

Selection against aggressiveness in pigs at re-grouping: practical application and implications for long-term behavioural patterns

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Abstract

The routine mixing of pigs causes aggression that cannot be greatly reduced by low-cost environmental changes. The variability and heritability of aggressiveness are discussed and both appear adequate to make selection against aggressiveness worthwhile in grower-stage pigs. Selection would require rapid phenotyping of many animals for which a validated indicator genetically correlated to aggressive behaviour is required. Three potential indicators are discussed (attack latency, number of skin lesions and relationship to non-social behavioural traits). Attack latency correlates with post-mixing aggressiveness under research conditions but attacks are delayed under commercial conditions reducing the practicability of the trait for selection. Correlations between aggressiveness and responses to non-social challenges, such as the back-test, are not always consistent. Lastly, the counting of skin lesions is rapid, and the number of lesions has a moderate heritability and is genetically correlated with involvement in aggressive behaviour. The wider effects of selection against post-mixing aggressiveness are discussed. Examining the behavioural strategies of unaggressive pigs, especially their response to defeat, would reveal how selection may alter aggressive tactics. Selection against lesions from mixing is also expected to reduce their number in more stable social conditions, but the implications for aggression between sows and that of sows towards their piglets and humans needs to be investigated. Aggressiveness is genetically correlated with response to handling involving components of social isolation, human presence and novelty. Identifying how unaggressive pigs respond to other challenging situations differing in these components may be worthwhile. Selection against aggression using skin lesions appears to be achievable although the full value of this would benefit from estimations of the genetic correlations with the traits outlined above.

Keywords: aggression, animal welfare, genetic correlation, heritability, pigs, selective breeding

The need for selection against aggressiveness

The mixing of pigs kept in commercial housing into new social groups is routine. It ensures that building space is utilised most efficiently, that single-sex groups can be formed and that group members reach slaughter weight at a similar time. However, mixing commonly results in aggression that in turn affects growth rate, feed conversion efficiency, immunocompetence and carcass quality (Tan *et al* 1991; Morrow-Tesch *et al* 1994; Warris *et al* 1998). Mixing of pregnant sows may also affect the subsequent stress responses of their piglets to mixing and non-social challenges as well as the piglets' own mothering ability (Jarvis *et al* 2006). The current paper assesses the degree to which individual differences in mixing-related aggressiveness are genetically determined and appraises how large numbers of pigs could be phenotyped for their total duration of involvement in post-mixing aggressiveness in a manner efficient enough to allow selective breeding. It also discusses the correlations between aggressiveness and other behavioural traits and poses issues that, if addressed, would contribute to a fuller understanding of the consequences of selection.

Under wild conditions, feral domestic pigs display mutual avoidance when two groups meet on overlapping home ranges (Gabor *et al* 1999) minimising inter-group aggression. Aggression within groups is limited by the gradual introduction of piglets to the social group after birth and by the stable dominance relationships encouraged by large differences in competitive ability between individuals (Mendl 1995). The quantity and quality of aggressive behaviour shown by domestic pigs released into naturalistic outdoor enclosures is similar to that of the wild boar (Stolba 1988). These observations indicate that the greater quantity of aggression shown in intensive conditions is primarily a product of the management conditions, whilst the quality of the behaviour itself remains similar to that of wild pigs. In particular, the suddenness with which mixing occurs and the practice of mixing animals of similar weight and therefore competitive ability exacerbates the likelihood and severity of fighting (Rushen 1987). Selective breeding for individual growth traits may also have affected behavioural traits. Løvendahl *et al* (2005) and Cassady (2007) have reported positive phenotypic correlations between growth rate and aggressiveness and have

speculated that past selection for performance may have inadvertently increased aggressiveness.

A number of husbandry changes have been investigated as means of minimising the duration of post-mixing aggression or the skin lesions that result. At best, these approaches delay the onset of aggression without reducing its total magnitude (Leuscher *et al* 1990; Arey & Edwards 1998; Spooler *et al* 2000). Those approaches that show promise, such as the presence of a mature boar at the time of mixing (Grandin & Bruning 1992), are not easy to integrate into routine management.

Considerable inter-individual variability in involvement in aggressive behaviour and the accumulation of skin lesions have been reported at mixing (Figure 1; see also Erhard & Mendl 1997; Mendl & Erhard 1997; Baumgartner 2007). Variability between individuals persists in the weeks after mixing when the initially high levels of aggression have subsided (Figure 2). These individual differences are reported to be stable over time and to therefore reflect a predictable personality trait. Mendl (1993), for example, found that sow aggressiveness was correlated across several parities and gestation groups.

