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Environmental and Biological Factors Influencing Aggression in Swine

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ABSTRACT

The aim of this review is to discuss the influence of environmental and biological factors on the development and expression of aggression in pigs. Inadequate resource distribution was found to be an incentive for competition, and aggressive competitions to be particularly encouraged when resources are defensible. Therefore, introduction of basic or additional resources should be carefully scattered. Less fighting was found in larger groups, as individuals have fewer opportunities to monopolize resources. Nevertheless, increasing group size may increase the risk of damaging behaviours. Greater space provides the opportunity to escape or avoid aversive interactions. Aggressive interactions at mixing appear to be necessary for assessing unfamiliar individual's competitive abilities and for the subsequent establishment of a social hierarchy. Thus, the pre-exposure and gradual introduction of a new individual will facilitate its assessment, helping to reduce aggression incidences. Resident pigs seem to be more driven to attack than intruders, as residents are generally highly motivated to defend their resources. Separating and reuniting pigs seems to be a problem when pigs are separated for longer than a few weeks, as pig's capacity to recognize individuals is limited by memory. Thus, pigs should be separated only for short periods of time. Aggression may be reduced by introducing either male or female dominant individuals. Proper social experiences seem to prepare animals to interact and adapt appropriately to future social situations and aggression modulation. In conclusion, pig welfare can be improved by controlling and modifying the animal's environment and by considering, identifying and managing the biological factors that potentially have an influence on aggressiveness.

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Keywords: Aggression, behaviour, domestic pig, motivation, social mixing, social stress, hierarchical structure.

RESUMEN

El objetivo del artículo es discutir la influencia de los factores ambientales y biológicos en el desarrollo y expresión de la agresión en cerdos. La distribución inadecuada de recursos es un incentivo para la competencia y las competencias agresivas son particularmente impulsadas cuando estos recursos son defendibles. Por consiguiente, la introducción de recursos básicos o adicionales se debe esparcir de manera cuidadosa: se dieron menos peleas en grupos más grandes, ya que los individuos tienen menos oportunidades para monopolizar los recursos; no obstante, aumentar el tamaño del grupo puede incrementar el riesgo de conductas perjudiciales. Una mayor disponibilidad de espacio parece proporcionar la oportunidad de escapar de o evitar interacciones aversivas. Las interacciones agresivas al mezclarlos parecen ser necesarias para evaluar las capacidades competitivas de individuos desconocidos y para el posterior establecimiento de una jerarquía social. Por lo tanto, la exposición previa y la gradual introducción de un nuevo individuo facilitarán su evaluación y ayudará a reducir las incidencias de agresión. Los cerdos residentes parecen ser más propensos a atacar que los intrusos, ya que generalmente están muy motivados para defender sus recursos. Separar y reunir a los cerdos parece ser un problema cuando se separan por más de una semanas, ya que la capacidad del cerdo de reconocer a los individuos está limitada por la memoria. Por lo tanto, solo se debe separar a los cerdos por periodos cortos. Es posible reducir la agresión introduciendo a individuos dominantes, ya sea macho o hembra. Las experiencias sociales adecuadas parecen preparar a los animales para que interactúen y se adapten adecuadamente a situaciones sociales futuras y a modular la agresión. En conclusión, es posible mejorar el bienestar de los cerdos mediante el control y la modificación del ambiente del animal y teniendo en cuenta, identificando y gestionando los factores biológicos que potencialmente influyen sobre la agresividad.

Palabras clave: agresión, comportamiento, cerdo doméstico, motivación, mezcla social, estrés social, estructura jerárquica.

Introduction

Aggression is thought to be motivated by emotions such as anger, irritation, frustration, fear, pleasure (Blair et al., 2006), and pain (Olivier et al., 1987). The motivation for agression has been categorized in different classification schemes. For example, Wingfield et al. (2006) classified aggression into different specific subtypes, including: spatial aggression, resources, related aggression, aggression over dominance status, sexual aggression, parental aggression, irritable aggression, anti-predator aggression, and interspecific aggression.

In its broadest sense, aggression refers to the disposition and performance of behaviours that intend to cause harm (Berkowitz, 1993). However, according to this definition, all behaviours that in-

volve harming could be categorised as aggressive, including abnormal damaging behaviours addressed to other animals (e.g. tail-biting), which are commonly influenced by different conditions related to farming practices. Therefore, for the purpose of this review, aggression will be considered as social behaviours intended to inflict harm in the context of defending or obtaining resources and the establishment of a social hierarchy.

Under natural conditions, pig social groups or "sounders" are relatively stable in composition (small, genetically related matriarchal groups) and new individuals generally join by being born to a sow in the group. Moreover, sows only withdraw from the group to make a nest and give birth. Within 1 to 2 weeks after giving birth, sows and piglets return to the group's communal nest where piglets socialize with piglets from other litters (Petersen et al., 1989). Furthermore, farrowing tends to be synchronized, so piglets in a sounder are often of a similar age (Held et al., 2009).

