

Individual variation in sow aggressive behavior and its relationship with sow welfare¹

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ABSTRACT: This study examined the relationships between individual sow aggressive behavior and sow welfare, based on aggression, skin injuries, and stress, in a total of 275 pregnant domestic sows. Over 4 time replicates, sows were randomly mixed into groups of 10 (floor space of 1.8 m²/sow) within 7 d of insemination in both their first and second gestations (200 sows per gestation with 126 sows observed in both gestations). Measurements were taken on aggression (both delivered and received) at feeding, skin injuries, and plasma cortisol concentrations at d 2, 9, and 51 after mixing. Live weight gain, nonreproductive removals, litter size (born alive, total born, and stillborn piglets), and farrowing rate were also recorded. In both the first and the second gestations, sows were classified at d 2 after mixing as “submissive” (delivered little or no aggression at feeding relative to aggression received), “subdominant” (received more aggression at feeding than delivered), and “dominant” (delivered more aggression at feeding than received). In both gestations, sows classified as dominant at d 2 subsequently

delivered more (gestation 1, $P < 0.01$; gestation 2, $P < 0.01$) and received less (gestation 1, $P < 0.01$; gestation 2, $P < 0.01$) aggression and gained the most weight (gestation 1, $P < 0.01$; gestation 2, $P < 0.01$). Dominant sows had the least skin injuries throughout gestation 1 ($P = 0.04$), and although submissive sows sustained the most skin injuries at d 9 and 51 of gestation 2, at d 2 the classifications did not differ in skin injuries ($P < 0.01$). Subdominant sows had the highest cortisol concentrations at d 2 of gestation 2, but there were no differences between classifications at d 9 and 51 in either gestation (gestation 1, $P > 0.05$; gestation 2, $P = 0.02$). There were no significant relationships between aggression classification and reproduction and nonreproductive removals ($P > 0.05$). In conclusion, sows classified as dominant at feeding at d 2 subsequently received less aggression at feeding, sustained fewer skin injuries, and had higher live weight gain. Submissive and subdominant sows in groups are likely to benefit from the provision of increased resources such as space and access to feed.

Key words: aggression, group housing, individual variation, productivity, sow, welfare

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INTRODUCTION

Research on group-housed gestating sows has predominantly used aggression, injuries, and physiological stress to assess animal welfare (Verdon et al., 2015).

Although aggression in itself is a normal social behavior, intense and prolonged levels are commonly observed in newly formed groups of sows (Velarde, 2007). This aggression has obvious welfare implications, particularly for subordinate animals, because of its consequences on injuries and stress and their association with pain and fear (Hemsworth et al., 2015; Verdon et al., 2015). Furthermore, although animal welfare is defined in terms of the individual (Broom and Johnson, 1993), it is often assessed at a group level, for example, group average or total injuries. Consequently, implications of aggression, injuries, and stress for the most vulnerable individuals may be underestimated.

There is limited evidence that the aggressive behavior of sows early after mixing is related to an in-

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dividual's welfare. In a study of 17 sows, Zanella et al. (1998) found that although middle-ranking animals had the highest cortisol concentration, the low-ranking sows had lost diurnal regulation of the hypothalamic–pituitary–adrenal axis, a characteristic of chronic stress (Harbuz and Lightman, 1992). Furthermore, Mendl et al. (1992) classified 37 gilts housed in a dynamic group based on their ability to displace others and also found distinct differences between the classifications in regard to behavior, physiology, and reproduction. The aims of the present research were to extend the research by Mendl et al. (1992) and Zanella et al. (1998) to better understand the implications of aggressive strategies on sow aggression, injuries, and stress.

MATERIALS AND METHODS

All animal procedures were conducted with prior institutional ethical approval under the requirement of the New South Wales Prevention of Cruelty to Animals Act (1979) in accordance with the National Health and Medical Research Council/Commonwealth Scientific and Industrial Research Organization/Australian Animal Commission *Australian Code of Practice for the Care and Use of Animals for Scientific Purposes* (NHMRC, 2013).

Facilities

This study was conducted between October 2010 and February 2012 in a gestation unit of a large commercial piggery in southern New South Wales, Australia. The 6-m-long and 19-m-wide building was equipped with adjustable blinds. Overhead water sprinklers covered 50% of the slatted floor area of the pens and were activated (3 min on and 15 min off) when the internal temperature exceeded 26°C. The maximum and minimum mean daily ambient temperatures for spring, summer, autumn, and winter of 2011 were 21.3 and 8.5°C, 29.2 and 15.2°C, 21.3 and 7.9°C, and 15.6 and 3.9°C, respectively.

Within the unit, 12 pens (3.7 by 4.8 m) were used. Each pen had partially slatted floors (50%) with a solid cement lying/feeding area and a slatted dunging area and was fitted with 2 overhead feed droppers and 1 nipple drinker. One video camera with built-in infrared lights was positioned above each pen and recorded from 0700 to 1700 h on the second day of mixing (labeled Day 2) and Days 9 and 51 after mixing. The camera covered most of the pen floor area (14 m²); however, some area in the corners of the pens could not be observed. Importantly, the area of the pen floor where feed was delivered was within the field of view of the camera and this was the area where most of the sow interactions at feeding occurred.

Animals and Experimental Design

A total of 275 pregnant Large White × Landrace sows (*Sus scrofa*) were used in this study so that 200 gilts (50 gilts per replicate) in 4 replicates were studied in their first gestation and 200 sows in 4 replicates were studied in their second gestation (200 animals per gestation with 126 animals common to both gestations). Gilts detected in estrus from 32 wks of age were transferred from groups of 30 gilts to stalls for insemination. Gilts were twice artificially inseminated (morning/afternoon insemination routine) and, within 7 d of insemination, were randomly mixed into groups of 10 (space allowance of 1.8 m²/gilt) between 0800 and 1300 h. Before mixing, symbols were sprayed on the backs of gilts allowing for individual identification.

