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Analysis of the phenotypic link between behavioural traits at mixing and increased long-term social stability in group-housed pigs

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1 Abstract

2 Mixing of growing pigs results in aggressive contests between group members. As
3 aggression serves to establish dominance relationships, it is possible that increased initial
4 aggression may facilitate the formation of social hierarchies. The objective of the study was to
5 investigate whether there is a phenotypic link between behavioural traits of aggression at
6 mixing and increased long-term group social stability. Aggressive behavioural traits were
7 recorded for 24 hours after mixing, whereas the numbers of skin lesions (anterior, central and
8 posterior) were obtained 24 hours (SL24h) and 3 weeks post-mixing (SL3wk) for 1,166 pigs. At
9 the group level, aggressive behavioural traits were positively correlated with anterior SL24h
10 (0.34 to 0.67; $P < 0.01$) at mixing, and negatively with central SL3wk (-0.28 to -0.38; $P < 0.01$) in
11 the stable group. At the individual animal level, most behavioural traits of aggressiveness
12 correlated positively with SL24h (0.09 to 0.53; $P < 0.001$), whereas the opposite associations
13 were found for SL3wk (-0.06 to -0.14; $P < 0.05$). Within aggressive cohorts, animals with a high
14 fight success rate received slightly fewer SL24h than equally aggressive, but unsuccessful pen
15 mates, while animals that avoided aggression received the fewest SL24h. Corresponding
16 associations were reversed in the stable group. These results provide evidence that increased
17 aggression at mixing may aid stable hierarchy formation. This raises an ethical dilemma in pigs
18 production, but potentially also in other species, that increased acute aggression during mixing
19 may actually decrease chronic aggression in groups and thus benefit the long term welfare of
20 the group.

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- 28 Keywords: aggressive behaviour; long-term social behaviour; mixing aggression; pigs, skin
- 29 lesions

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30 1. Introduction

31 Repeated mixing of livestock species that adopt social systems characterised by
32 dominance hierarchies disrupts social relationships and results in aggressive contests between
33 group members. This kind of aggressive behaviour serves to establish dominance hierarchies
34 (Meese & Ewbank, 1973) but may be associated with high stress and injury levels, especially in
35 pigs, where the costs of aggression can be particularly significant. These effects make social
36 aggression a known welfare and economic concern in pig production, affecting growth,
37 reproduction, and carcass quality (Faucitano, 2001; Marchant et al., 1995; Stookey & Gonyou,
38 1994). As well as the physical and metabolic demands of prolonged fighting, an uncertain
39 hierarchy position may be stressful to individuals (DeVries et al., 2003). In pigs, individuals that
40 were involved in aggression upon mixing but only achieved moderate fight success have been
41 shown to have higher baseline salivary cortisol levels than bottom and top ranking group
42 members (Coutellier et al., 2007; Mendl et al., 1992) implying that these animals may feel more
43 stressed than their subordinates. Methods of reducing aggression have been studied for over 30
44 years (Fraser 1984); however to date no practical, socially acceptable, low cost, high impact
45 solution has been found.

46

47 Physical aggression between pigs can cause injuries in the form of skin lesions. Lesions
48 to the anterior and central regions of the body have been shown to correspond with the
49 duration of reciprocal fighting, while lesions to the posterior region of the body are associated
50 with the receipt of non-reciprocal bullying (Turner et al., 2006^a). The number of lesions has
51 been found to moderately correlate with the duration of time spent engaged in aggression, and
52 combining the location and number of skin lesions has been shown to be a useful proxy
53 measure of aggression (Turner et al., 2006^a).

54

55 In commercial farming, once pigs are mixed for growing they will usually remain in
56 these groups for several months until regrouped again or marketed. As aggression serves to

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57 establish dominance hierarchies, it is possible that increased aggression upon first mixing may
58 actually lead to more stable dominance relationships in the long-term. Indeed, there is some
59 evidence that initial increased aggression at mixing results in lower aggression and improved
60 productivity over the entire growing-finishing period (Canario et al., 2012; D'Eath, 2005; Turner
61 et al., 2009). If this is the case, aggressiveness at mixing would be essential to improved long
62 term welfare and production.

63

64 Efforts to reduce aggression in commercial pigs either through different management
65 strategies, environmental manipulations, or via genetic improvement are on-going. If reduced
66 aggression in new social groups is found to be detrimental to long-term group stability, then it
67 will be important to quantify any continual welfare or production concerns that arise as a
68 consequence of reducing mixing aggression. Although this study focuses on pigs due to the costs
69 of aggression in this species, the existence of a trade-off between acute aggression at mixing and
70 subsequent chronic aggression may have implications for other species reliant upon dominance
71 relationships.

72

73 Many pig aggression studies use information taken from small group sizes or staged
74 interactions between individuals. Often they focus on one aspect of aggression, for example the
75 effects of body weight or previous fight success (Andersen et al. , 2000; Francis, Christisonl, &
76 Cymbaluk, 1996) . This study utilises a dataset comprised of extremely detailed behavioural
77 observations taken from more than 1,100 animals under commercially relevant conditions after
78 24 hours post mixing. This has provided an opportunity to study the behavioural repertoire of
79 the pig when placed in an unstable social environment, with no human interference. These
80 behavioural traits were compared to skin lesions at mixing (SL24h) and in the social stable
81 group (SL3wk).

82

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83 This study investigated whether there is a phenotypic link between aggression at mixing
84 and increased long-term group stability in the form of reduced skin lesions, and if so, to identify
85 mixing behaviours that improve long-term social behaviour. In particular it was of interest to
86 identify specific behaviours associated with skin lesions at mixing and three weeks post mixing.
87

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88 2. Methods

89 2.1. Animals and housing

90 The study comprised 1,166 pigs on a commercial farm in Ransta, Sweden, between
91 October 2005 and January 2007. Information gathered on all individuals included pen identity,
92 sex, breed, litter identity, and unique pig identification (ear tag or notch number). Single sex
93 (intact males, castrated males, and females) and single breed (703 purebred Yorkshire and 463
94 crossbred Yorkshire x Landrace) groups of 15 were created by mixing 3 pigs from 5 different
95 litters, resulting in 78 groups. Effort was made to standardise within-pen variation in body
96 weight across groups. Animals were weighed 24 hours post-mixing and showed an average live
97 weight of 27.6 kg ($SD = 5.6$) and an average age of 72 days ($SD = 4.3$). Pigs were housed in 4.0 x
98 3.2 m partially slatted pens (30% slats, 70% lightly bedded solid flooring) with a floor space
99 allowance of 0.85 m² per pig. Pigs were fed dry pelleted food *ad libitum* from a single space
100 feeder and had constant access to water via a nipple drinker.