Stable genetic ranking over time in a trait is a necessary condition for successful selective breeding. Evidence from other species suggests that aggressiveness is heritable (ie the additive genetic variance constitutes a significant proportion of the phenotypic variance; male rodents, heritability 0.22 to 0.34, Miczek *et al* 2001; fighting bulls, heritability 0.30, Silva *et al* 2006; aggressive anti-social behaviour in humans, heritability 0.46, Eley *et al* 2003). Some aggressive traits in pigs also appear to be heritable. Savaging of piglets by first parity sows and handler-directed aggression by lactating sows showed heritabilities of 0.40 and 0.08, respectively (Knap & Merks 1987; Grandinson *et al* 2003). In the latter case, aggression was recorded as a binary trait using a stockperson interview which may have contributed to its low heritability. If post-mixing aggressiveness is also heritable then selection against it may benefit animal welfare. To achieve this, a necessary first step is to identify a way of reliably phenotyping large numbers of individual animals for post-mixing aggressiveness.

Phenotyping aggressiveness

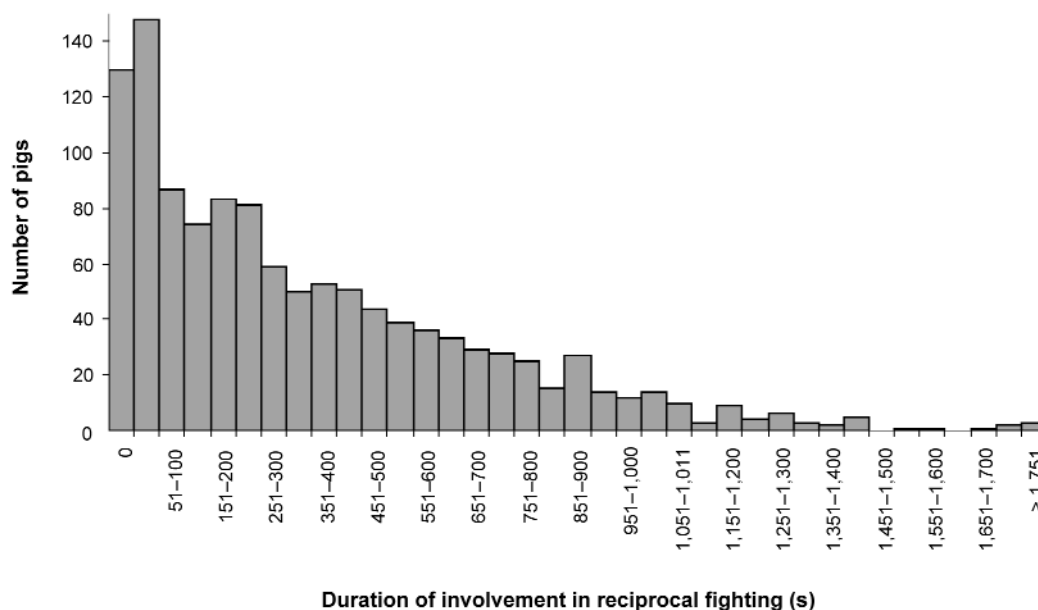
Aggressive behaviour is shown in various contexts which are driven by different motivations (see Fraser & Rushen 1987 for a review) and which may be independently genetically influenced despite utilising similar behaviours. In mice, for example, genetic correlations are low between inter-male, predatory and foot shock-induced aggression (Popova *et al* 1993). It also cannot be assumed that aggression measured at mixing is genetically associated with other stages in life or under more stable social conditions, even if phenotypic correlations are strong. This emphasises the need for a clear definition of the breeding goal and measurement of relevant phenotypes in the most relevant context. In practice, measuring a trait such as post-mixing aggressiveness in pigs must take less than around two minutes to have any possibility of being used in selection. Prolonged continuous observations of behaviour are not practical and an indicator trait is needed that predicts post-mixing aggressive-

ness. Other necessary features are that the trait recorded must be phenotypically stable over time, be feasible to measure in diverse husbandry conditions by non-scientists with little training and show strong inter-observer agreement. Furthermore, for maximum genetic progress, a trait measured on a continuous rather than a categorical or binary scale is preferable. In this paper, we discuss three candidate indicators whose phenotypic correlation with post-mixing aggressive behaviour has previously been examined.