One week before farrowing, gilts were moved to farrowing stalls where they remained until piglets were weaned at 25 d of age. After piglets were weaned, the parity 1 sows were housed in mating stalls, again twice artificially inseminated (morning/afternoon insemination routine), and within 7 d, were randomly mixed into groups of 10 (space allowance of 1.8 m²/sow). Females were allocated to different groups for their second gestation and remained in these groups for the remainder of the gestation. On average, the maximum number of sows in a group that has been housed together in the first gestation was 2.4 (range 0–4). The same farrowing management as for first gestation was applied. For convenience, in the remainder of this paper, gestating gilts will be referred to as sows. The gestation number of the sow will reflect her parity status: nulliparous or primiparous.

During gestation, sows were fed a standard commercial gestation pelleted diet (13.1 MJ/kg DM and 12.8% protein; 31.3 kg per feeder per drop and 2.5 kg per sow per d). Feed was delivered onto the floor in 4 feed drops (at approximately 0730, 0930, 1100, and 1500 h). Water was supplied ad libitum.

Aggressive Behavior at Feeding

Aggressive behavior of individuals was observed using continuous sampling for 30 min after each of 4 daily feed drops on the day after mixing (Day 2) and Days 9 and 51. Aggressive behavior was defined as bites, presses, and knocks (Samarakone and Gonyou, 2009) and also included fights, which were defined as aggressive interactions involving the same pair of animals and that continued for at least a 5-s duration. The numbers of aggressive acts delivered and received by each individual sow during the observation period were recorded. During fights, a bout criterion interval of 5 s was chosen to separate one bout of aggressive behavior from another bout (Hemsworth et al., 2013). Only when the full head

of the attacking animal and the identifying symbol of the animals delivering and receiving aggression were clearly in the field of view were aggressive interactions recorded.

From the observations of aggressive behavior at feeding at Day 2, sows were classified as “dominant” if they delivered more aggression than they received at Day 2, “subdominant” if they received more aggression than they delivered at Day 2, and “submissive” if they delivered very little or no aggression relative to aggression received at Day 2 (that is, the ratio of aggression delivered to aggression delivered + aggression received ≤ 0.05). Aggressive behavior at Day 2 was used because aggression between group-housed sows that are restrictively fed is most pronounced early after grouping (Barnett et al., 2001). This aggression classification is similar to that devised by Mendl et al. (1992) and used later by Zanella et al. (1998), but these researchers used displacements rather than aggression.

Cortisol Concentrations

Blood samples were taken by a single team at Days 2, 9, and 51 by venipuncture of the jugular vein while animals were restrained with a snout snare. Sampling commenced at approximately 1200 h and it took an average of 37 min to sample all sows in the replicate (average 7.5 min per pen). A 6-mL sample was taken in a heparinized tube (BD Vacutainer; Becton, Dickinson and Company, Belliver Industrial Estate, Plymouth, UK). For each animal, a maximum of 2 min from snaring was allowed to obtain the blood sample. This was so that an acute stress response associated with handling and blood sampling could be avoided, which would influence concentrations of plasma cortisol (Broom and Johnson, 1993). Karlen et al. (2007) found no effects of repeatedly sampling different animals within groups on salivary cortisol concentrations.

The individual samples were centrifuged for 10 min at $1,912 \times g$ at 4°C , and the plasma was poured off into individual microtubes and stored at -20°C until analyzed. During this study, the laboratory that analyzed the plasma samples for gestation 1 and for the majority of gestation 2 ceased to operate (Monash University, Melbourne, Australia). Consequently, 92 of 177 samples collected at Day 51 of gestation 2 (replicates 3 and 4) were analyzed elsewhere (The University of Western Australia, Perth, Australia).

The first laboratory measured plasma cortisol with an extracted RIA (Bocking et al., 1986), using hydrocortisone (H-4001; Sigma Chemical Co., St. Louis, MO) as the standard. The assay used [^3H]-cortisol (Amersham Pharmacia Biotech, UK, Buckinghamshire, England) as tracer and a dichloromethane extraction procedure. The second laboratory

measured plasma cortisol using a commercial RIA kit (Cortisol GammaCoat RIA kit CA-1549; DiaSorin Inc., Stillwater, MN). The intra- and interassay CV of the first and second laboratories were 7.81 and 12.06% and 5.13 and 4.85%, respectively.

Skin Injuries

The same assessment as described by Karlen et al. (2007) was used to assess skin injuries for individual sows in the morning of each of Days 2, 9, and 51 after mixing. Only skin injuries categorized as being fresh (scratches, abrasions, and cuts) were recorded. Each side of the sow's body was divided into 21 areas for injury data collection (see Karlen et al., 2007). The number and the type of skin injuries were recorded, and, from these records, the number of fresh injuries was collated for each sow on each observation day.

Live Weight Gain

Sows were individually weighed at Days 2 and 100. From this, live weight gain for the gestation was calculated.

Nonreproductive Removals

Removal of sows for injury, illness, or death was recorded as a nonreproductive removal.

Reproductive Performance

The reproductive performance data collected allowed for the farrowing rate percent of inseminated sows that farrowed (excluding those removed for injury, illness, or death) to be calculated. Litter size data (number of piglets that were born alive, total number born, and stillborns) as well as nonreproductive removals were also collected. Stillborn piglets were judged on the basis that they were fully formed at farrowing, covered in fetal membrane, had fully formed eponychia on their hooves, and were located behind the sow.