Therefore, a stable, linear dominance hierarchy persists and is regulated with minimal aggression by the infrequent and gradual integration of new members to the group (Mauget, 1981), close kinship, the preservation of individual space and the use of threats and non-aggressive behaviour to maintain dominance relationships (Mauget, 1981; Jensen & Wood-Gush, 1984; Mendl, 1994; Gonyou, 2001). Any further competition is infrequent and rarely harmful, and any overt aggression occurs only in the breeding season between adult males (Mendl, 1994).

In contrast, under farm conditions particularly under commercial production systems, repeated mixing and re-grouping of unrelated and unfamiliar animals is very common (Puppe et al., 2008). Mixing usually takes place at weaning, during the growing period, prior to slaughter and in group-housed sow system (Held et al., 2009), as this is beneficial for the producer, enabling batching and space efficiency (Kopecny, 2012). As unfamiliar pigs are frequently mixed, new dominance hierarchies have to be established after vigorous fighting (Meese & Ewbank, 1973; Puppe & Tuchscherer, 1994). During this fighting, injuries can occur through physical contact (Arey & Edwards, 1998; Turner et al., 2006), and the production of stress hormones such as adrenaline and cortisol can arise from unresolved aggression (Arey & Edwards, 1998). This could have serious consequences for the welfare of the individuals (D'Eath & Turner, 2009), and production traits such as daily weight gain, meat quality, impaired immunity (D'Eath, 2002) and fertility (Kongsted, 2004).

Moreover, aggression can be exacerbated under commercial conditions as a

consequence of a lack of space, which results in an animal that is unable to escape from aggressors or display an appropriate submissive behaviour (Turner et al., 2006), food restriction that results in a resource that is limited and defensible (Berkowitz, 1993) and other limited resources, which creates competitive situations that induce aggression or social stress (Hughes et al., 1997). Additionally, it has been suggested that aggressive behaviour is modulated by different biological factors. For example, researches have related aggression to serotonin levels in mammals (Reisner et al., 1996), and several studies have also demonstrated that aggressiveness traits are heritable in different species (e.g. Miczek et al., 2001; Edwards et al., 2006; Silva et al., 2006) including pigs (D'Eath et al., 2009).

Several attempts have been made to reduce aggression in pigs (Marchant-Forde, 2009). However, as aggression in pigs is mostly a multifactorial, socially induced problem (Held et al., 2009; Marchant-Forde, 2009). A combination of both environmental strategies and management of biological factors, taking into account the underlying causes of aggression, seems to be the best solution to deal with this problem.

The aim of this review is to study the influence of some environmental and biological factors related to aggression in pigs in order to identify housing and management options that can help to reduce the incidents and the detrimental effects. The review also discusses the existing remedies that are opted to reduce aggression among the pigs and the future solutions that can make a significant difference in permanently controlling aggression in the pigs.

Environmental influences for the presence of aggression

Resource availability

Overt aggression may occur when resources are restricted (Goméz, 2006) or not evenly distributed (Thomsen et al., 2010). In most pig housing systems resources are restricted, which leads to defence and monopolization of the resources (Brown, 1964; Emlen & Oring, 1977). Aggressive resource competitions tend to occur mainly when resources are defensible (Bryant & Grant, 1995). For instance, if food is concentrated in very few specific sites, these will be perceived as a defendable resource, and thus aggressive interactions around those sites will be frequent, whereas if food is scattered, dominant individuals will find it difficult to defend it and aggression levels are expected to be lower. For instance, during summer, aggressive interaction is low in feral pigs when food is abundant and evenly dispersed; in winter, aggression levels are higher, because food is scarce

and clumped (Graves, 1984). In fact, food competition starts early in life when piglets bite and shove their littermates to monopolise the most productive teats (Newberry & Wood-Gush, 1985). Similarly, aggression in group housing sows is very common at feeding, as they are feed restricted, while optional feeding times reduces aggression in sows (Graves et al., 1978; Petherick & Blackshaw, 1989) and young pigs (Kelley et al., 1980).

Several studies have shown that inadequate resource distribution leads to the occurrence of aggression (e.g. Andersen et al., 2000a; 2004). Ad libitum feeding, if done for 48 hours instead of 24 hours, showed less aggression among newly-mixed sows (Barnett et al., 1994). Pigs offered two feeder spaces per 20 animals experienced less feeder related aggression than pigs offered one feeder per 20 animals (Spoolder et al., 1999), and another study showed that wet food during feeding reduces the amount of aggressiveness and fighting among pigs. The average eating time of sows on this wet feeding is lower, which reduces the individual variation when compared to dry ration (Andersen et al., 1999). Since in wet feeding the individuals finish their meals simultaneously, the aggressive competition among them reduces (Andersen et al., 1999). In contrast, is aggravated in some cases due to electronic sow feeders, which conduct sequential feeding and hence increase competitive aggression due to the fact that dominant animals can be rewarded with extra food every time they return to the feeders and chase away subordinate animals that are feeding (Spoolder et al., 2009).