Attack latency in resident-intruder tests

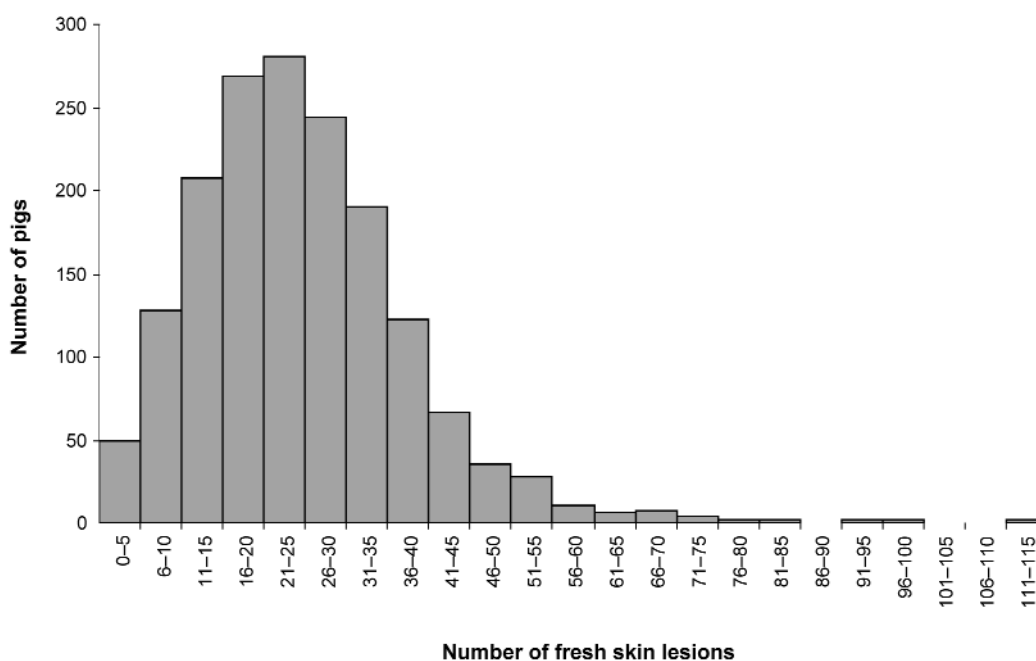
The latency of isolated male residents to attack male intruders introduced into their cage has been widely used as a model of mouse aggression. Successful divergent selection for this trait with heritabilities of around 0.30 has been achieved (reviewed by Miczek *et al* 2001). In group-housed pigs, a single resident of either sex is usually isolated by a partition in a section of its home pen and a smaller, unfamiliar intruder is introduced until the resident attacks or a predetermined test duration is reached (eg Erhard & Mendl 1997). Intruder-initiated attacks are rare (D'Eath & Pickup 2002). The latency to attack was shown by Erhard *et al* (1997) and D'Eath (2002) to be phenotypically associated with subsequent involvement in post-mixing fighting and the accumulation of skin lesions. The trait also shows some stability over time (between the ages of 7 and 11 weeks, Erhard & Mendl 1997; 8 and 24 weeks, Janczak *et al* 2003; 9 and 30 weeks, Clark 2007). D'Eath and Pickup (2002) failed to find a correlation between attack latencies measured on two consecutive days, but did find consistency in likelihood of attacking. Within the ranges studied in pigs, the resident's attack latency is unaffected by the relative weights between the opponents (Erhard & Mendl 1997; D'Eath & Pickup 2002). However, in rodents, resident aggressiveness is affected by the genetic line and mobility of the intruder (Miczek *et al* 2001), the degree of familiarity with the test environment (Benus *et al* 1992) and the frequency of handling (Benus 1999). Standardisation of the test environment and the intruder is likely to be necessary to allow all residents the same opportunity to show their aggressiveness. When performed in research environments, the proportion of resident pigs that attack is high, providing a continuously-based (non-categorical) measure of aggressiveness in the majority of animals (69%, 8-minute tests, neutral arena, Jensen 1994; 67%, 10-minute tests, Forkman *et al* 1995; 67%, 3.5-minute tests, Erhard & Mendl 1997; 38%, 5-minute tests, D'Eath & Pickup 2002; 91%, 10-minute tests, Janczak *et al* 2003; 75%, 5-minute tests, Clark 2007). Commercial husbandry conditions vary from those in which the test has previously been used in that there is commonly mixing of pigs at weaning, infrequent handling of the animals and the use of unbedded pens. Despite varying these factors, we have failed to replicate the high attack rates described above in small-scale trials performed on four commercial farms (Table 1). In each case, the tests were performed within the resident's home pen but the attack rate generally remained below 25%. These four farms were stocked with genetic lines of pigs produced by one and the same breeding organisation. A comparison was made between a line from one of these farms and that used previously by Clark (2007) to establish whether differences in

Figure 1



Duration of involvement in reciprocal fighting between grower pigs during the 24 hours post-mixing (n = 1,182). During this behaviour, bites were delivered at an approximate rate of ≥ 1 per 3 s.