Statistical Analysis

Due to removal of unproductive animals and to ensure each gestation had 200 animals at mixing, a total of 275 animals were selected for the study. Some animals were observed in the first gestation and not the second, and vice versa, but there were 126 animals common to both gestations. In gestation 1, 182 sows had complete injury and cortisol data sets (i.e., data collected at Days 2, 9, and 51). However, a technical malfunction meant there were no Day 51 behavioral data for replicate 4 in

the first gestation, and as such, only 137 sows in this gestation had complete aggressive behavior data sets. One sow in the second gestation escaped the pen before any data could be obtained. The numbers of sows with complete data sets for aggressive behavior, skin injuries, and cortisol in the second gestation were 177, 177, and 176 sows, respectively.

All analyses were conducted using SPSS statistical package (SPSS 17.0; SPSS Inc., Chicago, IL). Many variables did not conform to a normal distribution as indicated by visual methods (quantile-quantile plots and histograms). Aggression and injury data were square root transformed whereas cortisol and stillborn data were $\log_{10}(x + 1)$ transformed before analysis so that the residual variation was similar in both treatments. Data that were greater than the 75th percentile plus $1.5 \times$ the interquartile range or less than the 25th percentile minus $1.5 \times$ the interquartile range were removed as statistical outliers (Pallant, 2013).

Data on aggressive behavior (delivered and received), skin injuries, and cortisol were analyzed separately for each gestation using a general linear mixed model that included day, aggression classification, and their interaction as fixed effects. Repeated observations on the same sow were taken into account by including a repeated effect of day within sow. Random effects of group were included in the model to account for potential effects of the social environment across groups and on repeated measurements within sows. Where significant effects were found, the LSD test was conducted to compare means between the 3 classifications of sow. The LSD test was conducted at each day separately when there was an aggression classification \times day significant interaction. Differences in live weight (start weight and live weight gain) and reproduction (total born and born alive) were assessed using a general linear mixed model that included aggression classification as a fixed factor and group as a random factor. Data on stillborn piglets were discrete. A generalized linear model with an underlying Poisson distribution was fitted to this variable with aggression classification and group included in the model as fixed factors. This test generates a Wald statistic that is analogous to the χ^2 statistic. For the 126 sows common to both gestations, Kappa coefficients were calculated to assess the consistency of aggression classification between gestations 1 and 2. A χ^2 test for independence was used to determine the association between farrowing rate, nonreproductive removal, and the aggression classification of sows. Due to the low occurrence of removals (see results for details), the χ^2 analysis for nonreproductive removals was performed on combined data from gestations 1 and 2, whereas for the farrowing rate, it was performed on gestations 1 and 2 separately.

RESULTS

Aggression Classification

In both gestations, most sows were classified as subdominant (received more aggression than they delivered; 91 gilts [45.5%] in gestation 1 and 88 sows [44.2%] in gestation 2). Sows that delivered more aggression than they received were the next prominent (dominant; 71 gilts [35.5%] in gestation 1 and 66 sows [33.2%] in gestation 2), with sows that delivered very little or no aggression the least common (submissive; 38 gilts [19.0%] in gestation 1 and 45 sows [22.6%] in gestation 2). A Kappa statistic of 0.19 showed a low level of consistency in sow aggression classification between gestations 1 and 2.

Aggression Delivered and Received

Probability values and means for the interactive effects of sow aggression classification and day after mixing on aggression delivered and received are presented in Table 1 as well as graphically presented in Fig. 1.

There was an interaction effect of aggression classification and day on aggression delivered in gestations 1 and 2 (aggression classification \times day: gestation 1, $P < 0.01$, and gestation 2, $P < 0.01$; Table 1; Fig. 1a and 1c). At Days 2, 9, and 51 of both gestations, dominant sows delivered more aggression than submissive and subdominant sows; however, whereas aggression delivered by dominant sows declined over this period, aggression delivered by subdominant and submissive sows remained relatively constant (Table 1; Fig. 1a and 1c). It is of interest that aggression delivered by subdominant sows in both gestations more closely resembled that delivered by submissive sows rather than that delivered by dominant sows (Table 1; Fig. 1a and 1c).

There was no interaction effect of aggression classification and day on aggression received in either gestation 1 or gestation 2 (aggression classification \times day: gestation 1, $P > 0.05$, and gestation 2, $P > 0.05$; Table 1; Fig. 1b and 1d). Within each gestation, dominant sows received less aggression than submissive and subdominant sows (aggression classification: gestation 1, $F_{2,187} = 18.6$, $P < 0.01$, and gestation 2, $F_{2,189} = 45.8$, $P < 0.01$) although aggression received by each classification of sow declined over time (day: gestation 1, $F_{2,171} = 43.4$, $P < 0.01$, and gestation 2, $F_{2,186} = 42.3$, $P < 0.01$). Aggression received by submissive and subdominant sows did not differ throughout gestation 1 or 2 (Table 1; Fig. 1b and 1d).

Skin Injuries

Probability values and means for the interactive effects of sow aggression classification and day after