Group size

In commercial practice, the mixing of pigs is very frequent on more than one occasion, leading to high levels of aggression, which is believed to be required to establish a dominance hierarchy among the members of the new social groups (Fraser & Rushen, 1987). This is appears to be particularly true under commercial situations in small groups of pigs (Meese & Ewbank, 1973; Ewbank, 1976). However, it is not clear how pigs adapt to new social environments after regrouping in large groups (Samarakone & Gonyou, 2009) and how pigs assess their social status, if present (Mendl & Held, 2001), or whether the dominance relationships become more complex (Moore et al., 1996).

Pigs mixed in smaller groups are more likely to present aggression than if they are mixed in bigger groups (Nielsen et al., 1995; Turner et al., 2001). Many reasons have been suggested to explain this; one reason is that the probability of individuals being able to monopolize resources reduces as group size increases (Andersen et al., 2004) because the number of intrusions also increases, and

this reduces the effectiveness of aggression in controlling a resource and increases the costs in terms of time spent, energy expended, and injury (Davies & Houston, 1981). As a result, animals switch from a resource defence strategy to a tolerant social strategy (Samarakone & Gonyou, 2009). A "sub-group" model has also been recommended by Moore et al. (1993), who found that sows in large groups form distinct sub-groups rarely interact with each other.

Gonyou (2001) also proposed the formation of subgroups, as group size increases beyond the point that pigs can maintain a definitive social order, although no clear evidence of this has been found in domestic pigs in large social groups (Turner et al., 2003; Schmolke et al., 2004). Another explanation is that larger groups have more space and the availability of space affects aggressive interactions (Spoolder et al., 2009). It has also been suggested that pigs may reduce aggressive interactions, as group sizes increases due to an inadequate capacity for individual recognition (Turner et al., 2001). However, Rodenburg and Koene (2007) suggested that dominance relationships in large groups are not based on individual recognition but are instead based on other signals such as body size and avoiding costly fights.

Several studies have given evidence of the examples mentioned above. For example, sows in larger groups with a larger and more varied space generally fight less than sows in smaller groups (Mendl, 1994; Broom et al., 1995). Andersen et al. (2004) found that, after mixing, fighting was less frequent in groups of 24 pigs than in groups 6 and 12. Similarly, Turner et al. (2001) observed that aggression directed to unfamiliar individuals was less frequent and severe in pigs from a group of 80 compared with pigs from groups of 20. Samarakone & Gonyou (2009) found both that aggressive behaviours were higher when pigs were introduced into small groups than to large groups and that pigs derived from smaller groups spent a greater percentage of time in aggression compared to pigs derived from larger groups. Similar results have been reported when sows are mixed into large groups (Edwards et al., 1993).

It is also important to mention that intermediate group sizes can increase the aggressiveness of animals as compared to those in large or small groups (Croney & Newberry, 2007; Rodenburg & Koene, 2007). For example, intermediate group sizes of about 30 birds may constitute social problems that can affect production (Keeling et al., 2003) and increase aggression (Estevez et al., 2003). In intermediate group sizes, animals might fight to have a dominance relationship with every individual and end up making misjudgements, that might increase the aggressiveness, which cannot be

easily controlled. Thus, intermediate sized groups will continue being aggressive to maintain dominance among each other, whereas in large groups they tend to have competition among themselves to have their share in limited resources (Croney & Newberry, 2007). This behaviour differs between species depending upon its cognitive capacity (Croney & Newberry, 2007).

Space

Numerous studies have found that providing more space to pigs will reduce the level of aggression over the long term (Barnett et al., 1992; Edwards et al., 1993; Arey & Edwards, 1998; Docking et al., 2000; Barnett et al., 2001). For instance, a larger amount of space per sow (6.1 vs 3.7 m) tends to increase the number of interactions but decrease the number of lesions (Edwards et al., 1993) and reduces fights (Kelley et al., 1980). A clearer example is a study where sows were given different space allowances of 2.0, 2.4, 3.6 and 4.8 m2 per sow. As space allowance decreased, the total number of aggressive interactions increased (Weng et al., 1998). Similarly, for growing pigs the reduction of space increases aggression (Turner et al., 2000a) even when pigs were given a rooting material to manipulate (Jensen & Pedersen, 2010).

However, there are some studies regarding relation of floor space and aggression in pigs that have showed different results. It was reported by Kornegay et al. (1993) that pigs kept in restricted floor space were less aggressive than pigs housed in adequate floor space. Moreover, there is one short term study (which only considered the first 90 minutes post-mixing) that found that a decrease in space can suppress aggression (Barnett et al., 1993), though most other longer-term studies have found the contrary (Marchant-Forde, 2009); the number of lesions taken 10 days later were not different, and circulating free cortisol levels as well as measures of cell-mediated immunity were poorer in the animals with less space.