Figure 2



Number of fresh skin lesions on grower pigs 3 weeks post-mixing (n = 1,658).

genotype were responsible for the low attack rate. The two lines were housed contemporaneously on a fifth farm. Little difference in attack rate was evident between the lines whilst the genotype used by Clark (2007) showed a lower attack rate than previously reported. Finally, older pigs from a third breeding organisation were observed for 10 minutes in tests on

a sixth farm but only 11% attacked, confirming that a low attack rate was not restricted to pigs from the first breeding organisation. It was evident on each of the farms that a large number of skin lesions accumulated within 24 hours of mixing into new groups, suggesting that the absolute amount of aggression shown in mixed groups was high. The severity of

Table 1 Frequency of attacks in the attack latency test when used on six commercial farms stocked with pigs from three breeding organisations. All pigs experienced the test on two consecutive days with different intruders on each day.

Farm	Breeding organisation	Breed	Test duration (mins)	Weights			Treatments	Number of tests ending in		Total number of tests	Proportion of tests ending in resident attacks
				Resident weight (kg)	Intruder weight (kg)	Intruder weight as % of resident weight		Attacks by resident	No attacks by resident		
1	I	Damline LW × LR	5	38.4	27.0	70.3	None	0	30	30	0
2	I	Sireline (LW × LR) × LW	5	38.3	25.6	66.8	Unmixed litters	7	69	76	0.09
				36.6	24.8	67.8	Mixed litters	0	40	40	0
2	I	Sireline (LW × LR) × LW	5	43.9	26.6	60.6	Handled daily	16	24	40	0.40
				42.0	26.8	63.8	Handled infrequently	9	31	40	0.23
2	I	Sireline (LW × LR) × LW	5	32.3	21.8	67.5	Small, handled daily	2	28	30	0.07
				33.2	21.8	65.6	Small, handled infrequently	2	28	30	0.07
				45.5	31.0	68.1	Medium, handled daily	4	26	30	0.13
				45.5	31.0	68.1	Medium, handled infrequently	2	28	30	0.07
				62.1	40.3	64.9	Large, handled daily	5	25	30	0.20
3	I	Sireline pure LW	5	91.3	91.7	100.4	None	42	148	190	0.22
				61.1	40.3	66.0	Large, handled infrequently	7	23	30	0.23
4	I	Damline pure LW	5	43.1	31.4	72.8	Groups of 50, 3 straw yard	3	27	30	0.10
				65.6	51.7	78.8	Groups of 15, 7 unbedded, part slatted	7	23	30	0.23
5	I v 2	Sireline pure LW, Sireline LW × LR	5	41.1	29.3	71.3	Genotype from Farm 4	8	26	34	0.23
				38.5	28.1	72.9	Genotype from experimental farm (Clark 2007)	25	51	76	0.33
6	3	Sireline pure LW and pure LR	10	90.0	81.2	90.0	None	3	25	28	0.11

LW: Large White; LR: Landrace.

lesions varied on each pig and between pigs but was on average similar on each farm. The response in the attack latency test appears to represent a delay in the onset of aggression, rather than a reduction in its duration or severity in the longer term. Rather than any single factor being the cause of

this delay, the particular combination of management characteristics (eg handling frequency, use of bedding) that differ between research and commercial farms may be responsible. A delay in the onset of aggression resulting in few pigs attacking within a short observation period greatly limits the

practical value of the attack latency test as a means of selecting against post-mixing aggressiveness. A further limitation of the approach is its dependency on a supply of intruders that are not themselves potential selection candidates.

Skin lesions

Counts of skin lesions have been used to investigate aggression in large social groups or its change over prolonged periods following mixing (eg Erhard *et al* 1997; Spoolder *et al* 1999; Turner *et al* 2000). Using 75-kg pigs, Spoolder *et al* (2000) found a strong correlation between the duration involved in fighting during the first two hours post-mixing and the number of lesions 24-h later. Using similar time periods, Olesen *et al* (1996) also reported a significant correlation between the number of lesions and number of fights lasting longer than 10 s. Lesions accumulate from involvement in reciprocal fighting and the receipt of non-reciprocated aggression. Turner *et al* (2008) found that the number of lesions in different body areas provides information on the duration of involvement in these two traits. Specifically, lesions located on the head, neck and shoulders were phenotypically correlated with reciprocal fighting whilst those to the flanks, back and particularly the rump were phenotypically associated with the receipt of non-reciprocated aggression. This supports the suggestion of Burfoot *et al* (1995) and Baumgartner *et al* (2007) that to yield maximum information, lesions should be counted separately on different parts of the body.