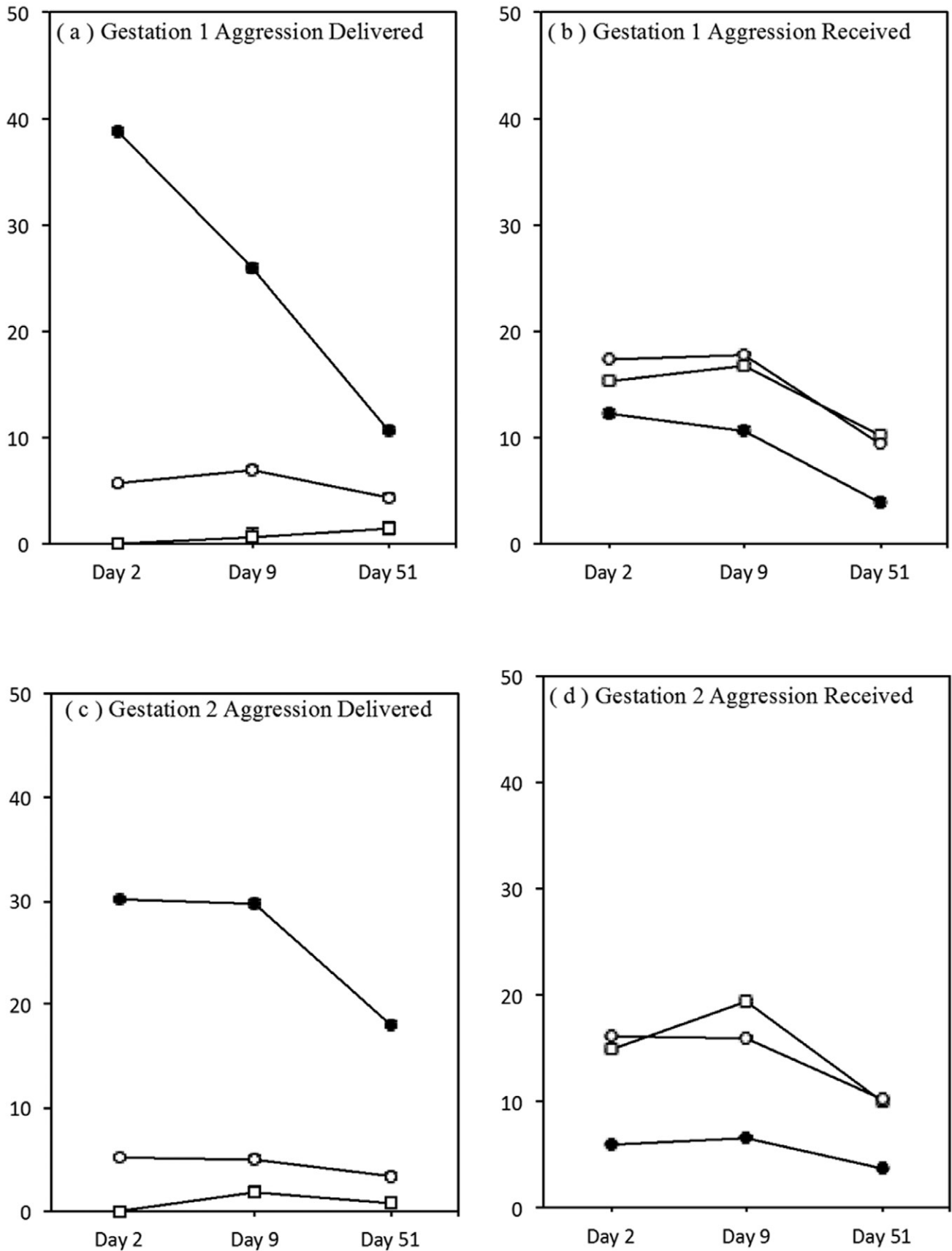


Figure 1. Mean frequency per sow per day ($\pm 2 \times \text{SEM}$) of aggression delivered and received (y-axis) by submissive (\square), subdominant (\circ), and dominant (\bullet) sows at Day 2, 9, and 51 after mixing in gestation 1 (a and b, respectively) and gestation 2 (c and d, respectively).

Table 1. Interactive effects of sow aggression classification and day after mixing on mean frequency of aggression delivered and received over 4 feed drops (total of 2 h per day) for sows in gestations 1 and 2

Variable ¹	Aggression classification ²				F-statistic	P-value ⁴
	SM	SB	D	SEp ³		
Gestation 1						
Aggression delivered, frequency per sow per day						
Day 2	0.00 ^a	5.64 ^b	38.8 ^c	0.53	$F_{4,166} = 24.2$	<0.01
Day 9	0.74 ^a	7.05 ^b	25.9 ^c	0.51		
Day 51	1.46 ^a	4.38 ^a	10.7 ^b	0.29		
Aggression received, frequency per sow per day						
Day 2	15.3	17.3	12.3	0.14	$F_{4,166} = 1.29$	0.28
Day 9	16.8	17.8	10.7	0.14		
Day 51	10.2	9.45	3.91	0.16		
Gestation 2						
Aggression delivered, frequency per sow per day						
Day 2	0.01 ^a	5.22 ^b	30.1 ^c	0.41	$F_{4,187} = 10.7$	<0.01
Day 9	1.84 ^a	5.01 ^b	29.8 ^c	0.48		
Day 51	0.79 ^a	3.36 ^b	18.0 ^c	0.30		
Aggression received, frequency per sow per day						
Day 2	14.8	16.1	6.02	0.14	$F_{4,186} = 2.04$	0.09
Day 9	19.4	16.0	6.62	0.17		
Day 51	9.99	10.2	3.64	0.14		

^{a-c}Within a row, least squares means lacking common superscripted letters differ ($P \leq 0.05$).

¹Back-transformed mean values \pm pooled SE.

²SM = submissive sow; SB = subdominant sow; D = dominant sow.

³SEp = Pooled standard error of the mean.

⁴Probability value for the aggression classification \times day interaction.

mixing on skin injuries are presented in Table 2 as well as graphically presented in Fig. 2.

There was an interaction effect of aggression classification and day on skin injuries in gestations 1 and 2 (aggression classification \times day: gestation 1, $P < 0.05$, and gestation 2, $P < 0.01$; Table 2; Fig. 2a and 2b). In both gestations, skin injuries did not differ between classifications at Day 2 but at Day 9, dominant sows had the least skin injuries, and at Day 51, submissive sows had the most (Table 2; Fig. 2a and 2b).

Stress Physiology

There were no differences between replicates 1 and 2 and replicates 3 and 4 in Day 51 gestation 2 plasma cortisol concentrations (back-transformed means [SD] for laboratories 1 and 2, 17.0 [0.89] and 18.9 ng/mL [0.65], respectively; $F_{1,176} = 1.32$, $P = 0.25$).