Not only amount of space but quality of space can have a large impact on aggression. The pen design is found to be beneficial to reduce aggression (Marchant-Forde, 2009). The pen divisions contribute to reducing overall aggressiveness levels (Waran & Broom, 1993) than reducing only the number of fights (Olesen et al., 1996). However, the optimum design and space allowance in pig husbandry for reducing aggression is still unclear. It has been argued that reducing space allowance increases aggressiveness, mainly due to a reduction in the opportunities for the pigs to escape or to avoid aggression (Spoolder et al., 2009). However, providing a pig with the necessary distance to escape is very difficult, as this can be quite large. For

instance, Edwards et al. (1986) found that 75% of interactions were associated with a chase of around 2.5 m. Similarly, Kay et al. (1999) found that 50% of flight distances were about 4.7 m. On some occasions, Kay et al. (1999) and Edwards et al. (1986) found that a flight distance could be > 20 m. The necessary space for pigs varies among authors and systems (Spoolder et al., 2009). Apparently, where food and space is virtually unlimited as in outdoor conditions the level of aggression is very low (Jensen & Wood-Gush, 1984).

Formation of new groups and integration of new members

In pig farming it is common to move individuals from an original group (e.g. from one in which they were raised) to new groups (e.g. breeding groups) for various reasons. The main reason for the mixing of unfamiliar pigs is to reduce the weight variation in the pen at market, with the ultimate aim of maximising profitability (Cottam & Morel, 2003). This practice may result in vigorous fighting, wounds, and, occasionally, death (Friend et al., 1983; Petherick & Blackshaw, 1987), as pigs tend to show more aggression towards unfamiliar animals than towards familiar ones (e.g. Zayan, 1990; Mendl et al., 2001). For instance, it has been found that levels of aggression after mixing are higher in dynamic groups (individuals entering or leaving the group on a regular basis) than in static groups (group composition remains unaltered after initial formation) (Gonyou, 2003; O'Connell et al., 2003). Thus, it seems advantageous in a husbandry system to have stable social organisations of pigs (Blackshaw & Allan, 1984).

Assessing others competitive abilities is necessary for the establishment of a hierarchy within a new social group (Meese & Ewbank, 1972; Held et al., 2002). Thus, aggressive behaviour at mixing among unfamiliar pigs seems to be motivated by the uncertainty of the competitive abilities of other individuals, and fighting might be prolonged by the necessity to accumulate information about the relative fighting ability of the opponent (Rushen et al., 1990). Thus, the reduction of aggressive interactions and their latency can be indicative of the fact that a dominance order between pigs is established (Meese & Ewbank, 1973; McGlone, 1986; Mount & Seabrook, 1993).

Fighting is generally more frequent and severe in the first day post mixing (Ewbank, 1976; Moss, 1978; Stookey & Gonyou, 1994), although aggression related effects of mixing can continue for up to three weeks after mixing (Tan & Shackleton, 1990). It has been observed that all individuals in newly formed groups of pigs are likely to be involved in aggressive interactions. In general, some animals

perform most of the agonistic behaviours and others receive most of them (Mount & Seabrook, 1993). Continued chasing and bullying frequently follows a fight, as the loser, who often ends up with physical injury, is unable to escape the aggressor. This can be an exhausting and a stressful situation for both the loser and the aggressor (Moore et al., 1994).

Resident individuals are more likely to attack unfamiliar, involuntary intruders, as residents are highly motivated to defend their resources (Leimar & Enquist, 1984; D'Eath, 2002). Thus, the introduction of a new individual into the residents' home frequently encourages aggression from the resident. For example, Turner et al. (2011) found that resident pigs are capable of displaying heightened aggressiveness in the presence of an intruder placed in their home pen despite the fact that in the wild these animals apparently do not display behaviours related with territorial defence. In fact, forced intruder pigs generally get severely injured despite displaying submissive behaviours (Leimar & Enquist, 1984; D'Eath, 2002).

Separating and reuniting

Farm animals are frequently separated and re-grouped together during their lifetime. Failing to recognize or remember members of a previous group may be a cause of aggression, as individuals may need to re-establish their social ranks (Ewbank & Meese, 1971; Croney & Newberry, 2007).

Several studies suggest that pigs use visual, olfactory and auditory cues to discriminate between familiar and unfamiliar conspecifics (Kristensen et al., 2001; McLeman et al., 2005; McLeman et al., 2008). For instance, pigs can use urine, faeces, bedding material (Horrell & Hodgson, 1992), recorded vocalisations (Illmann et al., 2002), whole body odours and live conspecifics (Kristensen et al., 2001) to discriminate between familiar and unfamiliar. However, the cues that pigs need to recognise group-members and hence reduce aggression, especially after periods of separation, are not clearly understood (McLeman et al., 2008). For example, the discrimination responses could be affected by novelty or conflicting motivational priorities, as the discrimination studies relied on subjects responding more vigorously to one stimulus than the other, spending longer investigating one stimulus over another, or showing a functional response such as aggression towards the unfamiliar animal (McLeman et al., 2008).

The cues used in the discrimination test could be different to those that pigs use to identify individuals under more natural conditions (Held et al., 2009). Also, for individual recognition, pigs may use idiosyncratic cues, rather than differences

in broader social classes (Zayan, 1994; Zayan & Vauclair, 1998), as well as one single, reliable cue in one modality, or any of a number of cues (McLeman et al., 2008). Finally, discrimination responses do not necessarily imply that the animals are able to recognise familiar individuals, as recognition implies not only responses to cues but mental representations of familiar conspecifics (Gheusi et al., 1997) and aspects of their behaviour that have social relevance (Held et al., 2009).