Counting lesions as a continuous trait takes less than two minutes per animal (Burfoot *et al* 1995; Turner *et al* 2009), requires no additional handling of animals, no equipment and minimal training, making it feasible for routine use in genetic nucleus herds. The severity of individual lesions is not normally recorded since to do so would greatly increase the time required for assessing each pig. High inter-observer correlations of 0.80–0.91 have also been reported (Burfoot *et al* 1995; Turner *et al* 2006a). Subtracting the number of lesions present before mixing from those present afterwards provides a more accurate assessment of the number resulting from mixing itself, but requires additional labour. A standardised mixing protocol is also needed to ensure that all pigs encounter the same number of unfamiliar animals in an area equally unfamiliar to all. Despite such standardisation, the aggressiveness of an individual is affected by the aggressiveness of its group mates and therefore the group into which a pig is mixed must be considered in the model of the genetic analyses (Turner *et al* 2006a). Furthermore, heavier pigs accumulate more lesions requiring liveweight to be recorded at or near the time of mixing (Olesen *et al* 1996; Turner *et al* 2006b). Where groups can be mixed in a standardised way and weights are recorded, the number of skin lesions may be used as an easily implemented method of assessing aggressiveness.

Response to non-social challenges

Several authors have presented evidence that post-mixing aggressiveness can be predicted from a pig's response to non-social challenges. Predicting aggressiveness through such responses would avoid the complexity of the subject's behaviour being affected by others and ease the standardis-

ation of the test environment for all animals. Terlouw (2005) reported that the extent of exploration of a novel object was positively correlated with post-mixing aggressiveness. Both Janczak *et al* (2003) and Jensen (1994) failed to confirm this link using the attack latency test, but a repetition of the Terlouw (2005) experiment recording post-mixing behaviour itself may be valuable. Some studies have suggested that a pig's response to inverted restraint in the back-test is predictive of its aggressiveness. In this test, the number of attempts to break free of restraint is recorded when a pig is held on its back by one hand placed over the throat and the second hand placed over the hind legs. Resistant pigs are regarded as those which show many escape attempts. Ruis *et al* (2000), for example, reported that the most resistant quartile of pigs were more frequently aggressive in a food competition test performed at 10 and 24 weeks of age than the least resistant quartile. In a subsequent study, mixed pairs of highly resistant pigs were more persistent in fighting and had higher body temperatures on the day of mixing (Ruis *et al* 2002). Supporting these earlier studies, Bolhuis *et al* (2005) found that the most resistant quartile of pigs had a shorter latency to fight, initiated more fights and fought for a longer duration in the first 3 h post-mixing than the least resistant quartile. Similarly, Bolhuis *et al* (2006) showed that high resisting pigs were also more aggressive under more stable social conditions. However, other studies have failed to find an association between back-test response and aggressiveness, either in the attack latency test (Forkman *et al* 1995; D'Eath & Burn 2002) or in a feed competition scenario (Geverink *et al* 2002). Finding evidence that the back-test response predicts post-mixing aggressiveness in the population as a whole rather than simply the extremes of the back-test distribution could make this approach an attractive option for phenotyping aggressiveness. Until then, its full value is difficult to judge. The value of using the response to non-social challenges to predict post-mixing aggressiveness is therefore currently unproven. In contrast, the case is stronger for using behaviour in the attack latency test, but the test does not transfer well to commercial conditions, the causes of which deserve further investigation. The counting of skin lesions, however, may be suitable for use in selection if the trait is heritable. As the strength and direction of genetic correlations cannot be inferred from phenotypic correlations, a significant genetic correlation between lesions and post-mixing aggressiveness must also be demonstrated.