Probability values and means for the interactive effects of aggression classification and day after mixing on plasma cortisol concentrations are presented in Table 2. Plasma cortisol concentrations did not differ between submissive, subdominant, and dominant sows in gestation 1 (aggression classification, $F_{2,119} = 0.96$,

Table 2. Interactive effects of sow aggression classification and day after mixing on mean frequency of skin injuries per sow and plasma cortisol concentrations per sow in gestations 1 and 2

Variable ¹	Aggression classification ²				F-statistic	P-value ⁴
	SM	SB	D	SEp ³		
Gestation 1						
Skin injuries, frequency per sow						
Day 2	23.3 ^{ab}	24.2 ^a	18.1 ^b	0.29	$F_{4,199} = 2.61$	0.04
Day 9	6.54 ^a	7.22 ^a	4.80 ^b	0.10		
Day 51	5.62 ^a	3.06 ^b	1.62 ^c	0.09		
Plasma cortisol, ng/mL						
Day 2	14.9	13.4	15.5	0.05	$F_{4,189} = 7.16$	0.13
Day 9	16.7	15.0	12.6	0.07		
Day 51	17.7	17.5	16.7	0.07		
Gestation 2						
Skin injuries, frequency per sow						
Day 2	22.2	23.5	27.8	0.23	$F_{4,197} = 1.79$	<0.01
Day 9	7.78 ^a	5.39 ^a	2.46 ^b	0.11		
Day 51	8.23 ^a	4.72 ^b	3.77 ^b	0.11		
Plasma cortisol, ng/mL						
Day 2	12.4 ^{ab}	15.4 ^a	11.0 ^b	0.08	$F_{4,197} = 2.94$	0.02
Day 9	12.9	13.5	13.9	0.06		
Day 51	18.6	16.7	19.2	0.06		

^{a,b}Within a row, least squares means lacking common superscripted letters differ ($P \leq 0.05$).

¹Back-transformed mean values \pm pooled SE.

²SM = submissive sow; SB = subdominant sow; D = dominant sow.

³SEp = Pooled standard error of the mean.

⁴Probability value for the aggression classification \times day interaction.

$P = 0.59$) nor was there an interaction effect of day and aggression classification on plasma cortisol in this gestation (aggression classification \times day, $F_{4,189} = 1.79$, $P > 0.05$; Table 2). In gestation 2, however, cortisol concentrations were higher for subdominant sows than for dominant sows at Day 2, but there was no difference between the cortisol concentrations for the 3 classifications of sow at Days 9 or 51 (aggression classification \times day, $F_{4,196} = 2.94$, $P < 0.05$; Table 2). For both gestations, cortisol concentrations increased as pregnancy progressed (day: gestation 1, $F_{2,189} = 4.13$, $P = 0.02$, and gestation 2, $F_{2,194} = 18.4$, $P < 0.01$; Table 2).

Live Weight

Probability values and means for the main effects of aggression classification on sow start weight and sow live weight gain are presented in Table 3. There was an effect of aggression classification on start weight in gestation 1 ($P = 0.01$) but not gestation 2 ($P > 0.05$). In gestation 1, submissive sows were lighter at Day 2 than subdominant sows but not dominant sows (Table 3). The CV for live weight at Day 2 in gestations 1 and 2 were 8.1 and 9.4%, respectively.