Others different factors may also affect pigs' capacity to recognize each other. For example, Li and Wang (2011) observed that pigs reared in a group-farrowing system discriminated between familiar individuals and non-familiar individuals more easily and were more tolerant of unfamiliar pigs compared to pigs reared in a confinement system. Other studies have found that pigs' capacity to recognize individuals is limited by the time they are able to memorise them. For instance, Hoy and Bauner (2005) reported that social memory in sows starts to deteriorate after the first week of separation. Spoolder et al. (1996) found that pigs have the capacity to remember other individuals for only four weeks following separation.

Life experiences

It has been shown that proper social experiences and interactions with conspecifics during the early stages of life prepare the animals to interact and adapt appropriately to future social situations as adults, including aggression modulation (Keverne & Curley, 2004; Cushing & Kramer, 2005). The importance of these early social experiences in pigs is supported by the study of Souza and Zanella (2008), who observed that early weaned piglets subject to social isolation presented more aggression compared to non-isolated pigs, due to the impairment in the ability to recognize familiar conspecifics.

Piglets first engage in playful social behaviour with their litter mates and learn dominance relationships with one another. At around two weeks of age they socialise with piglets from other litters by exploring each other and engaging in social play, which incorporates aggressive elements (Newberry et al., 1988; Petersen et al., 1989). It has been suggested that at playing that stage can possibly have a role in determining dominance relationships between piglets (Dellmeier & Friend, 1991).

Several experiences have been associated with aggression in pigs. For example, Moore et al. (1994) observed that pigs that were given the opportunity to acclimate to frequent changes in group composition presented shorter aggressive interactions when compared to pigs accustomed to stable groups. Olsson and Samuelsson (1993) observed that

sows that were mixed while still lactating showed less aggression than sows mixed after weaning. The exposure to unfamiliar social and spatial environments (Hötzel et al., 2011), pre-weaning enrichment (Melotti et al., 2011), lack of environmental stimuli (Schaefer et al., 1990; Blackshaw et al., 1997; Ishiwata et al., 2002) and confinement (Li & Wang, 2011) have also been associated with aggression in pigs.

Biological factors related to aggression

Age and sex

Domestic pigs show aggressive behaviours starting at birth (Newberry & Wood-Gush, 1985). Pre-pubertal males, females and castrates fight at about the same level (McGlone et al., 1987). As adults, it seems that pigs are less aggressive (Rydhmer et al., 2006) due to social experience gained during ontogeny (Puppe et al., 2008).

Puppe et al. (2008) found that, compared to weaned and growing pigs, sows showed fewer agonistic interactions and a higher amount of unidirectional dyads and directional consistency index (DCI) (DCI reflects the frequency with which wins occurred in the more frequent direction relative to the total number of agonistic interactions). This may indicate that experienced adult pigs can better judge the individual fighting ability of an opponent compared to younger individuals. However, it is important to highlight that, after puberty, all males can become increasingly aggressive (Cronin et al., 2003) due to the increasing levels of the hormone testosterone (Signoret, 1976). In fact, entire male groups are more likely than castrates to show aggressive behaviour (Ellis et al., 1983; Giersing, 1998; Cronin et al., 2003; Rydhmer et al., 2006). A higher frequency of aggressive behaviour (Cronin et al., 2003) and lesion score (Quiniou et al., 2010) have been observed in entire males than in barrows or gilts. Furthermore, Fredriksen et al. (2004) found more aggressive behaviour in pens with entire males and females than in pens with castrates and females.

The effect of raising pigs in mixed and single-sex groups on aggression has been studied but the results are not consistent. Conte et al. (2010) suggested that entire male pigs should be housed in mixed-sex groups. They found that skin lesion scores were highest in all-male with high weight variation groups and lowest in mixed-sex with low weight variation groups. Similarly, Boyle and Björklund (2007) found a higher rate of agonistic interactions during feeding between single-sex males compared to mixed-sex groups and single-sex females. Also, Schmidt et al. (2011) found that Gonadotropin Releasing Hormone (GnRF) vaccinated males were less aggressive

when they were raised in mixed-groups. In contrast, Rydhmer et al. (2006) found that single-sex female groups are less aggressive and rearing pigs in mixed-sex groups does not reduce aggression of males. These contradictory results may be explained by the housing conditions in all the studies mentioned above. Since the animals in the studies were housed in one single building separated just by sections, visual, olfactory and auditory cues might have confounded the results.

Size/weight

Contrary to the asymmetry in size and competitive abilities in natural social grouping, pigs under commercial systems are often mixed in homogeneous groups to facilitate their management and to make the most of the available space (Fredriksen et al., 2008). This may result in aggressive behaviours every time they are mixed and try to re-establish a hierarchy due to evenly matched opponents that have difficulties with determining relative strength or fighting ability (Rushen, 1987; Moore et al., 1994; Andersen et al., 2000a; Schmolke et al., 2003). Thus, the contestants are unwilling to give up early (Enquist & Leimar, 1983) and the fighting will be prolonged compared to a situation with unevenly matched opponents (Enquist et al., 1990).