Evidence for genotypic influences on post-mixing pig aggressiveness

The duration spent in reciprocal fighting and delivering non-reciprocated aggression during the first 24 h post-mixing has heritabilities of 0.43 and 0.35 (Turner *et al* 2009). These heritabilities are higher than those obtained for the number of mild (single blow or bite) and severe (multiple blows or bites) aggressive acts delivered by sows during the first 30 min post-mixing of 0.17 and 0.24 (Løvendahl *et al* 2005). With the exception of the receipt of non-reciprocated aggression which showed a low heritability (mild 0.06, severe 0.04, Løvendahl *et al* 2005; 0.08, Turner *et al* 2009), post-mixing

aggressive behaviour has heritabilities of a similar magnitude to growth traits (eg Haraldsen *et al* 2009). The number of skin lesions accumulated on the body as a whole in the 24 h following mixing was reported to have a heritability of 0.22 (Turner *et al* 2006a). This is consistent with the genetic parameters from a different, unrelated population, for which heritabilities were estimated for the number of lesions on the front, middle and rear thirds of the body of 0.26, 0.25 and 0.21, respectively (Turner *et al* 2009). Whilst the heritabilities of lesion traits on each body region are lower than those for the duration of fighting and delivering non-reciprocated aggression, they are still notably higher than for many reproductive traits commonly under selection (eg Kapell *et al* 2009). The heritable variation in both aggressive behaviour and skin lesions therefore seems adequate to justify selection. Furthermore, pleiotropy or linkage between genomic regions influencing both aggressive behaviour and lesions is apparent through significant genetic correlations, confirming that selection on lesions ought to lead to genetic change in aggressive behaviour (Turner *et al* 2009). The pattern of genetic correlations suggests that lesions to the front of the body should be treated as a different trait to those on the middle and rear. Selection against lesions to the front will act against reciprocal fighters, those that deliver non-reciprocated aggression and, at a slower rate, the receipt of non-reciprocated aggression (Turner *et al* 2009). Lesions to the middle and rear are highly genetically correlated ($r_g = 0.98$), indicating that they share a largely common genetic determination and can be regarded as a single trait. Selection for or against these will act to increase or decrease the receipt of non-reciprocated aggression (Turner *et al* 2009). Placing different selection pressures on front and middle/rear lesions treated as two traits could therefore be used to reduce aggressiveness in specific genotypes.

In other species, selection on reduced aggressiveness has resulted in correlated changes in other behavioural traits (eg fearfulness in mice; Guillot & Chapoutier 1996). Knowledge of correlated responses in pigs ought to inform whether selection on reduced aggression is appropriate. Below, we consider the current state of knowledge on these correlated effects and propose issues that may justify attention in order to fully understand the consequences of selection.

Wider behavioural effects of selection on aggressiveness

Assessment of fighting ability

D'Eath *et al* (2009) reported no significant genetic correlation between the level of activity 3 weeks post-mixing, measured as the proportion of times pigs were observed to be standing, and the duration of reciprocal fighting or delivering non-reciprocated aggression at mixing itself, suggesting that pigs do not avoid aggressive encounters simply by being lethargic. Selection against aggressiveness is therefore likely to operate through more direct changes in aggressive tactics. Defeat is known to be a potent modulator of future aggressiveness (Meerlo *et al* 1997). Less aggressive animals may be those that have either experienced defeat more frequently or who are more sensitive to its

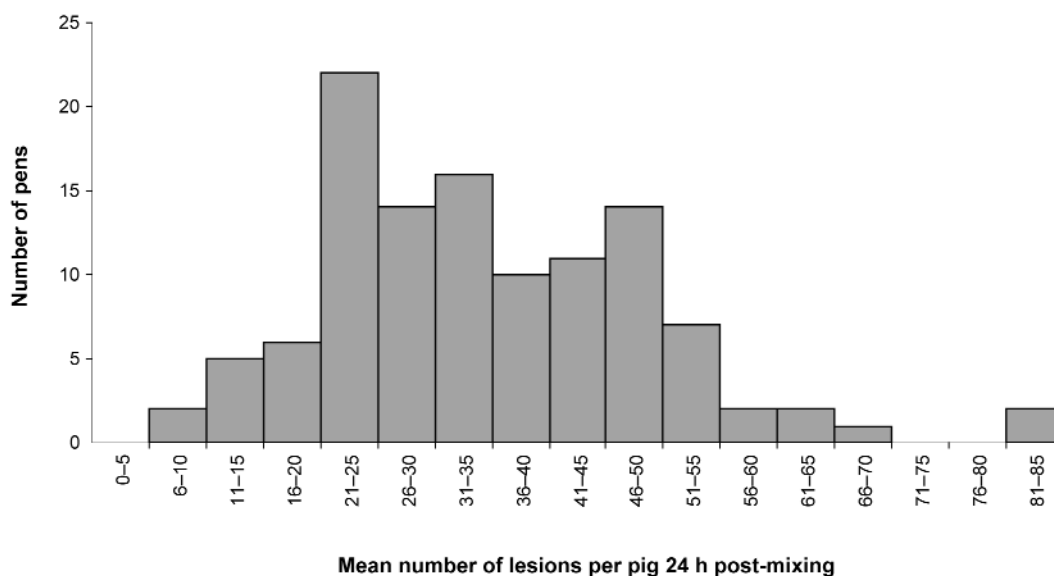
aggression-suppressing effect. In contrast, but possibly promoted by previous defeat, reduced aggressiveness could also be achieved through a better ability to assess the likelihood of success before engaging in actual fighting. This would be manifest in a reduced amount of fighting but a higher proportion of fights won. Turner *et al* (2006b) failed to find a phenotypic relationship between aggressiveness measured by the total number of lesions 24 h post-mixing and fight success, although it would be worth repeating this analysis with aggressiveness based on actual fighting behaviour. Elucidating the behavioural strategies and previous social history of unaggressive pigs would allow a greater understanding of how selection may alter social skills and aggressive tactics and, through this, the prudence of implementing selection. For example, selection which improved an individual's ability to assess its likelihood of winning before engaging in fighting may be viewed as preferable to selection which operated by enhancing the negative experiences of defeat.