101

102 2.2. Skin lesion traits

103 Lesions were counted immediately prior to mixing, and again 24 hours post-mixing by a
104 single observer, and were grouped by location on the body: anterior (head, neck, front legs, and
105 shoulders), central (flanks and back), posterior (rump, hind legs, and tail). The pre-mixing
106 lesion count was subtracted from that taken 24 hours post-mixing for each pig. This served to
107 ensure that only those lesions that occurred as a result of mixing aggression (SL24h) were
108 included in all analyses. Recently received lesions were counted again three weeks post-mixing
109 (89.8 days (SL3wk) [$SD = 5.2$]). One uninterrupted scratch was classed as a single lesion,
110 regardless of length or severity. A lesion was considered to be recent if it was vivid red in colour
111 or recently scabbed.

112

113 2.3. Behavioural traits

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114 Groups were video recorded for 24 hours post-mixing. Time, duration (s), and outcome
115 of reciprocal (RA) and non-reciprocal (NRA) aggression were recorded. Reciprocal aggression
116 was defined as a fight that lasted more than one second where both pigs were involved in
117 pushing, head knocking or biting. Non-reciprocal aggression involved the delivery of these
118 behaviours with no retaliation from the receiver. Non-reciprocal aggression could occur as a
119 unique event independent of a reciprocal fight, as a component of a reciprocal fight, or at the
120 end of a reciprocal fight as the loser retreated. In addition, for each fight, observers recorded the
121 duration of time spent engaged in injurious fighting. This is opposed to behaviour such as
122 pushing, head knocking, or chasing, which were not deemed injurious. These basic data were
123 used to derive quantitative aggressive behavioural traits that were used in the statistical
124 analysis in the current study (Table 1). Three observers used time-lapse video equipment to
125 extract the duration of each behavioural bout to the nearest second. Analysis of three 1-hour
126 samples of data showed a significant degree of inter-observer agreement ($r = 0.83$, $P < 0.001$)
127 (Turner et al. 2009).

128

129 *2.4. Characteristics of the data*

130 Skin lesion and behavioural data were available for all 1,166 animals in 78 groups.
131 Animals were mixed with an average growth rate of 881 g/day over an 86 day ($SD = 4$) growth
132 period (Yorkshire: 880 g/day [$SD = 155$]; Yorkshire x Landrace: 881 g/day [$SD = 186$]). The
133 average weight of pigs at the time of mixing was 27 kg (Yorkshire: 27 kg [$SD = 5.1$]; Yorkshire x
134 Landrace: 29 kg [$SD = 5.4$]) and the average weight at the end of the finishing period was 104 kg
135 (Yorkshire: 103 kg [$SD = 11.24$]; Yorkshire x Landrace: 106 kg [$SD = 12.49$]). The characteristics
136 of the data for the variables used in the analyses are presented in Table 2. Negative values for
137 skin lesions at 24 hours post mixing are partly due to observer error and partly due to lesions
138 healing between pre and post mixing lesion number counts. Within further analysis of the data,
139 these negative values were set to zero. The lesion numbers and behavioural traits showed

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140 skewed distributions (Table 2); therefore the data were log transformed ($y = LS + 1$) and the
141 transformed values were used in all subsequent analyses.

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142 2.5. Statistical Analyses

143 To account for systematic influences on behavioural traits and skin lesions, the effects of
144 breed type (purebred Yorkshire, Yorkshire × Landrace), sex (females, males, and castrates) and
145 experimental batch (pigs were mixed on 14 separate days) were fitted as class variables, and
146 body weight as a covariate in the statistical models. The group effect was modelled by including
147 the pen in which the animals were mixed as random effect. The analysis was carried out using
148 the MIXED procedure of SAS (version 9.1). To predict the individual animal associations and to
149 identify the change in aggression of animals over time, Pearson correlations were obtained
150 between the residuals of all behavioural traits and SL24h with SL3wks. Aggression is often
151 discussed in terms of the individual animal, however pigs are housed in social groups, and the
152 welfare of an individual is likely to be greatly affected by the level of social stability within the
153 group in which it is housed. In order to compare group-level associations between behaviour
154 and lesion numbers, correlations between estimates of pen effects were calculated.

155

156 To further explore the relationship between aggression at mixing and skin lesions for
157 individual animals at two time points, a multiple linear regression model was developed that
158 resulted in the best model to predict lesion numbers from a set of behavioural traits. A series of
159 multiple stepwise regression analyses using the REG procedure of SAS (version 9.1) were
160 performed, in which the estimated residuals for lesion and behavioural traits from the initial
161 mixed models for SL24h and SL3wk were set as response variables, and residuals for all
162 behavioural traits were set as predictors. Behaviour traits explaining significant variance in
163 lesion numbers ($P < 0.05$), as predicted by the regression analyses, were included in the final
164 model. Many behavioural traits may be correlated among each other; therefore multicollinearity
165 between behavioural variables included in the final model was estimated using variance
166 inflation factors (VIF); however no VIF were above 1.38, suggesting that multicollinearity was
167 not a concern. Using residuals of behavioural traits, the final model produced regression

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168 coefficients that predicted how various behaviours influenced lesion numbers at both time
169 points, independent of systematic effects described above.
170

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171 3. Results

172 There were large variations among pen group means of SL24h, suggesting that groups
173 differed significantly in levels of aggression. There was less variation among pen group means
174 for SL3wk than SL24h. However the averages of all pen group means for SL24h were similar to
175 SL3wk at the centre or posterior of the body but not for those observed at the anterior area
176 (Table 3). The distribution of pen group means of skin lesions was approximately normal, as
177 assessed by the skewness and kurtosis (Table 3), with the exception of posterior SL24h, which
178 was slightly negatively skewed.

179

180 3.1. Fixed and random effects on skin lesions

181 Batch and breed type*sex were included in the mixed models as fixed class effects while body
182 weight at mixing was included as a covariate. Batch effects were statistically significant for
183 almost all lesion traits except for anterior and central SL24h (posterior SL24h: $F = 8.59$; $P <$
184 0.001 ; anterior SL3wk: $F = 5.25$, $P < 0.001$; central SL3wk: $F = 7.70$; $P < 0.001$; posterior SL3wk:
185 $F = 5.72$, $P < 0.001$). Breed type*sex affected anterior and central SL3wk (anterior $F = 5.25$; $P <$
186 0.001 ; central $F = 3.12$; $P = 0.014$). Cross bred females received significantly fewer anterior and
187 central SL3wk ($P < 0.05$) than purebred females. Anterior and posterior SL24h showed
188 significant regression coefficients ($P < 0.001$ and $P = 0.046$) on body weight at mixing.