It has been demonstrated in pigs that larger animals have an advantage in settling disputes and that the probability of victory for the larger animal will increase with size difference (Andersen et al., 2000a). It has also been found that body weight plays an important role in aggressive interactions (Martin & Edwards, 1994; Andersen et al., 2000a; D'Eath, 2002). For instance, skin lesion score in groups with heavy start weight pigs (34.9 kg) was higher than compared to medium (29.6 kg) and light (24.5 kg) start weight groups (Turner et al., 2000a) on the 4th day post mixing. When there is a very similar weight between pigs, fighting lasts longer and biting is more frequent than when there is a large difference in pigs' weight (Rushen, 1987; Francis et al., 1996). Also, a larger weight asymmetry in pigs makes the ultimate loser cease fighting more quickly (Rushen, 1988). Nevertheless, it should be considered that previous experience and temperament also plays a fundamental role in aggressive interactions that have to be taken into account when assessing a pig's chance of winning an encounter (D'Eath, 2004). This will be discussed in the next sections.

Individual differences and coping style

A growing body of work has pointed out that both natural and artificial social groups of several species (wild and domestic) are formed by different individuals with different personality types

and coping styles (Benus et al., 1991; Koolhaas et al., 1999; Goddard et al., 2000; Réale et al., 2007; Wolf et al., 2007; Biro & Stamps, 2008). These individual differences are determined by both emotional and cognitive factors. Several research studies have been done in the study of the pig's emotional (Jensen, 1995; Andersen et al., 2000b; Janczak et al., 2002, 2003; D'Eath et al., 2005) and cognitive individualities (Arts et al., 2009; Jansen et al., 2009; Kouwenberg et al., 2009; Nielsen et al., 2009).

Coping style refers to the strategy (behavioural and physiological stress responses) that animals use to control, tolerate, reduce, and minimize stressful events (Benus et al., 1991; Koolhaas et al., 1999; Janczak et al., 2003). There are two main coping strategies, the fight-flight response employed by the proactive coping style individuals and the conservation-withdrawal response employed by the reactive coping style individuals (Koolhaas et al., 1999). Despite the fact that it has not been possible to support the existence of bimodal coping strategies in pigs (e.g. Janczak et al., 2003), some detectable individual differences possibly related to personality and diverse coping strategies apparently have an influence on aggression.

It has been reported that groups of unfamiliar pigs detected and classified as highly aggressive and low aggressive tend to fight less when mixed together in a group compared with groups containing just highly aggressive pigs or just low (Hessing et al., 1994; Mendl & Erhard, 1997). Additionally, it has been suggested that highly aggressive pigs tend to be more inflexible in their social tactics, while low aggressive pigs tend to moderate their behaviour, and this may help to minimize antagonistic displays of other pigs (D'Eath, 2002; Bolhuis et al., 2005).

The consistency of intra individual responses of coping varies in social and non-social situation in pigs (Janczak et al., 2003). At social situations the proactive individuals show more aggressiveness and avoidance when defeated, whereas reactive individuals have less aggression and withdraw more passively (Janczak et al., 2003). Individuals who are proactive develop routines and foresee the situation, but the reactive individuals generally react to environmental changes and do not foresee the situation beforehand and then react (Benus et al., 1991; Koolhaas et al., 1997). Thus, the coping style in proactive and reactive pigs differs, as well as reaching homeostasis in different environments. The proactive animals have difficulty in coping with the unstable environments, whereas the reactive individuals adapt to such environments in a better manner (Koolhaas et al., 1997).

Heredity and genes

Experiences during development are important to determine pigs' temperament (D'Eath & Lawrence, 2004; D'Eath et al., 2005). Nevertheless, temperament is also under genetic control (van Oers et al., 2005; Réale et al., 2007). Aggressiveness has been suggested to be a stable trait (D'Eath et al., 2009). Therefore, aggression is controlled and can be altered to some point by genetic selection in pigs (D'Eath et al., 2009).

It has been found that aggressive behaviours following the mixing of pigs are moderately heritable: $h2 = 0.17$ to 0.24 (Løvendahl et al., 2005); $h2 = 0.37$ to 0.46 (Turner et al., 2008); $h2 = 0.31$ to 0.43 (Turner et al., 2009). In fact, it has been found that several traits can be easily used as indicators of involvement in aggressive behaviour (Turner et al., 2010).

There are some examples of measuring both phenotypic and molecular traits to modify aggressiveness. Skin lesion scores 24 hours after regrouping has been used as a heritable trait that is related to aggression (Turner et al., 2008) without affecting key economic traits that are common in selection indexes (Løvendahl et al., 2005; Turner et al., 2006). Maternal ability has also been described as a trait related to aggression in sows. Pregnant sows that show low aggressiveness tend to savage their offspring after birth (McLean et al., 1998) but crush the piglets less (Andersen et al., 2005).

