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Function and strategies of a neonatal sibling competition during access to teats in domestic pigs

Bachelor's thesis

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Abstract

Domestic pigs have a high piglet mortality up to 20% during the first days post partum. It is unclear whether piglet mortality is caused by neonatal litter competition. Piglets are precocial and capable of active competition within minutes of birth on access to teats. There is very little known about this theme. The aim of the study is to review the behavioural mechanism of neonatal sibling competition during teat access and their consequences in domestic pigs. Factors which influence the level of neonatal litter competition should be considered. The consequences of the neonatal sibling competition should be reviewed on the survival and life history of individual piglets. Based on the knowledge from the literature an experimental design should be suggested for further experiments which clarify unknown aspects of litter competition.

Keywords: litter competition, teat order, domestic pigs, teeth, fighting behaviour

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1 Introduction

Domestic pigs have a high rate of piglet mortality during the first days post partum which may be caused by litter competition. Domestic pigs are polytocous animals producing many offspring in a single birth. Piglets are born extremely developed in a highly precocious state, which is relatively uncommon for a polytocous species among the mammals (Fraser 1980). Thus, they are capable to compete with their litter-mates for access to the functional teats immediately after birth. These competitions are made more dangerous because of fully erupted canines and third incisors. Pig producer often resected these teeth in order to avoid injures. Piglets tend to consistently suckle from one or two specific teat which they defend against littermates and they return to them at every nursing bout. They progressively establish relatively stable „teat order“ during the first weeks of life.

The fights can be disadvantageous for fighters and also for all littermates. On one side, loser can be excluded from the teat during milk ejection and threaten on life by starvation. On the other side, competition at the udder can cause failure of milk ejection due to inadequate and asynchronous teat massage. Inadequate milk intake may reflect piglet's weight gain and survival.

My bachelor's thesis should be based on the knowledge from the literature. The aim of the study is to review the behavioural mechanism of neonatal sibling competition during teat access and their consequences in domestic pigs.

2 Litter competition

Many animals grow up in the company of same or different-age siblings (Hudson and Trillmich 2008). The individual may have benefit from sibling presence but siblings may also compete among themselves for parental resources. We expect sibling competition particularly if resources are poor and the actually brood needs outweigh the supplies. Sibling rivalry can occur not only among young from one litter or clutch but also among young from different ones if offspring are not weaned before arrival of the next young. Presently, sibling competition is more and better studied in birds than in mammals but number of studies in mammals increases.

2.1 Sibling competition

Siblings growing up together inevitably compete among themselves over limited resources such as food, heat and parental protection and each tries to obtain a greater fitness benefit from the parental investment than received other members of the litter (Trivers 1974; Godfray 1995; Drummond 2006; Hudson and Trillmich 2008). Sibling rivalry is demonstrated by various behavioural mechanisms, such as agonistic interaction, scramble competition or aggression which can lead in extreme case to siblicide (reviewed by Hudson and Trillmich 2008). These competitive interactions presumably increase with number of offsprings, particularly in species that produce more young than is number of teats, for example guinea pigs (Fey and Trillmich 2008). In mammals, siblings often compete for the most productive teats, and growth rate of individual depends on the success in competition for these most productive sites whereas larger siblings may be more successful in acquiring them (Stockley and Parker 2002). Larger and heavier infants have generally greater advantage in competitions. Smaller and weaker infants thus may suffer from starvation, if they are excluded from the teat by stronger sibling or from injury if there is overt aggression. Postnatal growth rate thus depends on the amount of energy gained during suckling period and is low in species with intense sibling rivalry which may be explained by increasing energetic costs of competition (Stockley and Parker 2002). According to Drummond (2006), different competing and fighting ability is one of the mechanisms that generates later dominance relationship.

2.2 Parent-offspring conflict

Sibling rivalry may play a great role in reduction of litter size in animals that produce more youngs than can rear, particularly in unpredictable environmental condition. This is common for some kind of birds, for example great egrets. This phenomenon called „overproduction“ and it means that parents produce „core brood“ (the number of young ordinarily raised to independence) and „marginal brood“ (one or more youngs which are predetermined to die, though sometimes can survive) (Mock and Forbes 1995). This strategy involves some components, such as small investment to production of marginal young, intense sibling competition determining the number of offspring that will be raised and difference in body size among siblings producing competitive asymmetry (reviewed by Fraser et al. 1995). But why parents spend some cost by production supernumerary

offspring? According to Mock and Forbes (1995), there are three reasons. First, marginal offspring can replace youngs from core brood, that either died or develop poorly. Otherwise, marginal offspring may serve as a food for core brood members when food shortages arise. Finally, marginal offspring can enhance parental fitness, when unpredictable resources prove unusually rich and they survive. Supranumerous offspring may serve as an insurance of core brood survival and maximize thus reproductive success of parents.

Parental care is highly energy intensive process and can cause also conflict among parent and offspring mainly over the duration and amount of paternal investment. Trivers (1974) in his paper pointed out that parents and their offspring not always share the same interests. Parent-offspring conflict increases during the period of parental care and occurs when parents and offspring have different demands to maximize their inclusive fitness. Parents should invest in their offspring as long as the benefit to young from parental care exceeds costs to parents. Initially parent and offspring have the same interest. Parents are selected to feed and ensure survival of their offspring and offspring want to be fed. As time goes on, young become increasingly independent and benefits to them from parental care decrease whereas costs resulting from parental care increase. The added care may decreases parental investment in later posterity. Therefore parents are motivated to finish their care in current offspring whereas offsprings require more investment that parents wish to give and they employ psychological manipulation. Then, it can occur weaning conflict whose lenght and intensity is affected by degree of relatedness of current and future offspring (Trivers 1974). By lower degree of relatedness, for example if they are fathered by different male, we expect longer and more intense weaning conflict (Trivers 1974). The theory of parent-offspring conflict has been discussed by other authors (e.g. Harper 1986; Godfray 1995).

2.3 Models of litter competition in mammals

According to Nicholson (1954), there are two kinds of competition, scramble and contest. Scramble competition is contest over limited resources which are not sufficient for all competitors but they can equally share them. None of the competitors gains required amount of resource and in extreme case, if there is not enough, everyone die. In contest

competition, there are only winners and losers. An individual can gain either all or nothing (Parker 2000).

According to signalling theory, animals give some signals to other individuals. The question is whether individuals that are in conflict use honest signals during communication. Models of honest signalling propose that these signals may provide reliable information about needs and condition, whereas it exists negative relationship between soliciting and condition (Smith 1994). In case of parent-offspring conflict, parents monitor intensity of offsprings begging, they get a notion about their condition and on the basis of this information they allocate optimal resource (Godfray 1995). Based on Zahavi's studies (reviewed by Wells 2003), „reliable or honest signals between such individuals could evolve only if the signals were costly. Reliability is predicted to develop when the cost of the signal is such that the sender of false information must invest more in signalling than is gained from sending the false signal. Signalling then becomes more costly to cheaters than to honest individuals. "

3 Litter competition in pigs

Domestic pigs fit sibling competition in avian overproduction remarkably well. They produce many offspring in a single birth. Piglets are born small (often less than 1 % of the weight of their mother) with variability in body size (the smallest piglets have often only half on even one-third the weight of the heaviest) (Fraser et al. 1995). The expense of the overproduction some marginal offspring are very small. Moreover, piglets are born extremely developed in a highly precocious state which allows competing with their litter-mates for access to the functional teats immediately after birth. These fights can be disadvantageous for fighters and also for all litter-mates. On one side, loser can be excluded from the teat during milk ejection and threaten on life by starvation. On the other side, competition at the udder can cause failure of milk ejection due to inadequate and asynchronous teat massage for the whole litter.