189

190 3.2. Lesion numbers

191 The proportions of the phenotypic variance attributed to pen effects were significant (P
192 < 0.05) in the range from 4 to 12% and 3 to 21% for skin lesions (on the diagonal of Table 4)
193 and most behavioural traits, respectively (Table 5).

194 On the pen group level, lesions across body regions at the same time point were
195 positively correlated (SL24h: 0.28 to 0.77; $P < 0.01$, SL3wk: 0.65 to 0.75; $P < 0.001$). Between
196 time points, anterior or central pen group SL24h were positively correlated with anterior or
197 central SL3wk (0.24 to 0.36; $P < 0.05$). Lesions to the central region of the body were also

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198 positively correlated on a pen group level across time points (0.24; $P < 0.05$) (above diagonal,
199 Table 4).

200 At the individual animal level, lesions across body regions recorded at the same time
201 point were positively correlated for both SL24h (0.38 to 0.54; $P < 0.001$), and SL3wk (0.50 to
202 0.65; $P < 0.001$). Between these time points, there were significant but small positive
203 correlations between central (0.07; $P < 0.05$) or posterior (0.07; $P < 0.05$) SL24h and anterior
204 SL3wk. In contrast, there was a small negative but significant correlation between anterior
205 SL24h and central SL3wk (-0.06; $P < 0.05$) (below diagonal, Table 4).

206

207 *3.3. Correlations between behavioural and lesion traits on group (pen) level*

208 Between pen groups correlations of behavioural with lesion traits are presented in
209 Table 5. The aggressive behavioural traits showed mostly significant positive correlations with
210 SL24h (0.23 to 0.61; $P < 0.05$), except for the trait proportion of injurious fights, which was
211 negatively correlated with the posterior region at 24 hours (-0.27; $P < 0.01$). In contrast,
212 significant correlations of behavioural traits with SL3wk were consistently negative (-0.23 to -
213 0.33; $P < 0.05$). Between pen groups, behavioural traits were primarily associated with skin
214 lesions to the anterior regions of the body at 24 hours post-mixing, and to the central region of
215 the body at 3 weeks post mixing. In addition, most significant correlations were found for
216 behavioural traits that were defined as reciprocal aggression, with the exception of total non-
217 reciprocal aggression received (0.24; $P < 0.05$) which positively correlated with the posterior
218 SL24h, and duration of non-reciprocal aggression received, which positively correlated with
219 central (0.23; $P < 0.05$) and posterior (0.23; $P < 0.05$) SL24h (Table 5). A summary of the main
220 correlations found between pen groups is presented in Figure 1.

221

222 *3.4. Correlations between behavioural and lesion traits on individual animal level*

223 Under unstable social conditions at mixing, all behavioural traits included in the analysis
224 showed positive correlations with anterior SL24h (0.13 to 0.56; $P < 0.001$) (Table 6). Except for

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225 the behavioural traits proportion of fights won, all other analysed behavioural traits were
226 positively correlated with central SL24h (0.08 to 0.33; $P < 0.01$) but mostly at a lower
227 magnitude than those of anterior lesions. Even lower correlations were calculated between
228 behavioural traits and posterior SL24h (0.06 to 0.22; $P < 0.05$). The direction of these
229 correlations indicates that individuals that are involved in more aggression at mixing received
230 more SL24h, in particular to the anterior body region. A summary of the main correlations
231 found on individual animal level is presented in Figure 2.

232

233 Many measures of aggressive behaviours at mixing correlated negatively with anterior
234 and central SL3wk but at a lower magnitude than at those found at 24 hours (-0.07 to -0.18; $P <$
235 0.05). The behavioural traits number of RA involved with, the duration of RA and NRA initiated,
236 and the average fight duration, showed the largest negative correlation with central SL3wk. The
237 behavioural traits total NRA received, number of pen mates bullied by, and the proportion of
238 fights with an ambiguous outcome were not associated with the number of anterior or central
239 SL3wk. The duration of NRA received was negatively associated with central but not anterior or
240 posterior SL3wk (Table 6).

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241 3.5. Best model for prediction of lesion numbers

242 Of all skin lesion traits, anterior SL24h showed the highest predictability by behavioural
243 traits of aggression ($R^2 = 0.36$) (Table 7). Central SL24h were affected by the highest number of
244 behavioural traits. As found with the residual correlations, the regression model predicted a
245 positive association between behavioural traits of aggression at mixing and SL24h, with the
246 exception of the trait proportion of fights won, which was associated with slightly fewer central
247 ($P < 0.001$) and posterior ($P = 0.015$) SL24h. At three weeks, only lesions to the central region of
248 the body could be predicted by behavioural traits of aggression at mixing, however the R^2 value
249 was low. The model predicted a negative association between traits of aggression, with the
250 exception of the duration of NRA received, which was associated with slightly more SL3wk ($P <$
251 0.001) (Table 7).

252

253 Almost all behavioural traits included in all prediction models were significantly and
254 positively correlated with each other (0.06 to 0.93; $P < 0.05$). The proportion of fights won was
255 slightly negatively correlated with the total number of NRA received (-0.10; $P < 0.001$) and the
256 duration of NRA received (-0.10; $P < 0.001$). There was no statistically significant correlation
257 between the average duration of RA and NRA involved with and total number of NRA received
258 (Table 8). However, highly correlated behavioural traits were not selected for each prediction
259 model by the stepwise regression analysis so that multicollinearity was not a concern.

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260 4. Discussion

261 4.1. Behaviour and skin lesions on group level

262 Aggression can be defined at the level of individuals or at a group level. Numbers of
263 lesions have been previously validated as a method of measuring the aggressiveness of
264 individual pigs at mixing (Turner et al., 2006^a) but not as a measure of aggression across entire
265 groups. The current data set was an ideal opportunity to study the group level basis to skin
266 lesions. The direction of the correlations indicates that increased group level involvement in
267 reciprocal aggression, involving more pen mates, resulted in higher average anterior SL24h.
268 Pen level correlations between aggression and lesions at mixing suggest that skin lesions are a
269 useful measure of reciprocal aggression at mixing within a group, but only for anterior regions,
270 which have previously been linked to reciprocal aggression in individuals (Turner et al., 2008).