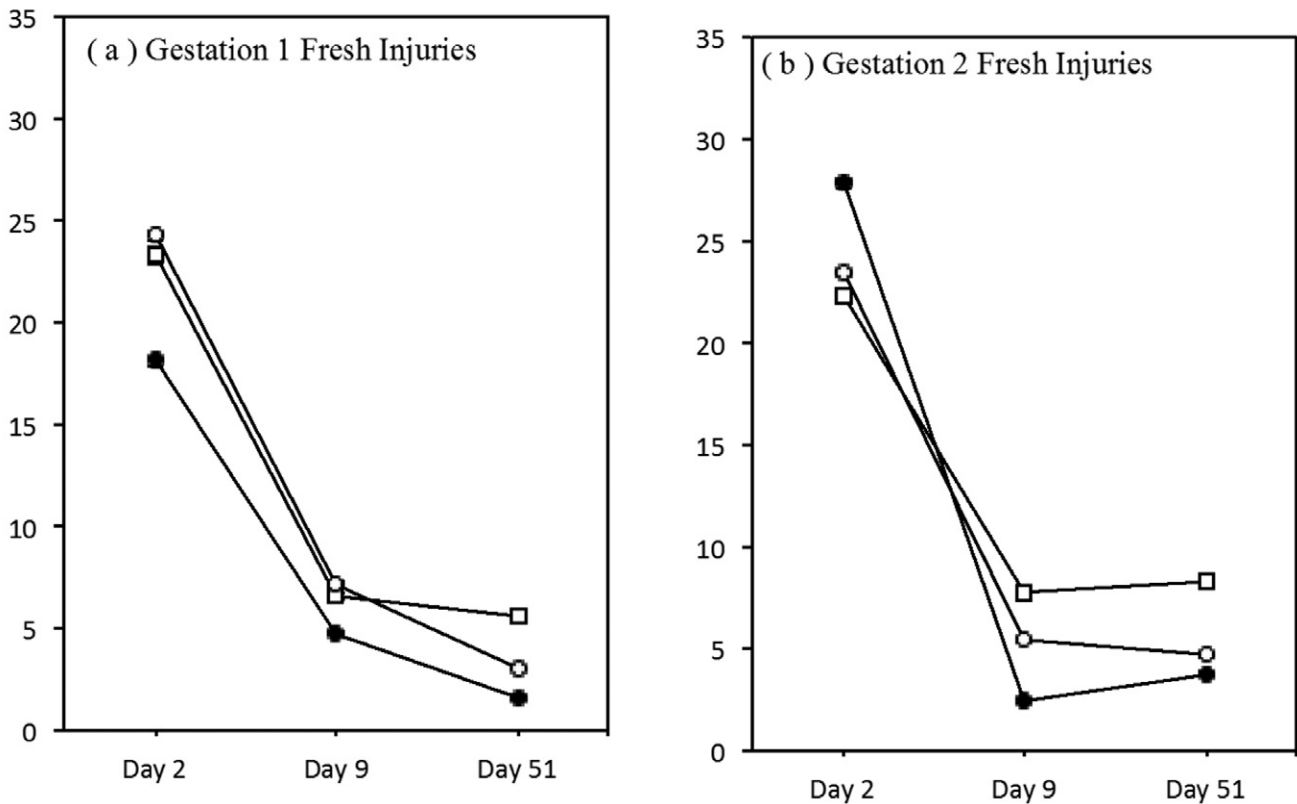


Figure 2. Mean numbers per sow ($\pm 2 \times$ SEM) of fresh skin lesions (y-axis) sustained by submissive (□), subdominant (○), and dominant (●) sows at Day 2, 9, and 51 after mixing in gestation 1 (a) and gestation 2 (b).

In both gestations, dominant sows gained the most weight but there was no difference in weight gained by subdominant and submissive sows (gestation 1, $P < 0.01$, and gestation 2, $P < 0.01$; Table 3).

Nonreproductive Removals

Over the 2 gestations, 7 submissive sows (4 sows in gestation 1 and 3 sows in gestation 2; 8.43% submissive sows), 7 subdominant sows (2 sows in gestation 1 and 5 sows in gestation 2; 3.91% subdominant sows), and 5 dominant sows (2 sows in gestation 1 and 3 sows in gestation 2; 3.65% dominant sows) were removed for nonreproductive reasons. The χ^2 test for independence indicated no significant association between nonreproductive removals and aggression classification ($\chi^2_{2, 399} = 3.13$, $P = 0.21$).

Reproduction

In gestation 1, 29 submissive sows (85.3% of submissive sows), 74 subdominant sows (83.1% of subdominant sows), and 60 dominant sows (87.0% of dominant sows) farrowed. In gestation 2, 36 submissive sows (85.7% of submissive sows), 77 subdominant sows (92.8% of subdominant sows), and 54 dominant sows (85.7% of dominant sows) farrowed.

The χ^2 test for independence indicated no significant association between farrowing rate and aggression classification in either gestation 1 ($\chi^2_{(2, 192)} = 0.45$, $P = 0.80$) or gestation 2 ($\chi^2_{(2, 188)} = 2.33$, $P = 0.31$).

Probability values and means for main effects of aggression classification on litter size data are presented in Table 3. Sow aggression classification was not related to the number of piglets born (either total or alive) in gestations 1 (born alive, $P = 0.59$; total born, $P = 0.20$) or 2 (born alive, $P = 0.17$; total born, $P = 0.13$). The average number of stillborn piglets (SEM) per litter born to submissive, subdominant, and dominant sows in gestation 1 were 0.38 (0.13), 0.45 (0.10), and 0.42 (0.10) piglets, respectively, and in gestation 2, the numbers were 0.39 (0.12), 0.39 (0.09), and 0.43 (0.10), respectively. The average number of stillborn piglets per litter was not affected by aggression classification in either gestation 1 (Wald statistic = 0.11, df = 1, $P = 0.95$) or gestation 2 (Wald statistic = 0.50, df = 1, $P = 0.78$).

DISCUSSION

Aggression Classification

Mendl et al. (1992) used a displacement success index to classify 37 gilts as no, low, or high success based on behavioral observations over 4 time periods on each

Table 3. Main effects of sow aggression classification on sow live weight gain and reproduction in gestations 1 and 2

Variable ¹	Aggression classification ²			SEp ³	F-statistic	P-value
	SM	SB	D			
Gestation 1						
Day 2 live weight, kg	146 ^a	152 ^b	150 ^{ab}	0.89	$F_{2,190} = 4.40$	0.01
Live weight gain, kg	69.5 ^a	66.9 ^a	73.9 ^b	0.97	$F_{2,126} = 9.50$	<0.01
Litter size, number of piglets						
Total	9.80	10.5	10.8	0.19	$F_{2,190} = 9.50$	0.20
Born alive	9.70	10.1	10.3	0.20	$F_{2,190} = 9.50$	0.59
Gestation 2						
Day 2 live weight, kg	191	190	195	1.28	$F_{2,183} = 1.46$	0.24
Live weight gain, kg	63.2 ^a	66.3 ^a	72.8 ^b	1.35	$F_{2,127} = 5.25$	<0.01
Litter size, number of piglets						
Total	11.0	11.0	11.9	0.21	$F_{2,190} = 9.50$	0.13
Born alive	10.6	10.6	11.4	0.21	$F_{2,190} = 9.50$	0.17

^{a,b}Within a row, least squares means lacking common superscripted letters differ $P \leq 0.05$.

¹Mean values \pm pooled SE.

²SM = submissive sow; SB = subdominant sow; D = dominant sow.

³SEp = Pooled standard error of the mean.

of 3 d in the first week and 2 d in the third week after mixing. By contrast, the present research classified 200 sows as submissive if they delivered little or no aggression, subdominant if they delivered less aggression than they received, and dominant if they delivered more aggression than they received based on behavioral observations for 30 min after each of 4 feed drops on the day after mixing. The use of aggressive behavior in preference to displacement behavior can be justified by the following: agonistic interactions early after mixing frequently include aggression (Jensen, 1982), aggression in group-housed sows that are restrictively fed is most pronounced early after grouping (Barnett et al., 2001; Hemsworth et al., 2013), the number of times a gilt is displaced/displaces another follows a pattern similar to the frequency with which she receives/delivers aggression (Mendl et al., 1992), and there may be difficulties in recognizing all agonistic interactions (e.g., submissive behavior; Meese and Ewbank, 1973). Nonetheless, both this study and that by Mendl et al. (1992) found that most animals were classified as subdominant with fewer numbers of submissive and dominant sows. The percentages of sows classified as submissive, subdominant, and dominant in the present study (gestations 1 and 2 combined) were 20.8, 44.9, and 34.3%, respectively, whereas in Mendl et al. (1992), the percentages were 18.9, 64.9, and 16.2%, respectively.