Piglets establish a relatively stable „teat order" during the first weeks of life, and number of fights gradually decreases. The question arises, whether piglets compete until they set up this „teat order", or whether their competition continues throughout lactation.

3.1 Direct and indirect neonatal competition in domestic pigs

Among littermates there can occur two kinds of competition, direct and indirect (Drake et al. 2008). Direct competition represents various form of fighting for access to the udder. Indirect competition occurs through unequal extraction of resources from the sow's mammary glands.

Direct competition is more dangerous because piglets are born with fully erupted deciduous canines angling outward from the jaw and third incisors assuming a canine-like orientation which they use against their littermates to displace them from the teat (Fraser and Thompson 1991; Drake et al. 2008). By this dentition piglets can deliver serious sideward bite to each other. It seems that these teeth have evolved as a weapon specialised against siblings solely in early intra-litter competition, at later age as other teeth erupt they become insignificant (Drake et al. 2008).

Indirect competition may be induced by weight of piglet or birth order. Earlier born piglets are often heavier and more vigorous then later born siblings (Hartsock and Graves 1976) and thus they are potentially capable to empty their teats more efficiently or to stimulate blood flow by more vigorous massage and thereby bring more hormones and nutrients to their own teats (Fraser 1984; Algers and Jensen 1991). However, larger and heavier piglets are more successfully also in fights and therefore suckle more frequently during the first hours after birth when the milk flow is steady than their lighter siblings (Hartsock and Graves 1976). So, piglets indirectly influence each other's milk intake and weight gain (Fraser et al. 1979). This is well documented by cross-fostering when piglets with medium birth weight reared in litter of lighter litter mates gain more weight than if they are reared in litters of heavier litter mates (Drake et al. 2008).

3.2 Nursing in domestic pigs

To understand to litter competition and teat order formation it is important to know the characterization of the nursing in pigs. Domestic pigs have a complex nursing-suckling behavioural pattern with a number of characteristic features, which makes them different from other mammals. After parturition, piglets are able to suckle colostrums continuously (Gill and Thomson 1956; Hartsock and Graves 1976). Then piglets progressively develop synchronized cyclical suckling (Fraser 1980). Piglets undergo several distinct phases during each nursing (Fraser 1980). To achieve a milk ejection, it is necessary to almost all

piglets participate in the teat massage before milk ejection. In addition, piglets have to massage the udder vigorously at least for a minute, which lasts longer than actual suckling. This initial massage lasts longer than in other mammals. Each suckling is accompanied by typical loud, rhythmic grunts of the sow.

3.2.1 The phases of the nursing

There are 5 distinct phases of suckling behaviour according to Whittemore and Fraser (1974), reviewed by Fraser (1980).

First, sow lies down and exposes the udder. She gives grunts by which she may call the piglets. Piglets assemble at the sow's udder. This lasts for several second or for several minutes.

Second, piglets start to massage the teats, usually for one minute or more. Sow grunts with rate gradually increasing.

Third, the mechanical stimulation of the udder causes a release of the hormone oxytocin from sow's pituitary which is accompanied by a rapid increase of sow's grunt rate. This may be a signal for piglets that milk ejection is approaching. Piglets suck with slow mouth movements. This phase lasts for 20 second.

Fourth, after 20 seconds milk ejection occurs. Actually milk flow is very brief, it lasts for 10-20 second. Because pigs have no cisterns for milk storage, milk is available for piglets only during this brief period. Piglets suck with rapid mouth movements.

Fifth, piglets start to massage teats again for up to 15 minutes although no more milk is available. It is not clear why piglets do it. It is possible that this massage influences the future milk production. Algers and Jensen (1985) showed a "restaurant hypothesis" when piglets "order" the volume of their own future meals. Gill and Thomson (1956) and Algers and Jensen (1991) found positive correlation between the duration of final massage and future total milk gain.

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3.2.2 Non-nutritive nursing

Not all nursing ends with milk ejection (Newberry and Woodgush 1985; Castrén et al. 1989; Illmann et al. 1999). This nursing which does not result in let-down of milk is called non-nutritive nursing, during which the sow's peak of grunting rate is significantly lower than during nutritive nursing, piglets do not display rapid mouth movements and they do

not gain weight (Illmann and Madlfousek 1995; Illmann et al. 1999). Non-nutritive nursing prolongs intervals between successful nursing (Fraser 1977; Castrén et al. 1989) and thus decreases piglets' milk intake (Illmann et al. 1998) and body weight gain (Spinka et al. 1997). Because piglets are fully dependent on maternal milk for the first weeks after birth and amount of milk consumption reflects piglets' growth and survival, it is important to know the causes of non-nutritive nursing.

It is sometimes assume that lower milk intake of piglets resulting from prolonged intervals between successful nursing with milk let-down is compensated by increasing of milk output from the udder during the next nursing. However, Spinka et al. (1997) found that this increase of milk amount is only slight because the mammary glands are refilled early after milk let-down. They observed that sows nursing in short intervals gave more milk and their litter gained more weight than sows nursing in long interval from 7^{th} to 8^{th} day post partum. This indicates that prolonged intervals between nutritive nursing decrease milk production.

The number of nursings without milk ejection can be up to 30% (Illmann et al. 1999). An adequate duration and intensity of massage is necessary to induce a milk ejection, piglets have to massage the teats synchronously and almost the whole litter have to take part (Fraser 1973; Algers et al. 1990). Also sow has to be motivated to nurse. This is confirmed in the study of Castrén et al. (1989) who found that most of nursing initiated by sow were nutritive whereas only half of the nursing initiated by piglets was succeeded. Any disruption of nursing behaviour, for example a lot of piglets are missing at the udder (Fraser 1973) or are busy by fighting, can result in non-nutritive nursing. Sow can terminate the nursing before milk ejection when she is disturbed by some external factor, such as unrest at the udder caused by fighting piglets (Illmann and Madlfousek 1995). However, Illmann et al. (1999) observed non-nutritive nursing even if all piglets were present at the udder and massaged the teats with the same intensity as in nutritive nursing. They suppose that non-nutritive nursing is an adaptive strategy for the sows because they can decrease milk output and thus decrease investment to the current progeny when parent-offspring conflict occurs. But more studies are needed to perform in order to confirm this suggestion. The influence of initial massage duration on non-nutritive suckling should be investigated.

3.3 Teat order

For suckling of pigs is characteristic that piglets tend to consistently suckle from one or two specific teat (Illmann et al. 2007) which they defend against littermates and they return to them at every nursing bouts. This stable arrangement is called the teat order.