271

272 At the group level, behavioural variables that were positively associated with anterior
273 SL24h were negatively associated with SL3wk; however this relationship was mainly significant
274 for the central body region only. The vigorous, reciprocal aggression that accounts for many
275 anterior lesions at mixing does not often occur in stable groups. Instead, aggression in stable
276 groups is primarily seen in the form of head knocks and bites, often over a resource (Bolhuis et
277 al., 2005), which could explain why a relationship was mainly found for the central region of the
278 body.

279

280 Very few traits related to non-reciprocal aggression were associated with skin lesions
281 on a group level, suggesting that skin lesions are not a useful measure of the amount of non-
282 reciprocal aggression a group has been involved in. The majority of behaviour at mixing related
283 to anterior SL24h on a group level, whereas lesions from non-reciprocal aggression are more
284 likely to be inflicted to the centre and posterior region of the body as the recipient is often
285 turned away from the attacker, as it attempts to escape. This is reflected in the group level

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286 correlations, as the number and duration of non-reciprocal aggression received were positively
287 correlated with central and posterior SL24h.

288

289 If increased aggression at mixing increases social stability, it would be expected that
290 SL3wks relates to the quality of aggression performed. For example if many fights within a
291 group have definitive outcomes and are rarely repeated, the individuals involved might be more
292 certain of their social position, resulting in a more stable hierarchy. There was little evidence of
293 this in the current study, as skin lesions at SL3wk did not relate to the proportion of repeated
294 fights, fight intensity or ambiguous outcomes at mixing. Groups with a high proportion of
295 successful fights (proportion of fights won) tended to have low SL3wks. Correlations between
296 behavioural traits (results not presented) indicate that groups with a high proportion of fights
297 success also had a large number of unambiguous, intense fights. It is possible that social
298 relationships are influenced by a combination of traits related to fight quality although
299 individual traits do not correlate with skin lesions when considered in isolation.

300

301 Negative correlations between reciprocal aggression at mixing and SL3wk offer some
302 support for the hypothesis that increased initial reciprocal aggression on a group level reduces
303 aggression in the long term. Reduced aggression at three weeks could indicate a more stable
304 social hierarchy. If this was the case, it could be that certain fighting experiences, in particular
305 those related to reciprocal aggression, lead to less ambiguity over hierarchy positions, resulting
306 in fewer conflicts over resources.

307

308 *4.2. Behaviour and skin lesions on individual animal level*

309 At the individual animal level, residual correlations between aggressive behavioural
310 variables and SL24h indicate that an increase in almost all measures of aggression at mixing
311 results in more skin lesions across all three body regions. Lesions to the anterior body region
312 have previously been shown to be associated with reciprocal fighting, and the posterior and

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313 central regions of the body associated with receipt of non-reciprocal aggression (Turner et al.,
314 2006^a).

315

316 A multiple regression model was developed in the current study in order to further
317 dissect the relationship between various aggressive strategies and the receipt of lesion
318 numbers. As predicted by residual correlations, a general increase in aggression - for example
319 long reciprocal fights - predicted higher lesions across all body regions 24h after mixing. Fight
320 success (proportion of fights won) predicted fewer SL24h to central and posterior body regions
321 when included in the model. This is likely to be because unsuccessful pigs receive more non-
322 reciprocal aggression, resulting in slightly more lesions than their successful pen mates.

323 Although the receipt of non-reciprocal aggression was weakly negatively correlated with fight
324 success, the number and duration of non-reciprocal aggression received were positively
325 associated with other measures of aggression, including the number of reciprocal interactions
326 involved in and the number of pen mates bullied. Combined, these results suggest that while
327 increased aggression of all descriptions increases the risk of receiving skin lesions, within this
328 more aggressive cohort, the animals with a high fight success rate receive fewer skin lesions
329 than their less successful but aggressive pen mates. Animals that avoid involvement in
330 aggression altogether receive the lowest skin lesions at this time.

331

332 Correlations between aggressive behaviour at mixing and skin lesions recorded three
333 weeks post-mixing were lower than those calculated for skin lesions 24 hours post mixing. As
334 described earlier, aggression at mixing and in established groups tends to differ in its form and
335 motivation, lacking the intense reciprocal aggression that constitutes the majority of aggressive
336 behaviour at mixing (Bolhuis et al., 2005; Fraser, 1984). A strong correlation between the two
337 traits was therefore not to be expected. Despite this, many measures of aggression were
338 negatively correlated with SL3wk, indicating that the more aggression an individual is involved
339 in at mixing, the fewer lesions it receives under stable social conditions, particularly to the

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340 anterior and central regions of the body. As found for associations with SL24h, behavioural
341 correlations with the posterior region of the body 3 weeks post mixing were lower than those
342 obtained for the anterior and central regions, resulting in extremely low correlations for this
343 body region at that time point. This pattern indicates that posterior lesions are not as
344 informative as lesions to the anterior body region. This may be because lesions are typically
345 inflicted to the rear of the body during the receipt of aggression, and are therefore not a
346 reflection of an individual's own behaviour, but rather that of its pen mates.

347

348 Behavioural traits accounted for very little variation in SL3wk, as predicted by the
349 multiple regression models. The models predicted that the proportion of fights won at mixing
350 accounted for most of the variation in central SL3wk, with the most successful animals receiving
351 the fewest lesions at this time. This implies that skin lesions in stable groups are chiefly related
352 to dominance, as it is likely that the most successful animals at mixing go on to achieve the
353 highest-ranking positions in stable groups. As reflected by the correlations on individual animal
354 level, the model predicted that an increase in the duration of non-reciprocal attacks received at
355 mixing was associated with slightly increased central SL3wk. The duration of non-reciprocal
356 attacks received was positively correlated with number and duration of non-reciprocal attacks
357 initiated, and the duration of reciprocal aggression involved in. Therefore the animals that
358 received much aggression were also actively involved in aggression. This finding reflects those
359 found in a previous study involving a different population (Turner et al., 2006^a). These results
360 demonstrate that non-reciprocal aggression at mixing is not received by the unaggressive
361 individuals in a group, but rather aggressive but unsuccessful animals, possibly as a means to
362 reinforce a fight outcome.