Long-term and wider impacts on aggression

Longer term social stress following mixing can have significant impacts on pig welfare and productivity. For example, de Groot *et al* (2001) described a long-term suppression of anti-viral immunity and an increased fever response many weeks after mixing and Stookey and Gonyou (1994) reported that acute and chronic aggression following mixing both decrease growth. The number of lesions recorded 24 h post-mixing appear to be significantly positively genetically correlated with the number of fresh lesions recorded 3 weeks post-mixing (Turner *et al* 2009). Although the strength of this correlation was not strong (0.28–0.50) it indicates that lesions received from mixing and those in more stable social conditions are to a degree commonly genetically determined and a longer term reduction in lesions ought to result from selection practiced at mixing.

Post-mixing aggression between breeding sows and gilts also poses welfare and economic challenges. Clark (2007) found significant correlations between the attack latency test behaviour of pigs as growers and again 26 weeks later as post-pubertal gilts. If the aggressiveness of young pigs turns out to be positively genetically correlated with that shown later as breeding females, this would substantially extend the benefits of selection in pre-pubertal pigs. However, sows show aggression in two other contexts that could also be affected by selection against post-mixing aggressiveness at any age. The first is savaging of their own neonatal piglets which appears to occur less in unaggressive gilts (Clark 2007). If this was confirmed at the genetic level it might be a further advantage of selecting against grower aggressiveness. The second context is aggression directed towards humans in defence of offspring. Løvendahl *et al* (2005) showed that sows which were unaggressive post-mixing responded more intensely to the handling of their piglets in which the most severe response was to attack the handler (genetic correlation -0.34). Whilst offspring defence may be regarded as a component of good mothering ability, selection against aggression may be less desirable if it compromises handler safety. Understanding the genetic

Figure 3



Mean number of lesions per grower pig in 111 mixed pens. Mixed groups comprised of three pigs from each of five pens. Lesions were recorded 24 hours post-mixing on the whole body and those present before mixing were subtracted.

relationship between post-mixing aggressiveness and these traits may help promote the uptake of selection or advise how undesirable consequences could be mitigated.

Changes in response to non-social challenges

The association between pig aggressiveness and responses to non-social challenges has been considered above. The evidence linking such traits at the phenotypic level is equivocal. However, studies identifying candidate genes for aggressiveness typically report pleiotropic effects on non-aggression traits, suggesting that these traits may be genetically associated (Balaban *et al* 1996). In pigs, D'Eath *et al* (2009) found that animals which showed a low duration of aggression at mixing were genetically less willing to move away from both a handler and group members into a novel weighing crate. This response could have arisen from a greater desire for social reinstatement, greater neophobia of the weighing crate or reduced fear of the handler. Given the difficulty in interpreting the underlying motivations and implications for welfare, an assessment of behaviour in situations designed to disentangle these motivations would be useful. A greater motivation for social reinstatement may have welfare implications if unaggressive pigs have a greater need for, or benefit more from, social support during times of stress. However, lines of quail (*Coturnix coturnix japonica*) selected for high or low social reinstatement behaviour were not found to differ in aggressiveness (Formanek *et al* 2008) and perhaps we should not expect a link between these traits in pigs. Mendl and Erhard (1997) have proposed that fear may inhibit the performance of aggressive behaviour in some pigs. The results of D'Eath *et al* (2009) suggest that aggressiveness is genetically associ-

ated with fearfulness in at least one context. It would be interesting to know whether unaggressive pigs do indeed avoid aggressive encounters as a result of heightened fearfulness. In addition to its effects on welfare, understanding how changes in fearfulness could affect handling ease may be an additional lever to encourage uptake of selection or may, in contrast, highlight a negative consequence of selection.