But why piglets establish this teat order? There may be several assumptions. A teat order may reduce fights at the udder and consequently reduce the risk of the milk ejection missing (Depassille et al. 1988a) and ensure survival of piglets (Hartsock et al. 1977). Piglets can influence productivity of their own teats in dependence on effectiveness of suckling behaviour, such as vigorous massage before milk ejection, efficient withdrawing of milk from teat (Fraser et al. 1979) and prolonged final massage (Gill and Thomson 1956; Algers and Jensen 1991). Moreover, there may be variability in the milk production of different teats (Gill and Thomson 1956). These factors influence weight gain of piglets, so it is advantage to return always to the same teat. Teat order can be also related to later social rank (Scheel et al. 1977), although Depassille and Rushen (1989a) consider teat order as a territorial system rather than a dominance hierarchy.

3.3.1 Ontogeny of the teat order

Soon after birth piglets begin to suckle from several different teats (Rosillon-Warnier and Paquay 1984), they suckle on average 7 different teats during the first eight hours postpartum (Depassille and Rushen 1989a). Later they begin to prefer one or two certain teats.

Hartsock and Graves (1976) classify behaviour of piglets during establishment of teat specificity into several phases. The time prior to physical contact with teat and suckling, when piglets search teats they classify as a “teat seeking”. In this phase usually occurs no aggressive behaviour. During the following phase, “teat sampling”, piglets move along the udder, sample teats and actively suckle. Piglets ordinarily show agonistic behaviour and competition for possession of the teat. This phase is followed by “teat defence”, when teat order begins to form. Piglets reduce their activities to a specific area of the udder and their interactions to an adjacent littermates and they vigorously defend possession of the teat. Last phase is relative calm “teat maintenance” when piglets suckle from their gained teats and usually no more aggression occurs. Scheel et al. (1977) suggested that the location of a teat from which piglet first suckle will influence subsequent searching pattern. “Piglets

which first suckled from teats on the upper row tended to continue suckling from teats on the upper row irrespective of which side the sow lay on" (Scheel et al. 1977). Although piglets generally tend to prefer anterior teats, there are strong preference of the first and second born piglet to suckle on posterior teats (Depassille and Rushen 1989a).

Suckling stability is developed gradually (Rosillon-Warnier and Paquay 1984; Depassille et al. 1988a) during the first several days after birth. There are different results among authors about the time of teat order establishment (summarized in **Table 1**). Puppe and Tuchscherer (1999) found that suckling stability increased rapidly up to fourth day after birth at all observed "territorial levels", udder region, teat pair and single teat. This phase was followed by moderate increase of suckling consistency up to the end of second week that was around 95%. Then suckling stability showed only small changes. Likewise other authors agree that teat order is established during second week. Rosillon-Warnier and Paquay (1984) found that teat order becomes stable after 7 days, according to Litten et al. (2003) it was by day 12 and according to Depassille et al. (1988a) teat pair stability was 85% by day 10. Hartsock et al. (1977) found that 51% of piglets achieved teat stability already by 72 hours. McBride (1963) reported much earlier achieving of teat stability with 75 % by 12 hours. Hemsworth et al. (1976) found teat stability already in the end of the first week. However, the time required to develop teat order may be influence by several factors, such as methods of determining teat specificity, mortality or litter size, when in larger litters the rate of teat order development is retarded (Hartsock et al. 1977).

It is remarkable that it has not been observed teat stability of 100%. After development of relatively stable teat order, there are always some piglets that change their preferred teat. Donald in his study (1937) observed a large number of changes at 1 month old piglets and he suggested several causes for this behaviour. First, milk supply is inadequate, pigs are more hungry and less tend to having their teats. Second, in large litter it may be difficult for a late-comer to find the right teat position at the udder. Third, the missing of some piglets in the litter which do not suckle gives opportunities for other to appropriate the free teats. Fourth, the number of the teats is not the same on each side of the sow's udder and for piglets it is more complex to assort themselves if the sow changes the position from one side to other. Some changes of the teat order can occur when a sow frequently changes the body position, when the litter is very large, when housing condition are inappropriate or when interaction between mother and her offspring is disturbed (reviewed by Puppe and Tuchscherer 1999). It would be interesting to focus on which piglets change their preferred

teat after an establishment of a relatively stable teat order, for example whether this change can be influenced by piglets' weight or the teat position. However, there are some studies that found that the stable teat order is established sooner at the ends of the udder than in the middle (Fraser 1975; Fraser and Jones 1975; Fraser and Thompson 1986; Depassille et al. 1988a; Puppe and Tuchscherer 1999; Puppe and Tuchscherer 2000; Mason et al. 2003). The reason may be that it is more difficult to find the correct position in the middle at the udder (Donald 1937) or because in the middle of the udder are more fights and piglets suckling here miss more milk ejection (Fraser and Thompson 1986).

The question is how piglets recognize their own teats and how they locate them. One suggestion is smell. Piglets rub the snout around their teats and thus they mark them (McBride 1963). In the sense of Donald's Gestalt theory (1937) the main means to identify of teats is sight by which piglets are able to appreciate the conformation of the sow as a whole and in secondary part with capability to recognize the feel of teats. Another possibility is that piglets recognize their neighbours at the udder (Donald 1937; McBride 1963). To locate the teats piglets may follow the sow's hair pattern (McBride 1963) or sow's vocalization (Jeppesen 1982). Rosillon-Warnier and Paquay (1984) suppose that piglets are oriented by angles formed by the dam's leg and the body.

3.3.2 Factors affecting the ontogeny of the teat order

There are several aspects that may influence the ontogeny of the teat order. These aspects are summarized in **Table 2**.

In general, it is assumed that piglets with greater birth weight tend to occupy more anterior teats. Scheel et al. (1977) found negative correlation between birth weight and teat position with heavier piglets suckle more on anterior teats. This is in agreement with Hartsock and Graves (1977) and Mason et al. (2003). Other authors found only a weak relationship between birth weight and location of the suckled teat (Fraser and Jones 1975; Fraser et al. 1979; Depassille et al. 1988a) or no relationship (Hartman et al 1962; Fraser and Lin 1984; Rosillon-Warnier and Paquay 1984 with the exception of the lightest piglets; Depassille and Rushen 1989a; Kim et al. 2000; Litten et al. 2003). To summarized, there are approximately the same number of the studies that confirmed or rejected the prediction that piglets with greater birth weight tended to occupy more anterior teats. Based on these

results it is not possible to make any definite conclusion and it is still unclear which piglets occupy anterior teats. Other studies may be helpful.

Birth weight appears to be influenced by birth order and earlier born piglets are heavier than later born littermates (Harmon et al. 1972; Hartsock and Graves 1976; in contrast to Scheel et al. 1977), with tendency earlier born piglets to occupy more anterior teats. But studies confirming this relationship are missing. Rosillon-Warnier and Paquay (1984) found no influence of birth order on teat order development.

Scheel et al. (1977) showed a correlation between sex and teat position where males occupied anterior teats because males are usually slightly higher than female. But Rosillon-Warnier and Paquay (1984) claim that the development of teat order is not influence by sex. There is almost no knowledge about the influence of sex as well as birth order on the teat order development.