363

364 The results from the correlations and mixed model predictions indicate that while high
365 fight success at mixing results in the lowest stable lesions, involvement in aggression at mixing,
366 even when unsuccessful, leads to fewer lesions in the stable group than animals which avoid

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367 aggression at mixing altogether. The simplest explanation is that pigs which avoid aggression
368 are simply the most subordinate individuals; however this does not explain the observations
369 made on a pen group level. It could be that simply engaging in aggression leads to less
370 ambiguity over social standing, resulting in fewer challenges to hierarchy positions.
371 Alternatively, it is possible that experience in physical aggression is necessary in learning to
372 convey both dominant and submissive behaviours. Studies involving repeated mixing of pigs
373 (Coutellier et al., 2007; Giersing & Andersson, 1998) have shown that the amount of aggression
374 displayed reduces with increased mixing, whereas D'Eath (2005) found that early socialising of
375 piglets leads to faster hierarchy formation. Frischknecht et al., (1982) demonstrated how mice
376 that had experience of being defeated displayed significantly more submissive behaviours than
377 those that had never experienced agonistic interactions. In the present study, pen group lesions
378 at three weeks were negatively associated with traits related to reciprocal fighting. If important
379 social skills are learned via fighting experience, this may explain why we see more social
380 stability in groups that involved more reciprocal aggression between more group members.
381

382 Social instability in the form of long-term aggression may be caused by several factors. It is
383 possible that groups with increased aggression 3 weeks post mixing have a less stable hierarchy
384 than other groups, and therefore frequent physical aggression is required in order to re-
385 establish or maintain dominance relationships. Alternatively, it may be that some individuals
386 fail to recognise dominance relationships, or continue to fight at inappropriate times. As no
387 behavioural data were available three weeks post-mixing, the stability of dominance
388 relationships could not be assessed. As such, it is impossible to deduce whether long-term social
389 instability was the result of unstable dominance relationships or socially dysfunctional
390 individuals within a group.
391

392 The results of these analyses confirm that skin lesions are a useful alternative measure of
393 aggressiveness displayed by individual pigs in the first 24 hours post mixing. While increased

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394 aggression at mixing leads to more injuries at first, it may be beneficial for the individual in the
395 long term, even if the animal is not successful at fighting.

396

397 *4.3. Lesion correlations*

398 Lesions across body regions at the same time point were positively correlated meaning
399 that animals that received high lesions to one region of the body were likely to receive lesions to
400 other body regions. This is in accordance with the findings from the behavioural data in which
401 animals that engage in a high amount of aggression of any form receive many lesions to all body
402 regions.

403

404 Individuals that received high central and posterior SL24h were also somewhat likely to
405 receive high anterior and central SL3wk, although the correlations were of a very low
406 magnitude. These results appear to conflict with the direction of the correlations between
407 aggression at mixing and SL3wk. Although this seems counterintuitive at first, the correlations
408 between skin lesion traits are low, and contradicting correlations can occur due to the various
409 effects that influence the correlations. It can be hypothesised that the contradictory relationship
410 between aggressive behaviour and lesions at different time points may contribute to the
411 reduced correlations between lesions at mixing and the stable group.

412

413 Genetic correlations using the same population showed a moderate to strong positive
414 correlation between SL24h and SL3wk (Turner, 2009); however the same study also found
415 negative residual correlations between these traits. This relationship was also observed on a
416 group level, although the correlations were of a higher magnitude than those observed for
417 individuals.

5. Conclusions

Research into reducing aggression via a combination of genetic and management strategies are on-going. Phenotypic correlations such as those explored in the present study offer some evidence that within groups of mixed aggression levels, increased reciprocal aggression may be beneficial to long term group dynamics. It may prove challenging to identify any single management strategy that will simultaneously reduce both mixing-induced aggression and on-going chronic aggression. In contrast, genetic correlations (Turner et al., 2009) and experiments in which animals were grouped according to aggressive personalities (Erhard et al., 1997) support the theory that reducing the level of aggression displayed by individuals may result in reduced long term aggression. The environment (O'Connell & Beattie, 1999), group size (Andersen et al, 2004; Hemsworth et al., 2014), genetics (Canario et al., 2012; Turner et al., 2006b; Turner et al., 2009), early life experience (D'Eath, 2005) and prenatal stress (Jarvis et al., 2006) have all been shown to affect social aggression in pigs. Further work is clearly required to disentangle these factors in order to better predict the possible consequences on aggression. In terms of genetic strategies to control aggression in pigs, this study raises the interesting question that selection for reduced aggression at mixing could result in increased levels of chronic aggression. Further studies should seek to calculate the genetic correlation between metrics of aggression at mixing and then during the stable state to uncover the genetic architecture of these two distinct traits.

The current study cannot address the question of whether skin lesions at three weeks not only relate to aggression, but that increased aggression in stable groups translates to poor welfare. Published studies examining the long term effects of social stress (usually by measuring cortisol or immune responses) have produced conflicting results (Blanchard et al., 1993; Mendl et al., 1992; Tuchscherer et al., 1998; Ekkel et al., 1997). In the present study, SL3wk were similar in number to SL24h for central and posterior lesions, indicating a comparable level of aggression at the two time points. It could be argued that dominance relationships are a part of the pig's

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natural behaviour and therefore individuals should be equipped to deal with the stress that arises from these encounters. However in space-restricted pens animals are often unable to adequately avoid persistent attacks (Fraser et al., 1995).

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Tables

Table 1. Definitions of skin lesion traits and behavioural traits used in the analyses

| Trait | Description |
|---|---|
| Skin lesions at 24 hours (SL24h) | Number of skin lesions counted 24 hours post mixing |
| Skin lesions at three weeks (SL3wk) | Number of skin lesions counted 3 weeks post mixing (stable groups) |
| Reciprocal aggression (RA) | A fight lasting >1s in which the recipient of the attack retaliated |
| Non-reciprocal aggression (NRA) | An attack in which the recipient did not retaliate |
| RA involved with | Total number of reciprocal fights the focal pig was involved with, regardless of which pig initiated the attack |
| NRA involved with | Total number of non-reciprocal fights the focal pig was involved with, regardless of which pig initiated the attack |
| Total RA initiated/received | The total number of times an individual initiated or was the recipient of an attack which was reciprocated |
| Total NRA initiated/received | The total number of times an individual initiated or was the recipient of an attack which was not-reciprocated |
| Number of pen mates focal pig attacked (RA) | The number of pen mates the focal pig attacked in which the attack was reciprocated |
| Number of pigs attacked by (RA) | The number of pen mates the focal pig was attacked by which the focal pig retaliated against |
| Number of pen mates focal pig bullied | The number of pen mates the focal pig attacked which did not reciprocate |
| Number of pen mates bullied by | The number of pen mates the focal pig was attacked by which it did not reciprocate against |