Practical implementation

There remain practical issues relating to the implementation of selection that must be addressed. Aggression is context specific and pigs can probably alter their aggressiveness depending on the aggressiveness of other group members. It may be advantageous for an otherwise unaggressive pig to show more aggression when mixed with other passive animals, which could counteract the benefits of selection. However, when pigs that are unaggressive in the attack latency test are subsequently mixed, the levels of aggression are low (Erhard *et al* 1997; D'Eath 2002) and with a larger dataset, Figure 3 confirms that some pens of pigs do appear to come through mixing with a very low mean number of lesions per animal. Estimation of breeding values for aggressiveness in one environment (for example small social group sizes) and their application in another environment (large groups) does pose the risk of genotype \times environment interactions affecting the success of selection and it would be appropriate to quantify these interactions before commencing selection. There is also a need to determine the optimum age at which to phenotype pigs and to estimate the genetic correlations between aggressiveness and all relevant traits commonly used in selection indices. Turner *et al* (2006a) found no significant genetic correlation between

the total number of lesions and either growth rate or back-fat depth, the two most important production traits in sire-line pig breeding. From this, selection on lesions should not inhibit progress in performance traits through antagonistic relationships but the sample size of 657 pigs was small for this type of analysis and there is still a need to examine the correlations with other economic traits. Aggressiveness can also be viewed as both a market and non-market trait (Kanis *et al* 2005) in which the latter recognises its social or ethical value. Estimating the value of both components, taking into account the correlated effects on traits, such as aggression between sows and the savaging of piglets, may greatly assist in promoting the uptake of selection by breeding organisations. For this, there may be a role for approaches such as contingent valuation that measure a consumer's willingness to pay for non-market traits (Lawrence *et al* 2004). An alternative approach to selection which may circumvent the need for behavioural phenotyping is to place selection pressure on the effects that individuals have on the growth of other group members ('associative effects'; Bijma *et al* 2007). Behaviour is likely to be the mechanism through which associative effects operate, but it is not yet clear if selection will favour less aggressive pigs or whether other behavioural phenotypes will be changed independently of aggression, such as activity levels, feeding behaviour or libido (Canario *et al* 2008). The potential for this approach to reduce aggressiveness ought to be explored as well as its impacts on animal welfare.

Animal welfare implications and conclusion

Severe post-mixing aggression has been accepted as unavoidable on many farms. It is not easily minimised by low-cost environmental changes and, whilst effort should continue to find feasible environmental solutions, aggressiveness is adequately variable and heritable to make selection worthwhile. The use of skin lesions appears to offer the most practical and accurate way of estimating the duration of involvement in aggressive behaviour on a large number of animals. Alternative approaches have not been fully proven to correlate with aggressive behaviour or are not transferable to commercial environments. Selection on lesions at mixing, particularly with reference to their location, is expected to lead to a reduction in their number in the longer term. It is unclear at present how a reduction in severe aggression that causes lesions may affect the occurrence of less severe forms of aggressive behaviour which could also significantly affect the welfare of pigs. Whilst a reduction in aggression is unlikely to result in more lethargic pigs, the response to handling is expected to change slowly over time. Disentangling how selection on lesions might separately affect responses to challenges involving humans, novelty and social isolation would elucidate the costs/benefits for welfare and handling ease, as would a better understanding of the post-mixing behavioural strategies of unaggressive pigs. The mixing of pigs selected for low aggressiveness with unselected animals may occur in practice. This would be expected to increase the proportion of mixed groups in which unaggressive animals encounter

aggressive ones. Whilst groups comprised of animals of contrasting aggressiveness are formed in current populations by the random mixing of unselected pigs, there may be welfare implications of increasing the proportion of these where selected and unselected pigs are mixed together. As long as space allowances are adequate to allow retreat and avoidance, the accumulation of skin injuries on unaggressive pigs can probably be minimised. Where space is more limiting, the consequences for unaggressive pigs may be more severe and the benefits of selection partially masked. Finally, estimating the genetic correlations between post-mixing aggression of immature pigs and that of sows, together with the tendency to savage piglets and attack handlers during lactation, could greatly facilitate the implementation of selection, particularly if these genetic correlations were favourable. This may aid the estimation of the market and non-market values of post-mixing aggression, the unawareness of which probably remains the most significant barrier to the implementation of selection.

Acknowledgements

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