The establishment of teat order can be affected by litter size. This is confirmed by Hartsock et al. (1977) where only 44% of piglets in the seven largest litters achieved teat consistency by 72 h whereas piglets' teat consistency in six smaller litters achieved at the same time was 63%. Likewise, Milligan et al. (2001a) reported lower teat consistency in larger litters. According to Hemsworth et al. (1976), teat order were unstable also in larger litters and litters had lower growth rates. In contrast to Rosillon-Warnier and Paquay (1984), who concluded that the time of teat order establishment does not necessarily vary with number of piglets in the litter. These findings are also insufficient.

The other factor affecting rate of teat development may be mortality in the litter. Piglets that die vacate their teats and other litter mates may occupy them, which cause the changes in the teat order (Hartsock et al. 1977). But evidence is missing whether piglet mortality is associated with the establishment of the teat order.

3.3.3 Differences in the teat quality

Piglets do not demand all teats equally. Anterior teats are more desirable and more preferred (Hartsock et al. 1977; Fraser and Lin 1984; Fraser and Thompson 1986; Dyck et al. 1987; Depassille et al. 1988a; Depassille and Rushen 1989a; Fraser and Thompson 1991; Puppe and Tuchscherer 1999; Kim et al. 2000) and piglets actively compete for them, with larger piglets usually win their possession.

There are some assumptions why piglets prefer these teats. First, piglets may be attracted to anterior teats by sow's voice (Jeppesen 1982). Second, the pattern of hair on the sow's belly leads piglet in the direction of posterior to anterior teats (McBride 1963). Third, the massages of the anterior teats are necessary for the milk ejection (Fraser 1973). Fourth, anterior teats may be more productive than others (Gill and Thomson 1956; Rosillon-Warnier and Paquay 1984). If these teats are indeed superior and more productive, then we can assume that piglets suckling here will gain more weight and enhance their growth. Many authors found enhanced growth of piglets suckling at the anterior teats (Hartsock et al. 1977; Fraser et al. 1979; Rosillon-Warnier and Paquay 1984; Dyck et al. 1987; Mason et al. 2003). However, piglets with greater birth weight are more capable to obtain and maintain ownership of anterior teats and larger piglets may have greater potential for growth and they may withdraw teats more effectively (Drake et al. 2008). The other possibility may be that the anterior teats produce more milk because of more vigorous stimulation they receive by larger piglets (Fraser and Jones 1975).

Several studies were done in order to determine if anterior teats are more productive than other or not. Hartman et al. (1962) showed that mammary glands differ in the milk production but milk yield was not significantly associated with the teat position. Orihuela and Solano (1995) in their experiment forced piglets with heavier birth weight to suckle at the posterior teats and lighter birth weight piglets to suckle at the anterior teats in order to increase uniformity at weaning time but they found that heavier piglets continued to be heavier independent of the suckled udder region. Depassille et al. (1988a) showed very low effect of teat position on weight gain manifesting only between days 4 and 6 of piglets' age.

This is in contrast to other studies that observed greater growth rate on anterior, sometimes also on middle teats. Kim et al. (2000) found that the first 5 pairs of mammary glands had greater wet and dry weights and piglets suckling there had greater weight gain. They found no difference in growth rate among piglets suckling anterior and middle teat pairs. Also Skok et al. (2007) observed no significant difference between anterior and middle teat pairs but piglets suckling on posterior teats took less milk and thus gained less weight than piglets on anterior or middle teats. Rosillon-Warnier and Paquay (1984) observed lower growth rate on the last three teats whereas first four teats were more productive and show no difference among themselves. Puppe and Tuchscherer (1999) observed that only piglets suckling on teat pair 7 gained significantly less weight, other

teats showed no difference. Gill and Thomson (1956) found that piglets suckling on anterior teats gained up to 15.3% more milk than piglets suckling on posterior teats which confirm that anterior teats are more productive. Likewise, Fraser and Lin (1984) showed that mean colostrum yield from the most anterior teats was about three times greater than from the most posterior teats near the time of farrowing. However, in later lactation, there were no differences in milk production between anterior and posterior teats. There is no difference between right and left row of the sow's udder in milk yield (Hartman et al. 1962; Fraser and Lin 1984) and piglets chose right teats as often as left teats (Hartsock et al. 1977). Studies that found greater weight gain of piglets occupying more anterior teats compared with those occupying posterior teats are summarized in **Table 3**.

It seems that only piglets suckling on posterior teats often gain less weight. The influence of middle and anterior teats on piglet weight gain is disputable. Some authors suppose that greater weight gain of piglets suckling at the more anterior teats occurs with increasing parity (Dyck et al. 1987; Fraser et al. 1992). Although it is often assumed that anterior teats are more productive there are only few studies confirming this suggestion. The true reason why piglets favour anterior teats remains unclear.

3.4 Fights

Fights over teats play significant part during establishment of teat order (McBride 1963). Piglets show overt, agonistic behaviour during suckling at a very early age (Depassille and Rushen 1989a). Success or failure in fighting may influence milk intake and thus reflect growth rate and survival. These fighting may contribute to piglets' preweaning mortality which is relatively high, ranging between 20 and 30% being most frequent during the first three days (Hartsock et al. 1977). As the most often cause of piglets death it is usually reported to be starvation and crushing (Dyck et al. 1987; Depassille and Rushen 1989b).

3.4.1 Occurrence of fights after birth

Scheel et al. (1977) and Depassille et al. (1988a) observed occurrence of fights for 10 days after birth and they found most fights occurring during the first day. Hartsock and Graves (1976) observed fighting frequencies of piglets during the first 24 hour after birth

and found that number of fights per piglet were maximal during the second and third hours. Depassille and Rushen (1989a) investigated suckling behaviour of piglets during the first 10 hours post partum and they observed more frequent fights during 3rd hours, then its frequency decreased. In contrast, Rosillon-Warnier and Paquay (1984) did not find any fights during the establishment of teat order. Scheel et al. (1977) reported very little aggression after the establishment of teat order.

Very disputable is the influence of the litter size. Some authors claim that in larger litters fights are more common than in smaller (Fraser 1975; Fraser and Thompson 1986; Milligan et al. 2001a), other authors did not agree (Scheel et al. 1977; Depassille and Rushen 1989a) (see **Table 4**).

It has already been mentioned before that piglets prefer anterior teats and actively compete for them. Several authors indeed observed more fights towards anterior teats (Hartsock et al. 1977; Scheel et al. 1977; Fraser and Thompson 1986) than towards the posterior ones. However, Depassille and Rushen (1989a) found also more fights at anterior teats but they suppose that piglets do not compete to access to anterior teats but to access to any functional teat during brief time of milk ejection. More fights were there simply because there were more piglets. This is in contrast to Fraser and Thompson (1986) who reported that piglets at the ends of udder fight less than piglets occupying middle teats. Fraser (1975) found piglets occupying teats in the middle of the udder to have more facial wounding which suggests that piglets suckling these teats fight more. Number of teats occurring at right and left side of sow's udder shows no differences (Scheel et al. 1977).