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| Trait | Description |
|--|---|
| Pen mates involved with | Total number of pen mates with which the focal pig had any aggressive interactions |
| Average duration RA & NRA involved (s) | Average duration of all aggressive encounters in which the focal pig was involved |
| Duration of RA initiated (s) | Duration of time spent in RA in which the focal pig was the initiator |
| Duration of RA received (s) | Duration of time spent in RA in which the focal pig was the recipient of the attack |
| Duration of NRA initiated (s) | Duration of time spent in NRA in which the focal pig was the initiator |
| Duration of NRA received (s) | Duration of time spent in NRA in which the focal pig was the recipient of the attack |
| Proportion of fights won | Proportion of all reciprocal fights which the focal pig won |
| Proportion of repeated fights | Proportion of all pen mates fought with which the focal pig had more than one aggressive interaction |
| Proportion with ambiguous outcome | Proportion of reciprocal fights the focal pig was involved with in which the winner could not be determined |
| Proportion injurious RA involved with | Proportion of time the focal pig spent in reciprocal fights engaged in what was deemed to be injurious fighting |

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Table 2. Characteristics of behavioural and skin lesion data for individual animals included in the statistical analysis (SK = skewness; K = kurtosis)

| <i>Trait</i> | Original scale | | | | | Log transformed scale | | | |
|---|-----------------------|----------------|------------------|-----------|----------|------------------------------|-----------|-----------|----------|
| | <i>N</i> | <i>Min-Max</i> | <i>Mean (SD)</i> | <i>SK</i> | <i>K</i> | <i>Mean</i> | <i>SD</i> | <i>SK</i> | <i>K</i> |
| Anterior SL24h | 1166 | -17 to 99 | 18.84 (17.32) | 1.38 | 2.31 | 2.56 | 1.09 | -0.88 | 0.34 |
| Central SL24h | 1166 | -30 to 100 | 10.71 (12.02) | 1.42 | 5.99 | 2.05 | 1.10 | -0.63 | -0.55 |
| Posterior SL24h | 1166 | -42 to 41 | 3.70 (8.26) | -0.72 | 4.12 | 1.36 | 1.02 | -0.11 | -1.30 |
| Anterior SL3wk | 1166 | 0 - 63 | 10.4 (5.63) | 1.57 | 8.67 | 2.30 | -1.13 | -1.13 | 2.60 |
| Central SL3wk | 1166 | 0 - 40 | 10.35 (5.94) | 1.03 | 1.86 | 2.28 | 0.6 | -0.93 | 1.58 |
| Posterior SL3wk | 1166 | 0 - 30 | 4.51 (3.51) | 1.21 | 3.07 | 1.48 | 0.71 | -0.51 | -0.35 |
| RA involved with | 1166 | 0 - 56 | 8.36 (7.14) | 1.37 | 3.05 | 1.90 | 0.90 | -0.58 | -0.38 |
| NRA involved with | 1166 | 0 - 69 | 7.65 (6.95) | 2.86 | 15.27 | 1.89 | 0.75 | -0.29 | 0.23 |
| Total RA initiated | 1166 | 0 - 36 | 4.19 (4.29) | 1.76 | 4.99 | 1.32 | 0.85 | -0.13 | -0.90 |
| Total RA received | 1166 | 0 - 25 | 4.17 (3.77) | 1.44 | 3.06 | 1.36 | 0.79 | -0.31 | -0.74 |
| Total NRA initiated | 1166 | 0 - 66 | 3.84 (5.54) | 3.84 | 25.9 | 1.14 | 0.91 | 0.33 | -0.70 |
| Total NRA received | 1166 | 0 - 25 | 3.81 (3.17) | 1.57 | 3.89 | 1.36 | 0.67 | -0.26 | -0.28 |
| Number of pen mates focal pig attacked (RA) | 1166 | 0 - 11 | 2.84 (2.32) | 0.66 | -0.19 | 1.13 | 0.69 | -0.38 | -0.96 |
| Number of pigs attacked by (RA) | 1166 | 0 - 9 | 2.84 (2.06) | 2.06 | -0.52 | 1.17 | 0.64 | -0.57 | -0.69 |
| Number of pen mates focal pig bullied | 1166 | 0 - 14 | 2.56 (2.68) | 1.32 | 1.55 | 0.99 | 0.75 | 0.06 | -1.10 |
| Number of pen mates focal pig bullied by | 1166 | 0 - 9 | 2.56 (1.67) | 1.67 | 0.09 | 1.15 | 0.52 | -0.56 | -0.10 |
| Pen mates involved with | 1166 | 0 - 14 | 6.67 (3.06) | 0.02 | -0.67 | 1.94 | 0.49 | -1.12 | 1.43 |
| Average duration of NA & NRA involved (s) | 1159 | 1 - 249 | 42.48 (27.82) | 2.04 | 8.33 | 3.58 | 0.64 | -0.38 | 0.45 |
| Duration of RA initiated | 1166 | 0 - 2394 | 286.26 (364.26) | 2.09 | 5.41 | 4.27 | 2.34 | -0.87 | -0.56 |
| Duration of RA received | 1166 | 0 - 2997 | 326.45 (351.62) | 2.09 | 6.68 | 5.08 | 1.46 | -1.09 | 1.49 |
| Duration of NRA received | 1166 | 0 - 996 | 41.61 (68.46) | 2.87 | 13.79 | 3.11 | 1.34 | -0.88 | 0.32 |
| Duration of NRA initiated | 1166 | 0 - 444 | 41.29 (46.46) | 4.63 | 40.84 | 2.52 | 1.82 | -0.19 | -1.27 |
| Proportion of fights won | 1066 | 0 - 1 | 0.30 (0.25) | 0.57 | -0.22 | 0.25 | 0.19 | 0.22 | -0.82 |
| Proportion of repeated fights | 1159 | 0 - 1 | 0.50 (0.25) | -0.34 | -0.35 | 0.39 | 0.18 | -0.74 | 0.02 |
| Proportion with ambiguous outcome | 1066 | 0 - 1 | 0.27 (0.24) | 0.87 | 0.67 | 0.22 | 0.18 | 0.44 | -0.37 |
| Proportion injurious | 1156 | 0 - 1 | 0.59 (0.24) | -1.07 | 0.76 | 0.45 | 0.17 | -1.46 | 1.66 |