Neurological influences

Aggression among groups of pigs can also develop due to changes in the concentration of brain amines-neurotransmitters (Poletto et al., 2011). Aggression in pigs is controlled by neural pathways that include different areas of the brain, such as the frontal cortex, hypothalamus and amygdale (Davidson et al., 2000). The underlying cellular mechanisms within these brain areas are extensively linked to serotonergic and dopaminergic systems represented by the biogenic monoamines and catecholamines (Nelson & Chiavegatto, 2001; Nelson & Trainor, 2007).

Dysregulation of serotonergic and dopaminergic systems in neural pathways controlling aggression trigger aggressive and defensive behaviours (Miczek et al., 1994; Miczek et al., 2002). The serotonergic system is interconnected with the noradrenergic system (Clement et al., 1992), which is also linked to the regulation of aggression (Miczek & Fish, 2006). Poletto et al. (2010a) suggested that in gilts feeding the β-adrenoreceptor agonist ractopamine (RAC) leads to a noradrenergic depletion, which may increase aggression by association with parallel alterations of other neurotransmitter systems such as dopamine (DA), serotonin (5-HT) or both (Haden &

Scarpa, 2007). Moreover, RAC-fed gilts showed a trend for reduced blood 5-HT concentration (Poletto et al., 2010b), and 5-HIAA (5-hydroxyindoleacetic acid, which is a 5-HT metabolite) in amygdale (Poletto et al., 2010b), compared with standard diet gilts.

In general, low serotonergic activity and elevated dopaminergic activity invoke aggressiveness (Haney et al., 1990; Miczek et al., 2002; De Almeida et al., 2005; Miczek & Fish, 2006), which has also been found in gilts (Poletto et al., 2010b). However, fluctuations in serotonergic and dopaminergic activity do not necessarily lead to aggressiveness (Nelson & Trainor, 2007), as this response is also dependent upon the interaction between dopamine and serotonin with other molecules (steroid hormones, vasopressin, histamine, substance P, Monoamine oxidase A, Neural cell adhesion molecule, Interleukins and nitric oxide), and receptor subtypes and their loci in the neurons (Nelson & Chiavegatto, 2001).

Despite the numerous molecules and interactions that influence aggression, serotonin (5-HT) remains the primary molecular determinant of aggression (Nelson & Chiavegatto, 2001). Physiological (Poletto et al., 2010a; Poletto et al., 2010b) and genetic (D'Eath et al., 2005; Poletto et al., 2011) evidence for a role of 5-HT in aggression have been found in pigs.

How can we reduce aggression incidence?

Several attempts have been made to reduce aggression between newly mixed pigs. It has been observed that the mixing of gilts during darkness has been shown to reduce aggressive interactions compared to mixing during light (Barnett et al., 1994; 1996). The dimming of light from 100 to 5 lx was also found to reduce aggression (Christison, 1996). Similarly chemical intervention through the use of sedatives seems to reduce aggression (Blackshaw, 1981; Gonyou et al., 1988; Tan & Shackleton, 1990) as the use of anti-aggression drugs does (Barnett et al., 1993, 1996) and the spread of pheromones (McGlone et al., 1987). However, these techniques have a temporary effect on aggression that only last for a short period of low activity (e.g. sunset) or as long as the chemical has efficacy, and in some cases such as the use of sedatives, aggression can be higher once the effects of the drug have ended (Luescher et al., 1990). Moreover, these techniques do not take into account the causes of aggression.

The most logical management system would be to avoid mixing wherever possible from birth to slaughter and returning animals to their original groups as fast as possible when separated. If mixing is unavoidable, as is the case in most commercial situations, different mana-

gement options can be used to reduce aggression amongst pigs.

Firstly, enhancing asymmetries between group members reduces uncertainty about relative fighting abilities (Rushen et al., 1990; Andersen et al., 2000a), which in turn will allow the rapid establishment of social status and thus reduce aggression. However, mixing pigs of different sizes and weights is opposite to the main reasoning for mixing pigs that are for batching and space efficiency (Kopecny, 2012). In fact, the ideal would be a pen where all the animals reached the slaughter weight at the same time as soon as possible with the ultimate aim of maximizing profitability. Therefore, farmers may be reluctant to mix outmatched pigs. Other ways to increase asymmetries is by introducing superior individuals or through using other individual characteristics such as aggressiveness and sex.

Presence of a boar has been proposed to reduce aggression at mixing (Grandin & Bruning, 1992; Barnett et al., 1993; Docking et al., 2000). However, in some recent studies this did not reduce agonistic interactions and skin lesions in sows, and there was also a low or none impact of a boar on the social structure of the group (Séguin et al., 2006; Borberg & Hoy, 2009). Moreover, this seems an unpractical solution as a boar can be difficult to handle, and requires a big amount of space and food. Whether a mixed-sex pen can reduce aggression is still unclear, and further investigation is necessary before drawning conclusions on it.