Piglets that win more fights usually suckle more frequently (Hartsock and Graves 1976; Depassille and Rushen 1989a), suckle more on one preferred teat pair (Hartsock et al. 1977; Scheel et al. 1977; Depassille and Rushen 1989a) and have greater weight gain from birth to 3rd day (Hartsock et al. 1977). This larger preweaning weight gain of piglets with greater fighting success may be associated with more frequent access to teats prior to establishment of the nursing order or by ability to claim more productive teats (Hartsock et al. 1977). However, Depassille et al. (1988a) found that more successful piglets had greater weight gain only during first day. Conversely, piglets that fail in competition move along the udder, try to gain ownership of other teats and thus they initiate more fights (Depassille and Rushen 1989a). Piglets that more fight have a low teat consistency, miss milk ejection more often (Fraser and Thompson 1986) and have lower weight gain (Depassille et al. 1988a). The losers are handicapped because they can miss milk ejection while they try to

exclude littermates from teats, they spent much energy, have reduced weight gain and thus decrease their survival (Scheel et al. 1977). Depassille and Rushen (1989b) found that in litter with higher piglet mortality fights are more often and also the total time spent in teat disputes was longer.

There is some evidence that piglets actively compete with littermates during access to the teats. Based on mentioned studies, we can assume that litter competition will decrease in time as teat order became more stable. However we do not know if these competitions last only up to teat order establishment or throughout the lactation. More studies investigating frequency of fighting from birth to weaning will be helpful. Because it has never been observed teat order of 100%, it is very probable that after relatively stable teat order some piglets will change their preferred teats and initiate other fights. We have also insufficient information on which part of udder piglets fight more. Although piglets prefer more anterior teats, it is still unclear, if there are also more fights.

3.4.2 Occurrence of screams after birth

Domestic pigs have a rich repertoire of vocalization which is very important for their communication. Sows give grunts in time of milk ejection and piglets vocalize when they are isolated from the sow (Weary and Fraser 1995; Weary et al. 1997) and excluded from the nursing episode (Appleby et al. 1999), when they are injured (Weary et al. 1998) or handled by human. Piglets also give some loud screams when they compete for teats during establishment of teat order but these calls are not ubiquitous (Appleby et al. 1999). In agreement with honest signalling theory, these calls may provide information about current state and condition of individual, with those that are more in need call more (Godfray 1991; Smith 1991). The lightest piglets with the lowest growth rate and hungry piglets vocalize more and use more high-frequency and longer calls and calls that rose more in frequency than their fed and more thriving littermates (Weary and Fraser 1995). Appleby et al. (1999) deprived some piglets of milk by covering their preferred teats and observed that these hungry piglets vocalized more frequently before milk ejection than piglets having access to their teats. It was surprising that these signals became neither more intensive nor more frequent in time as piglets were deprived of teats and were presumably hungrier. They suggest that the piglets' screams are mainly signal for the sow that some piglets have not access to the teat. The other hypothesis, why piglets scream during

nursing, was that piglets' calls may intimidate their littermates. But this suggestion was not confirmed.

These loud vocalizations emitted by fighting piglets seem often to upset the sow (Fraser 1975). Sows often respond to fighting screams by terminating of nursing (Newberry and Woodgush 1985). But too high responsiveness to piglets' screams is undesirable because sow often changes her body position and this can lead to crushing the piglets; moreover, too frequent terminating of nursing before milk ejection can also jeopardize the piglets because of decreased milk intake and weight gain (Illmann et al. 2008).

Other studies should investigate fights and screams together during access to the teats.

3.4.3 Factors affecting success in fights

Birth weight is a good predictor of fighting success because piglets larger at birth usually win more fights, suckle more frequent and so gain more weight (Hartsock and Graves 1976; Hartsock et al. 1977; Scheel et al. 1977; Depassille and Rushen 1989b) because of improved birth vigour (Neal and Irvin 1991). Depassille et al. (1988a) reported that larger piglets won more fights only from 1st to 6th days post partum, after 6th day body size had no influence on success during fighting. Conversely, piglets with poor weights won fewer disputes (Depassille and Rushen 1989b). Larger piglets also suckle more often (Hartsock and Graves 1976), had greater weight gain (Hartsock et al. 1977; according to Depassille et al. 1988a more successful piglets gain more weight only on day 1) and lower mortality (Hartsock and Graves 1976; Hartsock et al. 1977; Scheel et al. 1977). Also Neal and Irvin (1991) and Bereskin et al. (1973) reported that birth weight is positively correlated with survival. So, it seems that some influence of birth weight on success in fights really occurs.

Heavier piglets at birth are often those that are born earlier (Harmon et al. 1972; Hartsock and Graves 1976) and thus win more fights (Hartsock and Graves 1976; Depassille and Rushen 1989a). However, there is almost nothing known about the influence of the birth order on the success in teat disputes.

The influence of sex and teat position on success in fights has not been investigated. Only Scheel et al. (1977) showed that males tended to win more fights and they had a position at the anterior teats because they were slightly larger than female. The same author observed greater success in disputes by piglets occupying anterior teats.

Hartsock and Graves (1976) showed that piglets have a “home court advantage”. It means that when piglets fight at their “home teats”, then they win on average 80,8 % of the fights.

There is some evidence that piglets with greater birth weight are more successful in fights. However, other factors affecting success in fights are very little examined. Studies that confirm or not the influence of above mentioned factors on success in fights are summarized in **Table 4**.

3.5 Effect of teeth as a weapon on neonatal litter competition and teat access

Piglets are born with surprisingly developed dentition. Newborn piglets have fully erupted deciduous four canines which angle outward from the jaw and four third incisors which assume a canine-like orientation (Figure 1). This position of teeth allows piglets to give sideways bites to each other and thus incur serious lesions. Piglets use their teeth during early competition for teats in order to displace their littermates from teats. In later age, as jaw grows and other teeth erupt, these teeth become insignificant (Drake et al. 2008). It has been suggested that they may have been developed as an arms race.

By these sharp teeth piglets often cause facial injury to each other (Fraser 1975; Brown et al. 1996; Gallois et al. 2005; Figure 2). It is also believed that they can cause damage of the sow’s udder. Thus, many pig producers routinely resect these teeth soon after birth. They can clip them by pliers either at the gum line or only one-third of the tooth or grind by rotating grindstone. However, if these procedures are perform incorrectly, they can cause wounds of the teeth, gum or lips because of splinters or sharp edges of clipped teeth, pulp cavity exposing, haemorrhage, infiltration or abscess (Hay et al. 2004; Gallois et al. 2005). These wounds can be place of entry for an infection. The question is which wounds are more acceptable, facial wounds resulting from intact teeth or mouth and dental wounds resulting from resected teeth and if teeth resection has any impact on pig performance and preweaning mortality.