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Table 3. Variations between 10% lowest and highest in pen group means for lesion numbers (SL24h = lesion numbers at 24 hours post mixing, SL3wk = lesion numbers 3 weeks post mixing. SK = skewness, K = kurtosis).

| Trait | Lowest 10% in group means | Average over all group means (SD) | Highest 10 % in group means | SK | K |
|--------------|--|--|--|-----------|----------|
| SL24h | | | | | |
| Anterior | 8.07 | 18.82 (6.65) | 32.68 | 0.80 | 2.54 |
| Central | 2.91 | 10.71 (5.39) | 21.43 | 0.70 | -0.09 |
| Posterior | -9.66 | 3.69 (5.79) | 10.87 | -1.91 | 4.93 |
| SL3wk | | | | | |
| Anterior | 6.77 | 10.40 (2.21) | 14.34 | -0.53 | 0.02 |
| Central | 6.28 | 10.34 (2.58) | 15.37 | -0.64 | 0.86 |
| Posterior | 1.79 | 4.51 (1.62) | 7.46 | -0.85 | 0.86 |

Running head: Long-term Social Stability

Table 4. Phenotypic proportions of skin lesion number (SL) variance attributable to pen group effects (on diagonal in bold) and the correlation between pen group effects (above diagonal), and individual animal (residual^a) correlations (below diagonal) between lesion numbers recorded 24 hours post mixing and three weeks post mixing.

| Trait | SL24h | | | SL3wk | | |
|--------------|----------------|-----------------|-----------------|---------------|-----------------|----------------|
| | Anterior | Central | Posterior | Anterior | Central | Posterior |
| SL24h | | | | | | |
| Anterior | 0.08 ** | 0.45 *** | 0.28 ** | -0.07 | -0.09 | 0.06 |
| Central | 0.53 *** | 0.11 *** | 0.77 *** | 0.20 | 0.24 * | 0.11 |
| Posterior | 0.38 *** | 0.54 *** | 0.12 *** | 0.36 *** | 0.32 ** | 0.19 |
| SL3wk | | | | | | |
| Anterior | -0.00 | 0.07 * | 0.07 * | 0.04 * | 0.65 *** | 0.69 *** |
| Central | -0.06 * | 0.00 | 0.01 | 0.65 *** | 0.09 *** | 0.75 *** |
| Posterior | -0.02 | 0.01 | 0.04 | 0.50 *** | 0.58 *** | 0.07 ** |

^a Residual correlation after accounting for all systematic effects and the group (pen) effects.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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Table 5. Phenotypic proportions of behavioural variance attributed to pen group effects (column 1), and correlations of estimates of pen group effects between aggressive behaviour and skin lesion numbers recorded 24 hours (SL24h) and 3 weeks (SL3wk) post-mixing.

| Trait | Proportion of pen | SL24h | | | SL3wk | | |
|---|-------------------|----------|---------|-----------|----------|----------|-----------|
| | | Anterior | Central | Posterior | Anterior | Central | Posterior |
| RA involved with | 0.10 *** | 0.61 *** | -0.04 | -0.19 | -0.21 | -0.33 ** | -0.10 |
| NRA involved with | 0.21 *** | 0.09 | 0.14 | 0.16 | 0.03 | -0.11 | -0.10 |
| Total RA initiated | 0.06 ** | 0.59 *** | -0.01 | -0.17 | -0.23 * | -0.32 ** | -0.10 |
| Total RA received | 0.10 *** | 0.63 *** | -0.03 | -0.18 | -0.22 | -0.33 ** | -0.09 |
| Total NRA initiated | 0.04 * | 0.21 | 0.08 | 0.08 | -0.06 | -0.20 | -0.15 |
| Total NRA received | 0.20 *** | 0.07 | 0.22 | 0.24 * | 0.10 | -0.01 | -0.05 |
| Number of pen mates attacked (RA) | 0.07 ** | 0.58 *** | -0.04 | -0.17 | -0.21 | -0.30 ** | -0.08 |
| Number of pigs attacked by (RA) | 0.10 *** | 0.60 *** | -0.07 | -0.18 | -0.20 | -0.30 ** | -0.07 |
| Number of pen mates focal pig bullied | 0.03 * | 0.23 * | 0.08 | 0.08 | -0.10 | -0.21 | -0.21 |
| Number of pen mates bullied by | 0.15 *** | 0.12 | 0.22 | 0.21 | 0.02 | -0.05 | -0.13 |
| Pen mates involved with | 0.12 *** | 0.41 *** | 0.06 | 0.02 | -0.14 | -0.26 * | -0.20 |
| Average duration of RA & NRA involved (s) | 0.17 *** | 0.37 *** | 0.03 | -0.08 | -0.18 | -0.14 | -0.11 |
| Duration of RA initiated (s) | 0.05 ** | 0.55 *** | 0.01 | -0.12 | -0.18 | -0.26 * | -0.06 |
| Duration of RA received (s) | 0.08 ** | 0.57 *** | 0.10 | 0.01 | -0.24 * | -0.24 * | -0.14 |
| Duration of NRA initiated (s) | 0.03 | 0.21 | 0.08 | 0.07 | -0.10 | -0.21 | -0.23 * |
| Duration of NRA received (s) | 0.13 *** | 0.07 | 0.23 * | 0.23 * | 0.07 | 0.01 | -0.10 |
| Proportion of fights won | 0.03 | 0.23 * | -0.13 | -0.18 | -0.24 * | -0.28 ** | -0.11 |
| Proportion of repeated fights | 0.05 ** | 0.23 * | -0.01 | -0.07 | -0.10 | -0.15 | 0.01 |
| Proportion with ambiguous outcome | 0.11 *** | 0.00 | 0.01 | 0.06 | 0.13 | 0.08 | 0.02 |
| Proportion injurious | 0.07 ** | 0.37 *** | -0.14 | -0.27 ** | -0.12 | -0.09 | 0.10 |

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

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Table 6. Correlations^(a) between estimates of aggressive behaviour and skin lesion numbers recorded 24 hours (SL24h) and 3 weeks (SL3wk) post-mixing at the individual animal level.