It should be recognized that in the present study, sows were classified on the basis of aggression at feeding and not aggression in other contexts. Nevertheless, most aggression between floor-fed group-housed sows occurs at feeding (Csermely and Wood-Gush, 1987). Furthermore, Csermely and Wood-Gush (1990) and Brouns and Edwards (1994) found that sows with a high dominance

index, calculated from observations of agonistic behavior during both feeding and nonfeeding periods, delivered more and received less aggression at feeding in a floor-feeding system than sows with a low dominance index.

There was a low level of agreement between sow aggression classification in gestations 1 and 2 of the present study. Although an individual sow may have a general tendency to deliver more or less aggression, she may also display flexibility around this general tendency depending on prior experiences, the environment (including the social environment), internal state, and stage of development (Sih et al., 2003; Bell, 2007).

Aggression and Skin Injuries

Sows classified as dominant delivered the most aggression at Days 2, 9, and 51 after mixing for both gestation 1 and 2, whereas those classified as submissive delivered the least. Aggression delivered by dominant sows declined over time and this decline coincided with a reduction in aggression received by each classification of sow and, consequently, a reduction in the frequency of skin injuries over the same period, although in both gestations, dominant sows received the least aggression and sustained the least skin injuries. When unfamiliar sows are mixed, aggressive animals fight for dominance but also deliver aggression to those that are lower ranking or become lower ranking. Therefore, both dominant and lower-ranking sows receive aggression and sustain skin injuries early after mixing. Sows that are successful in achieving a dominant status at mixing are likely to receive less aggression in the future and, consequently, sustain fewer skin injuries. These results contrast a previous finding in young pigs that the number of skin injuries

sustained 24 h after mixing correlated to that sustained 3 wk after mixing (Turner et al., 2009). However, these results support studies on the sow that have found no relationship between sow aggression and injuries early after mixing and that dominant sows have fewer injuries in the long term (Arey, 1999; O'Connell et al., 2003).

Aggression delivered by dominant sows in the present study remained high at Day 9 but was markedly reduced at Day 51 in both gestations. Aggression associated with the mixing of unfamiliar sows is reported to reach baseline levels within 1 to 2 d (Marchant-Forde, 2009), but when sows are floor fed, aggression around feeding does not stabilize until at least 28 d after mixing (Arey, 1999). Therefore, aggression delivered by dominant sows in the present study may have remained high at Day 9 as these animals defended their access to a limited supply of food (Edwards, 1992). Although aggression delivered by dominant sows in the present study declined from Days 2 to 51, skin injuries for all sows declined markedly from Days 2 to 9. This marked decline in skin injuries is likely a consequence of high-intensity aggression early after mixing, which is associated with unfamiliarity between sows. Furthermore, the removal of sows throughout gestation (for reproductive failure or injury, a total of 23 and 22% of sows removed throughout gestations 1 and 2, respectively) may have affected aggression and, subsequently, injuries because of the potential reduction in interactions and the increase in space allowance with removals from a pen. However, Hemsworth et al. (2013) found no effect of increasing space allowance (1.4–3.0 m²/sow) on feeding aggression 8 d after mixing and Taylor et al. (1997) found no effect of group size (5, 10, 20, and 40 sows) with the same space allowance on skin injuries at Days 5 and 53 after mixing.

In gestation 1, aggression received and skin injuries sustained by dominant sows declined in a way similar to those received and sustained by subdominant and submissive sows. In gestation 2, however, dominant sows consistently received low levels of aggression whereas aggression received by subdominant and submissive sows declined over time. Furthermore, skin injuries sustained by each classification of sow in gestation 1 declined by approximately 70% from Day 2 to 9, but in the second gestation, skin injuries sustained by dominant sows declined by 91% over the same period. Older and more socially experienced sows may form a stable social hierarchy more quickly and with less aggression. Indeed, aggressive behavior is strongly influenced by experience of social aggression, as prior winning experiences raise and losing experiences lower an individual's perceived fighting ability (for review, see Hsu et al., 2006). Consequently, following the experience of group housing in the first gestation, low-ranking sows may have learned to avoid high-ranking sows, whereas

the latter sows may be more confident in their fighting ability and respond accordingly.

The level of aggression delivered and received by subdominant sows was more similar to those delivered and received by submissive sows than by dominant sows. Interestingly, Mendl et al. (1992) also found the frequency of aggression delivered and received (per hour) by middle-ranking gilts to be more similar to low-ranking gilts than to high-ranking gilts, even though agonistic behavior was recorded in a variety of contexts, whereas in the present study, aggressive behavior was observed only at feeding. Mendl and colleagues hypothesized that middle-ranking gilts continued to deliver aggression despite facing repeated defeat from those more dominant, whereas the lowest-ranking gilts reduce their involvement in aggression by avoiding competition. Considering the above results in the context of social dynamics may prove to be revealing. Once a hierarchy has been established, dominant sows receive little aggression yet continue to deliver aggression to those of lower rank, especially when defending a high-priority resource such as food. Subdominant sows receive aggression from dominant sows, and we speculate that subdominant sows risk aggression by feeding at the same time as dominant sows. The submissive sows receive aggression from both dominant and subdominant sows. In groups where sows compete for access to food and space is limited, it may become increasingly difficult for submissive sows to show submissive behaviors (i.e., fleeing) and avoid aggression, particularly if they are to maintain an adequate intake of food. Therefore, although, in the present study, subdominant and submissive sows receive comparable amounts of aggression, the former may do so because they continue to risk aggression whereas the latter receive aggression because they cannot avoid aggression. That submissive sows sustained the most skin injuries in the long term suggests that they are receiving aggression at times other than feeding or of greater severity than subdominant sows. These results raise an important question: can the welfare of the most vulnerable sows practically be improved through an increased provision of resources (e.g., food, straw, space, barriers and kennel areas)? Presumably, a point will be reached when extra provisions cease being monopolized by dominant sows and are increasingly available to be used by subordinate sows.