Mixing pigs of contrasting aggressiveness seems sensible. For instance, when mixing highly aggressive animals (proactive) with less aggressive (reactive) animals, they rapidly developed a stable social order, which helped to reduce aggression (Hessing et al., 1994). However, this approach requires using an aggressiveness test, which seems more likely to be adopted by breeding units rather than farmers. Therefore, the mixing of pigs selected for low aggressiveness with unselected animals (Turner et al., 2010) could be a more realistic option. For this purpose, the use of skin lesion locations appears to offer a practical and accurate indicator that is genetically correlated to aggressive behaviour (Turner et al., 2010).

Secondly, social experience plays a key role in reducing aggression (Kennedy & Broom, 1994; Jensen et al., 1996; Jensen & Yngvesson, 1998), and thus familiarization of individuals prior to mixing should be enhanced. For example, Weary et al. (1999) found less aggressive behaviour at weaning when piglets from different litters were mixed in their farrowing pens, enabling them to become familiar at an early age when the level of aggressiveness is lower. Moreover, the mixing of

piglets prior to weaning has been shown to benefit social skills in the long term (D'Eath, 2005). Similarly, Kennedy and Broom (1994) found that, by allowing gilts a degree of contact (smell, hearing, and occasionally touch) for five days prior to introduction with the group of sows they were going to be housed with, the gilts received less aggression. Also, if pigs are mixed more than once, there is less aggression with each successive mixing (van Putten & Buré, 1997; Spoolder et al., 2000). Enhancing pigs' social experiences appears to be an applicable solution in commercial situations, as this does not sacrifice livestock productivity and its implementation may be achieved through a reasonable cost.

Environmental factors may also be manipulated to reduce aggression. Numerous studies have reported that providing complex and spacious environments reduced aggression (Lammmers & Schouten, 1985; Weng et al., 1998; O'Connell & Beattie, 1999; Docking et al., 2000; Barnett et al., 2001). However, in a commercial situation it is difficult to establish the minimum optimal space and its relevant characteristics, as it remains scientifically undefined (Spoolder et al., 2009). Furthermore, the kilogram of pork produced per floor space would be less at larger floor space allowances and hence may not be viable in a commercial setting.

Minimizing the opportunities for resource monopolization could also reduce aggression. A way to do this is to increase group size (Andersen et al., 2004); however, some important considerations must be taken. Firstly, resources such as feed, water, or space cannot be limited in quantity, distribution, or temporal availability (Turner et al., 2000b), even in big groups. Secondly, new members of a group need to be familiarized with the resources (e.g., feeding system) prior to introduction to a large group (Spoolder et al., 2009). Thirdly, regarding feeding systems, it seems that individual feeding stalls and electronic feeders are the most appropriate existing systems for big groups of pigs, though all possible measures should be taken (e.g. enclosing the sows, ad libitum feeding) to enable animals to complete their ration allowance without being displaced by others (Andersen et al., 1999).

Several studies have related pen design, cover, and barriers with aggression in pigs, as they provide opportunities to avoid each other. For example, rectangular pens were more efficient in reducing aggression compared with square pens (Barnett et al., 1993). McGlone and Curtis (1985) found that providing shelter helped to reduce pig aggression, and Waran and Broom (1993) suggested that pen divisions are likely to reduce aggression.

Additionally, numerous enriched housing systems have been reported to have an effect in aggression. For example, a "multi-activity pen system" (Simonsen, 1990), straw (Andersen et al., 2000a), toys (Blackshaw et al., 1997) and bedding in electronic sow feeders (Jensen et al., 2000) resulted in less aggression in groups of pigs. Nevertheless, it is important to consider that competition for any type of resource can encourage aggressive interactions in pigs, with subordinate individuals typically being the most affected (Dantzer et al., 1987; Lewis, 1999; Olsen et al., 2002; O'Connell et al., 2003). Therefore, environmental enrichment use and other resources (e.g. laying areas) should be provided carefully in any type of housing system.

Finally, as previously described, genetic selection on lesions at mixing is expected to lead to a reduction in the number of lesions in the longer term (Turner et al., 2010). Moreover, many of the husbandry solutions that we mentioned above are sometimes prohibitively expensive and difficult to incorporate into routine management. Meanwhile, genetic selection for non-aggressive pigs may provide a long-term solution for aggression at relatively little cost to individual producers (Wall et al., 2010). However, further investigation in unexpected genetic correlations and genotype × environment interactions are necessary before implementation. For instance, McLean et al. (1998) reported that low aggressiveness in pregnant sows was associated with a subsequently elevated risk of savaging the piglets after birth.

Conclusion

There are several reasons that lead to aggression in pigs. Several methods have been used to reduce the aggression among them, but in most cases it is delayed rather than suppressed. Pig welfare should be improved by the control of environmental and biological factors that have an influence on aggressiveness. Moderation of aggression can be achieved by appropriate resource distribution, mixing and selecting pigs according to aggressiveness, facilitating individual recognition, gradual introduction of new individuals, maintaining stable groups, and exposing animals to positive life experiences.

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