| Trait | SL24h | | | SL3wk | | |
|---|----------|----------|-----------|-----------|-----------|-----------|
| | Anterior | Central | Posterior | Anterior | Central | Posterior |
| RA involved with | 0.56 *** | 0.32 *** | 0.20 *** | -0.14 *** | -0.18 *** | -0.08 ** |
| NRA involved with | 0.34 *** | 0.25 *** | 0.15 *** | -0.09 ** | -0.09 ** | -0.05 |
| Total RA initiated | 0.43 *** | 0.22 *** | 0.13 *** | -0.12 *** | -0.14 *** | -0.05 |
| Total RA received | 0.48 *** | 0.29 *** | 0.17 *** | -0.10 *** | -0.16 *** | -0.08 ** |
| Total NRA initiated | 0.28 *** | 0.17 *** | 0.08 ** | -0.12 *** | -0.15 *** | -0.07 * |
| Total NRA received | 0.18 *** | 0.20 *** | 0.18 *** | 0.03 | 0.05 | 0.00 |
| Number of pigs attacked (RA) | 0.50 *** | 0.32 *** | 0.20 *** | -0.11 *** | -0.15 *** | -0.09 ** |
| Number of pigs attacked by (RA) | 0.50 *** | 0.32 *** | 0.20 *** | -0.11 *** | -0.15 *** | -0.09 ** |
| Number of pen mates focal pig bullied | 0.30 *** | 0.19 *** | 0.09 ** | -0.12 *** | -0.16 *** | -0.08 ** |
| Number of pen mates bullied by | 0.21 *** | 0.20 *** | 0.17 *** | 0.03 | 0.04 | -0.02 |
| Pen mates involved with | 0.48 *** | 0.29 *** | 0.17 *** | -0.14 *** | -0.15 *** | -0.09 ** |
| Average duration of RA & NRA involved (s) | 0.48 *** | 0.23 *** | 0.18 *** | -0.07 * | -0.12 *** | -0.09 ** |
| Duration of RA initiated (s) | 0.49 *** | 0.23 *** | 0.14 *** | -0.14 *** | -0.17 *** | -0.07 ** |
| Duration of RA received (s) | 0.54 *** | 0.33 *** | 0.22 *** | -0.10 *** | -0.14 *** | -0.10 *** |
| Duration of NRA initiated (s) | 0.29 *** | 0.17 *** | 0.10 *** | -0.12 *** | -0.17 *** | -0.09 ** |
| Duration of NRA received (s) | 0.23 *** | 0.22 *** | 0.21 *** | 0.04 | 0.08 ** | 0.00 |
| Proportion of fights won | 0.13 *** | -0.05 | -0.07 * | -0.12 *** | -0.13 *** | -0.05 |
| Proportion of repeated fights | 0.35 *** | 0.21 *** | 0.16 *** | -0.08 ** | -0.08 ** | -0.04 |
| Proportion with ambiguous outcome | 0.18 *** | 0.08 ** | 0.06 * | 0.03 | -0.01 | 0.00 |
| Proportion injurious | 0.30 *** | 0.12 *** | 0.08 ** | -0.12 *** | -0.13 *** | -0.03 |

^a Residual correlation after accounting for all systematic effects and the group (pen) effects.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Long-term Social Stability

Table 7. Regression model predicting skin lesions recorded 24 hours (SL24h) and 3 weeks (SL3wk) post-mixing from aggressive behavioural traits based on the individual animal information

| Skin lesions predicted by | <i>P</i> Value | Regression coefficient (SE) | Cumulative <i>R</i> ² (a) |
|---------------------------------------|-------------------|--------------------------------|---|
| SL24h | | | |
| <i>Anterior</i> | | | |
| RA involved with | <0.001 | 0.47 (0.04) | 0.30 |
| Average duration of RA & NRA | | | |
| involved (s) | <0.001 | 0.53 (0.05) | 0.35 |
| Total NRA received | <0.001 | 0.21 (0.04) | 0.36 |
| <i>Central</i> | | | |
| Number of pigs attacked by (RA) | <0.001 | 0.34 (0.07) | 0.08 |
| Total NRA received | <0.001 | 0.30 (0.05) | 0.10 |
| Average duration of RA & NRA | | | |
| involved (s) | <0.001 | 0.32 (0.06) | 0.12 |
| Proportion of fights won | 0.001 | -0.69 (0.17) | 0.13 |
| Number of pen mates focal pig bullied | 0.002 | 0.15 (0.05) | 0.13 |
| <i>Posterior</i> | | | |
| Duration of NRA received (s) | <0.001 | 0.11 (0.02) | 0.04 |
| Average duration of RA & NRA | | | |
| involved (s) | <0.001 | 0.17 (0.06) | 0.05 |
| Proportion of fights won | 0.015 | -0.51 (0.15) | 0.06 |
| RA involved with | <0.001 | 0.15 (0.04) | 0.07 |
| SL3wk | | | |
| <i>Central</i> | | | |
| Duration of NRA initiated (s) | <0.001 | -0.04 (0.01) | 0.02 |
| Duration of NRA received (s) | <0.001 | 0.05 (0.01) | 0.03 |
| Average duration of RA & NRA | <0.001 | -0.11 (0.03) | 0.04 |
| Proportion of fights won | 0.044 | -0.20 (0.10) | 0.05 |

^a For each body region, cumulative *R*² values represent the proportion of the total phenotypic variance explained by the corresponding predictor in addition to predictors listed in previous rows of the table.

Running head: Long-term Social Stability

1 Table 8. Residual correlations between estimates of aggressive behaviours included in final models, as presented in Table 7

| Trait | b | c | d | e | f | g | h |
|--|----------|----------|----------|-----------|----------|-----------|----------|
| a RA involved with | 0.52 *** | 0.19 *** | 0.84 *** | 0.37 *** | 0.65 *** | 0.19 *** | 0.61 *** |
| b Average duration of RA & NRA involved (s) | | 0.01 | 0.46 *** | 0.20 *** | 0.14 *** | 0.13 *** | 0.16 *** |
| c Total NRA received | | | 0.16 *** | -0.10 *** | 0.06 * | 0.88 *** | 0.07 ** |
| d Number of pigs attacked by (RA) | | | | 0.18 *** | 0.49 *** | 0.17 *** | 0.46 *** |
| e Proportion of fights won | | | | | 0.32 *** | -0.10 *** | 0.29 *** |
| f Number of pen mates focal pig bullied | | | | | | 0.07 * | 0.93 *** |
| g Duration of NRA received (s) | | | | | | | 0.07 * |
| h Duration of NRA initiated (s) | | | | | | | |

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3 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

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