Figure 1. The teeth of domestic pigs at three ages (birth, day 21 and 84 after birth) showing the changing orientation of the anterior portion of the jaw during growth: third incisor (arrow) assume a canine-like orientation at birth and more forward orientation at later ages. Drake et al. 2008

3.5.1 The influence of teeth treatment on piglets injury

Many studies investigating piglets' injures minimally up to 3rd week post partum have shown fewer and less severe facial lesions in litters with grinding or clipping teeth than in litter with intact teeth (Fraser 1975; Brown et al. 1996; Bates et al. 2003; Holyoake et al. 2004; Gallois et al. 2005; Lewis et al. 2005a; see **Table 5**). When only clipping and grinding were considered, then some authors observed more facial lesions in piglets with grinding than clipping teeth (Gallois et al. 2005; Lewis et al. 2005a). Also partial tooth clipping significantly reduces incidence of facial wounds but do not cause more injury than fully clipped teeth (Weary and Fraser 1999). When only litters with intact teeth are taken into account then no significant correlation between litter size and severity of damage was found by Brown et al. (1996), in contrast to Fraser who found a positive correlation (1975).

The teeth resection is advantageous because it reduces facial injuries of piglets, but the disadvantage is that it may cause serious dental and mouth injury. When teeth were intact, these injuries almost did not occur (Holyoake et al 2004; Gallois et al. 2005; Lewis et al. 2005a). When teeth were resected, then more wounds occurred in piglets with ground teeth according to Holyoake et al. (2004) and conversely more wounds were found in piglets with clipped teeth according to Gallois (2005). Lewis et al. (2005a) found more mouth and

gum damage for piglets with clipped teeth and more lip lesions for piglets with ground teeth.

Figure 2. Facial laceration caused by sharp teeth. Reese and Straw 2005

It seems that intact teeth cause more facial injury whereas teeth resection, both clipping and grinding, reduces these injury but cause more dental and mouth damage. Although all above mentioned studies investigated the effect of teeth treatment on piglets' injury and did not focus on association between treatments and neonatal litter competition, we can conclude that piglets with more face injury more fight. Only Fraser (1975) found that clipped teeth do not decrease incidence of fights during development of stable teat order. Taken together, these results suggest that the reduction of facial damage in piglets due to resected teeth can be an indicator for decrease litter competition. However, the dental and mouth damage seems to be a serious welfare problem.

3.5.2 The influence of teeth treatment on piglets preweaning mortality

Some authors found no significant differences in preweaning mortality among teeth treatment (Brown et al. 1996; Weary and Fraser 1999; Gallois et al. 2005; Lewis et al. 2005a; see **Table 6**). Holyoake et al. (2004) observed higher mortality in litters with intact and ground teeth whereas litters with clipped teeth had fewer deaths because there were fewer overlay deaths. Likewise, Lewis et al. (2005a) observed that most common causes of piglets' death in teeth intact piglets were crushing. This may be because intact teeth cause injury and discomfort to the sow, she often changes posture and this behaviour can result in

increased piglet crushing. This suggestion was confirmed by Lewis et al. (2005b), as was mentioned above, where intact and ground teeth caused sows' udder damage in the middle lactation and where sows showed increased avoidance.

Bates et al. (2003) found an interaction between teeth treatment, piglets mortality and number of sow's parity. They showed that only in parity of 1, 6 or more litter with intact teeth had lower mortality rate compared with litter with clipped teeth. In parity of 2-5 mortality rate among treatment were similar. When selective teeth clipping has been performed, when piglets with low birth weight had their teeth intact whereas their heavier littermate had clipped teeth, Robert et al. (1995) showed an effect of litter size. Only in large litters (12-14 piglets per litter) piglets with low birth weight and intact teeth had lower mortality than their heavier littermates with clipped teeth. Fraser and Thompson (1991) also perform selective teeth clipping and they found mortality rate to be similar in low-birth-weight piglets with teeth and higher-birth-weight piglets without teeth.

Although piglets in litter with intact teeth have evidently more face injures, there are no evidences, that these damages affect preweaning mortality of piglets. Only Holyoake et al. (2004) found higher mortality and higher face damage in piglets by intact teeth but these deaths were caused not by facial lesions but by crushing. Leaving teeth intact seems not to improve survival of piglets with low birth weight. Also evidences that piglet with resected teeth have higher mortality because of dental or mouth damage are missing.

3.5.3 The influence of teeth treatment on piglets weight gain

Many authors did not found any association between different teeth treatment and piglets' growth within the first 3 weeks after birth (Fraser 1975; Brown et al. 1996; Bates et al. 2003; Gallois et al. 2005; Lewis et al. 2005a; see **Table 7**). Holyoake et al. (2004) found that piglets with clipped teeth were around 200 g heavier at weaning then unclipped littermates. Conversely, Weary and Fraser (1999) showed lower weight gain during first week post partum in litters whose teeth were resected compared with litters with intact teeth. Fraser and Thompson (1991) observed matched pairs of litter mates and found that in litters of 12 piglets, piglets with intact teeth had greater weight gain to day 21than their clipped litter mates. Thus, they concluded that only in large litters containing 12 and more piglets occurs an effect of teeth resection on piglets' growth rate with greater advantage for piglets with intact teeth. In smaller litters there were a tendency in the same direction but it

was not significant. This suggestion of litter size may confirm why above mentioned authors did not find a differences in weight gain between teeth treatment. All these authors used in their investigation 12 and fewer piglets per litter. It suggests that intact teeth in small litters give only little advantage to their owner if any. Only in larger litters with more than 12 piglets, where competitive pressure is most intense, intact teeth improve weight gain to their owner and also improve survival of piglets with low birth weight (in agreement with Fraser and Thompson 1991). Piglets with clipped and ground teeth may have lower competitive ability (which allows the smaller piglets to gain their own teat) or may suffer from mouth and dental damage resulting from teeth resection which may cause lower growth rate. But there are only few studies using large litters and confirming this effect (Fraser and Thompson 1991; Weary and Fraser 1999).

Because of worse performance and high mortality of piglets with low birth weight there were carried out studies in order to investigate whether intact teeth give some advantage to the lightest piglets in the litter whereas their heavier litter mates had teeth clipped. According to Fraser and Thompson (1991) small piglets with intact teeth had only slightly lower growth rate from birth to Day 21 and according to Weary and Fraser (1999) even greater weight gain during first week of age compared to heavier littermates with clipped teeth. Both of these studies used litters with mainly 12 piglets. Hovewer, Robert et al. (1995) observed improved growth rate of low birth weight piglets with intact teeth only in litters of 9-11 piglets but not in larger litters. They speculated that it may be because in large litter, where growth rate is strongly influenced by competition, advantage resulting from intact teeth was insufficient. The average litter weight gain was not altered by teeth treatment. So, leaving teeth intact in piglets with low birth weight leads to their greater weight gain at the expense of heavier littermates with clipped teeth and overall weight gain of litter is not affected, thus intact teeth lead to more uniform weight at weaning (Fraser and Thompson 1991; Robert et al. 1995).

There are not enough evidences that treatment has a significantly effect on piglets weight gain. Also evidences that piglets' lesions affect weight gain are missing.

3.5.4 The influence of teeth treatment on development of teat order

Effect of teeth treatment on development of teat order was investigated only in few studies and they found no substantial influence on rate of teat order establishing (Fraser

1975). Weary and Fraser (1999) did not observe any effect on suckling position. This is in contrast with Fraser and Thompson (1991) who observed that piglets with intact teeth, which had competitive advantage, gained anterior teats more often than piglets with clipped teeth.