Stress Physiology

In the present study, there was no effect of aggression classification on cortisol concentrations at Day 2 in the first gestation. However, there was a significant aggression classification × day interaction in the second gestation, with subdominant sows having

the highest plasma cortisol concentrations at Day 2. Other studies that have similarly categorized sows into 3 dominance classifications have reported that middle-ranking gilts experience the highest stress in the first week after mixing (Nicholson et al., 1993), at 5 wk after mixing (Mendl et al., 1992), and 8 to 12 d after estrus detection (Zanella et al., 1998). Mendl et al. (1992) suggested that repeated attacks and defeat experienced by middle-ranking gilts resulted in a chronic stress response. Sow experience may partially explain why, in the present study, there was an effect of aggression classification on cortisol in gestation 2 but not in gestation 1; however, considerable variation in individual plasma cortisol concentrations may also have contributed to this discrepancy. More research may determine whether the interaction effect reported in the second gestation is a real effect.

Physiological stress is affected by stage of reproduction in that total cortisol concentrations increase throughout gestation (Barnett et al., 1985; Hay et al., 2000), and indeed, in the present study, plasma cortisol concentrations increased throughout both gestations.

Productivity (Live Weight, Removals, and Reproduction)

Submissive sows were lighter than subdominant but not dominant sows at Day 2 of gestation 1, but there was no relationship between aggression classification and weight at Day 2 of gestation 2. In mixed-parity groups, high social rank has been correlated with sow weight and parity in some studies (Arey, 1999) but not in others (Mount and Seabrook, 1993; Brouns and Edwards, 1994). Weight differences between sows in mixed parity groups, however, are likely to be much greater than those observed in uniform parity groups, which were used in this study. Indeed, in both gestations of the present study, the CV was low (<10%) for live weight at Day 2. Where physical differences between sows are limited, engagement in aggression may be more dependent on factors such as genetics and experience.

Dominant sows gained more weight than subdominant and submissive sows in both gestations. Dominant sows may gain priority access to food but submissive animals that avoid aggression may be sacrificing the opportunity to feed for safety (Verdon et al., 2011). On the other hand, subdominant animals may risk receiving aggression to access feed or improve their social order or both, but the associated energy expenditure and stress from consistently engaging in aggression could result in reduced weight gain. Interestingly, both Mendl et al. (1992) and Kranendonk et al. (2007) found sows of high social rank to gain the most weight during gestation, even though animals were fed using an

electronic sow feeder. Mendl et al. (1992) suggested that increased fear and anxiety of attack could increase basal metabolic rates and, thus, expenditure of energy of middle-ranking sows, compromising growth.

The frequency of removals for injury including lameness, illness, or death did not differ for submissive, subdominant, or dominant sows. The total number of removals over both gestations for nonreproductive reasons was low (19 sows total), and only approximately a quarter of these removals were dominant sows.

There were no differences in litter size, still births, or farrowing rate of dominant, subdominant, and submissive sows in either gestation of the present study. The literature regarding social rank and sow reproduction is inconclusive. For instance, although middle-ranking sows have been found to have lower farrowing rates (Nicholson et al., 1993) and produce piglets of lighter weight (Mendl et al., 1992), no effects have been reported on litter size (Mendl et al., 1992) or on embryo survival (Tsuma et al., 1996). Although stress can interfere with reproduction, some sows are resistant to the effects of prolonged stress or a sustained increase in cortisol on reproduction (Turner et al., 2005). Furthermore, ovulation rate and litter size may, in part, be determined by genetics (Rothschild et al., 1996; Rathje et al., 1997). These inconsistencies highlight how little is known about the relationship between dominance, stress, and reproduction, a topic that requires further research.

There are some conflicting results between the present study and those conducted by others (e.g., gestation 1 stress physiology, sow reproduction) as well as between the first and second gestations of the present study (e.g., start weight, stress physiology at Day 2). These inconsistencies between studies may be attributed to varying research methodologies (i.e., context in which agonistic behavior was observed [mixing, feeding, under stable conditions, and aggression classification method]), pen designs (i.e., floor space allowance and feeding system), and social factors (i.e., stage of gestation at mixing and group composition; for review, see Verdon et al., 2015).

Conclusions

Although analysis based on group data plays an important role in research of the welfare of group-housed animals, this study demonstrates the importance of understanding welfare implications at the individual animal level. Under the group-housing conditions described in this study, aggressive sows risk injury early after mixing by engaging in fights in an attempt to gain a high position in the dominance hierarchy but submissive sows may have had difficulty avoiding those that were more dominant. Consequently, most animals in a group receive skin injuries early after grouping. Once

a dominance hierarchy is established, dominant sows have a reduced risk of receiving aggression and, hence, reduced skin injuries. They are also more likely to gain greater weight. Identifying the most compromised sows, however, is complicated. Although subdominant and submissive animals were comparable in terms of aggression received, live weight gain, and reproduction, subdominant sows may be more likely to experience greater stress early after mixing but submissive sows have more skin injuries later in gestation. Therefore, although the dominant sows receive skin injuries early after grouping, in the long term, they have priority of access to feed, fewer skin injuries, and higher growth rates. However, both subdominant and submissive sows in groups may benefit from the provision of increased resources such as access to feed, lying space, and access to drinkers, particularly in the period immediately after mixing as the hierarchy is being established. Further research is required to assess this.

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