasing litter size in this line was accompanied by a longer interval between nursings, fewer piglets securing a teat during milk letdown, and higher maternal crushing and overall piglet mortality without any additional increment in the number, weight or weight uniformity of piglets at weaning with increasing litter size (litter size by breed, $P > 0.1$).

Acknowledgements

This study was financed by the Norwegian Research Council, Animalia, Nortura and Norsvin (grant number 207804). The authors wish to acknowledge staff at the Pig Research Unit for their technical assistance and for taking good care of the animals.

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