Most of studies investigating teeth treatment focused on injury, piglets' prosperity or welfare. The influence of the teeth treatment on teat order development should be examined in the other studies.

3.6 Cross-fostering

In domestic pigs, piglets within litter often vary in birth weight (Milligan et al. 2001a). Small piglets are disadvantaged in competition and thus they may suckle less because they are not successful in gaining some functional teats or they are not able to defend them and they often miss milk ejection. This leads to reduced weight gain and survival of these piglets and also to a higher variation in piglets' weaning weight. To increase survival of light piglets and reduce differences in body size within litter pig producers often use cross-fostering between litters. Cross-fostering is also used when sow having large litter has not enough functional teats for all piglets. Then farmers manipulate with litter size according to supposition that in smaller litter there are more milk available to each piglet (Fraser and Thompson 1986; Auldist et al. 1998). Cross-fostering may be linked with increased aggression and number of fights among siblings and disrupts establishing of teat order, especially when it is carried out in late piglet age.

3.6.1 The influence of age of fostered piglets on fights and weight gain

During the first days after birth piglets develop teat fidelity to some teat or teat pair (Fraser and Jones 1975; Depassille et al. 1988a). Cross-fostering of unfamiliar piglets to a new litter can disturb the teat order and suckling behaviour of the whole litter. Price et al. (1994) observed in their experiment an interaction between resident and fostered piglets of the same age, when cross-fostering was performed during the first day after birth (2-9 hr post partum) and in later age (day 2, 4 and 7). Piglets which were fostered in early age reached much higher successful suckling within experimental 6 hours after fostering than piglets fostered in late age which showed greater reluctance to engage in suckling, greater

restlessness and more frequent vocalization. They conclude that cross-fostering of piglets older than 2 days retards an integration of those piglets into the new litters. Giroux (2000) done cross-fostering at 6 days of piglets age. Fostered piglets had lower weight gain compared to resident piglets from 6 to 45 days and also whole litter with adopted piglets had lower growth rate and higher rate of aggression then litter without fostered piglets. Similar results showed also Horrell and Bennett (1981). Wattanakul et al. (1998) done cross-fostering on day 14 after birth of piglets. They observed significantly reduced weight gain in litter with fostered piglets in the week after cross-fostering but within these litters, the growth rate of resident and fostered piglets were not significantly different. However, Stewart and Diekman (1989) done cross-fostering during first day post partum and they also found slower growth of adopted piglets to day 21 compared with resident piglets.

Robert and Martineau (2001) carried out repeated cross-fostering, when every 3 days (day 1, 4, 7, 10, 13 and 16 post partum) three piglets were switched between two fostered litters. Resident piglets had greater weight gain and were heavier at weaning than fostered. Except for day 1, they observed more frequent fights and more skin lacerations in litter with cross-fostering than in litter without alien piglets during and between nursings with most fights occurring between resident and fostered piglets. More injury occurred mainly in fostered piglets. Milligan (2001b) found no significant differences between fostered and resident piglets in the number of teat disputes during nursing.

According to above mentioned studies, it seems that cross-fostering, especially it is done in late age of piglets, disturbs growth of fostered litter compared to non-fostered litters and impairs growth resident and adopted piglets. Adopted piglets may have reduced access to the teats during nursing (Giroux et al. 2000), they compete with resident piglets and disturb teat order (Horrell and Bennett 1981; Horrell 1982). Resident piglets often show aggression towards fostered piglets when they attempt to suckle from their preferred teats (Price et al. 1994). Also the sow sometimes shows an aggression towards adopted piglets during nursing (Price et al. 1994; Olsen et al. 1998).

3.7 The influence of litter competition on life history of piglets

Suckling behaviour of piglets in early life may have an impact on the physical and behavioural development of piglets. Competition during access to the teats, teat order development and other suckling behaviour may affect not only piglets' growth and survival

but also may contribute to stress of piglets. Litter competition may also form the basis for the dominance hierarchy (Scheel et al. 1977; Puppe and Tuchscherer 1999).

3.7.1 Stress

The influence of stress resulting from litter competition has never been studied in domestic pigs. It is possible that in large litter where competition pressure is most intense piglets have higher cortisol level which is an indicator of stress (Fey and Trillmich 2008). Further studies should investigate if piglets in litter with more fights are more in stress and how this early stress affect life history of piglets.

3.7.2 Dominance

Sometimes it is believed that there is relationship between teat order and social dominance with the supposition that heavier and in competition more successful piglets occupy anterior teats and are higher up in the social hierarchy. Dominant piglets may gain possession of some teat earlier in neonatal life and hence improve their growth and survival (Litten et al. 2003).

It has been observed that dominant piglets were those that had higher birth weight (Scheel et al. 1977), they were more successful in competition (Scheel et al. 1977), fought more during nursing but initiated fewer fights (Scheel et al. 1977), tended to occupy anterior teats (Scheel et al. 1977; Rosillon-Warnier and Paquay 1984), had greater weight gain before weaning (Scheel et al. 1977; Litten et al. 2003) and lower mortality (Scheel et al. 1977) than subordinates. However, some authors did not find relationship between dominance and birth weight (Rosillon-Warnier and Paquay 1984; Litten et al. 2003) and between dominance and teat order (Litten et al. 2003).

After weaning and mixing with unfamiliar pigs, vigorous fighting occurs which leads to development of dominance hierarchy (Meese and Ewbank 1973). Scheel et al. (1977) found that dominance rank during suckling and after weaning was highly correlated which shows that dominance rank of piglets remains relatively stable before and after weaning. Puppe and Tuchscherer (1999) reported that piglets suckling at the posterior teats (teat pair 6 and 7) showed lower dominance values after weaning and mixing. Algers et al. (1990) found relationship between social rank of piglets and a productivity of the sows' teats.

Piglets suckling on teats with poor quality (mostly posterior) were more submissive after weaning and mixing.

Although there are some evidences that social hierarchy has roots in early ontogenetic life, we know very little about the circumstances under which it is developed. Dominance hierarchy formulated during nursing can persist also in later age after weaning and mixing with unfamiliar pigs but there are not enough studies.

4 Conclusion

The aim of the study was to review the behavioural mechanism of neonatal sibling competition during teat access and their consequences for piglet survival in domestic pigs.

There is evidence that piglets begin to compete and fight for teat immediately after birth before the teat order is established. The teat order is relatively stable after first week post partum. However, there are contradictory results about the time of the establishment of teat order post partum. This may be because of different methods of determining of teat specificity or different mortality rate in the litter. Other important and very little examined factor affecting the rate of teat order development is litter size.

Most authors agree that anterior teats are preferred. However, evidence is missing that more fights occur among piglets occupying anterior teats. It has been observed that at the end of the udder there is higher teat consistency than in the middle. But higher teat consistency does not have to be linked with lower occurrence of fights. Piglets are simply more capable to demand ownership of their teats. Further studies should investigate at which part of the udder piglets fight more.

It is still unclear why piglets prefer anterior teats. It has been suggest that anterior teats are more productive. However, clear evidence from studies is missing. It seems that piglets grow slower on posterior teats compared with middle and anterior teats which may indicate that these teats produce less milk. But it is possible that posterior teats are occupied by the lightest piglets which have a lower potential for growth. Factors affecting the development of the teat order (birth weight, birth order or sex of piglets) should be more investigated.

The number of fights should decrease when the teat order becomes stable. There are almost no studies which investigated the number of piglets' fight during teat access in the neonatal period. There is no study which focused on the frequency of fights during the course of lactation. It seems that some piglets will always fight because any author did not

found a teat consistency of 100 %. It is possible that piglets with heavier birth weight win more fights but other factors that affect teat access are very little investigated. Further studies should focus on which piglets are more successful in fights (especially birth order, sex and position of preferred teat).

There is some information that intact teeth cause facial lesions in piglets. The reduction of facial damage due to resected teeth can be an indicator for decrease litter competition. However, any effect on litter competition is unknown. There are also not enough evidences that teeth treatment affect weight gain and mortality of piglets.

Long lasting effect of litter competition on life history of piglets should be also more investigated (especially stress and dominance).

More detailed studies are necessary in order to understand the association between neonatal litter competition and the effect of weight gain and survival of individual piglets.

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Table 1. Overview of studies which analyzed the establishment of the teat order. The proportion of teat stability indicates which proportion of piglets suckled permanently from one specific teat during one day

Study	Number of sows	Proportion of teat stability (%) in dependence from the days after parturition																														
		12 h	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	32	35
Hemsworth et al. 1976	9	-	68	75	73	-	87	-	91	-	-	92	-	-	-	-	94	-	-	-	-	-	95	-	-	-	-	-	-	-	-	-
Puppe and Tuchscherer 1999	39	-	47	56	70	81	83	86	87	89	90	92	-	-	-	94	-	-	-	96	-	-	97	-	-	-	96	-	-	95	97	98
DePassillé et al. 1988a	6	-	-	-	5	13	20	20	17	15	30	53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rosillon-Wamier and Paquay 1984	8	-	34			62				93																						
Hartsock et al. 1977	13	-	30	43	51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
McBride 1963	5	75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fraser 1975	8	-	69	79	83	89	89	90	96	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-
Donald 1937	5	-	-	-	-	40 - 50		-	-	50 and more							-	-	-	-	-	-	-	-	-	-	-	-	-	--	75 - 80	

Tab. 2 Studies confirming (+) or not (-) the influence of specific factor on development of the teat order

Birth weight Heavier piglets occupy more anterior teats		**Birth order** Earlier born piglets occupy more anterior teats		**Sex** Males occupy more anterior teats		**Litter size** In larger litters slower development or lower stability of teat order	
+	–	+	–	+	–	+	–
Fraser and Jones 1975 [a)]	Litten et al. 2003		Rosillon-Warnier and Paquay 1984	Scheel et al. 1977	Rosillon-Warnier and Paquay 1984	Milligan et al. 2001	Rosillon-Warnier and Paquay 1984
Hartsock et al. 1977	Rosillon-Warnier and Paquay 1984					Hemsworth et al. 1976	
Fraser et al. 1979 [a)]	Hartman et al. 1962					Hartsock et al. 1977	
Scheel et al. 1977	Kim et al. 2000						
Depassille et al. 1988a [a)]	De Passillé and Rushen 1989a						
Mason et al. 2003	Fraser and Lin 1984						

a) only weak correlation

Table 3. Studies that found (+) or not (−) greater weight gain of piglets occupying more anterior teats compared with posterior

+	−
Harstock et al. (1977)	Hartman et al. (1962)
Fraser et al. (1979)	Orihuela and Solano (1995)
Rosillon-Warnier and Paquay (1984)	Fraser and Lin (1984)
Dyck et al. (1987)	
Mason et al. (2003)	
Depassille et al. (1988a) [a)]	
Kim et al. (2000)	
Skok et al. (2007)	
Puppe and Tuchscherer (1999)	
Gill and Thomson (1956)	

a) between days 4 and 6 after birth

Table 4. Studies confirming (+) or not (-) the influence of specific factor on success in fights

Birth weight Heavier piglets are more successful in fights		**Birth order** Earlier born piglets are more successful in fights		**Teat position** Piglets suckling on anterior teats are more successful in fights		**Sex** Males are more successful in fights		**Litter size** In larger litters are more fights	
+	–	+	–	+	–	+	–	+	–
De Passillé and Rushen 1989a		De Passillé and Rushen 1989		Scheel et al. 1977		Scheel et al. 1977		Milligan et al. 2001	De Passillé and Rushen 1989a
De Passillé et al. 1988a [a)]		Hartsock and Graves 1976						Fraser and Thompson 1986	Scheel et al. 1977
Hartsock et al. 1977									
Hartsock and Graves 1976									
Milligan et al. 2001									
Scheel et al. 1977									

a) from Day 1 do Day 6

Table 5. Influence of teeth treatment (intact, ground, clipped teeth) on frequency and/or severity of face injury of piglets as an indicator of piglet competition

Study	Time of observation (days post partum)	Frequency and/or severity of face injure rate		
		Intact teeth	Ground teeth	Clipped teeth
(Holyoake, Broek et al. 2004)	4-6	Higher	Lower	Lower
(Bates, Hoge et al. 2003)	3, 13	Higher	-	Lower
(Fraser 1975)	7, 14, 21	Higher	-	Lower
(Brown, Edwards et al. 1996)	7, 14, 22	Higher	-	Lower
(Gallois, Le Cozler et al. 2005)	8, 27	The highest	Medium	The lowest
(Lewis, Boyle et al. 2005a)	1, 4, 11, 18, 27	The highest	Medium	The lowest
(Weary and Fraser 1999)	3, 7, 14	Higher	-	Lower

Table 6. Studies that observed (+) or not (−) an influence of teeth treatment on piglets preweaning mortality

+				−
	Preweaning mortality rate			
	Intact teeth	Ground teeth	Clipped teeth	
Holyoake et al 2004	Higher	Higher	Lower	Brown et al. 1996
Bate et al. 2003[a)]	Lower	-	Higher	Robert et al 1995[c)]
Robert et al. 1995[b)]	Lower	-	Higher	Gallois et al. 2005
a) Only in sow's parity 1, 6 and more b) Only in litters of 12-14 piglets c) Only in litter size of 6-8 and 9-11 d) Only in sow's parity 2-5				Lewis et al. 2005a
				Weary and Fraser 1999
				Bates et al. 2003[d)]

Table 7. Studies that observed (+) or not (−) an influence of teeth treatment on piglets weight gain

+				−
	Weight gain rate			
	Intact teeth	**Ground teeth**	**Clipped teeth**	
Holyoake et al 2004	Medium	The lowest	The highest	Fraser 1975
Robert et al. 1995[a)]	Higher	-	Lower	Brown et al. 1996
Fraser and Thompson 1991	Higher	-	Lower	Robert et al. 1995[c)]
Weary and Fraser 1999[b)]	Higher	-	Lower	Gallois et al. 2005
a) only in litter size 9-11 b) only during the first week post partum c) only in litter size 6-8 and 12-14 d) after first week post partum				Lewis et al. 2005a
				Weary and Fraser 1995[d)]
				Fraser and Thompson 1991
				Bates et al. 2003