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1 **Prediction of reduction in aggressive behaviour of growing pigs using skin**
2 **lesion traits as selection criteria**

3

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26 **Abstract**

27 Aggression at regrouping is a common issue in pig farming. Skin lesions are
28 genetically and phenotypically correlated with aggression and have been shown to
29 have a significant heritable component. This study predicts the magnitude of
30 reduction in complex aggressive behavioural traits when using lesion numbers on
31 different body regions at two different time points as selection criteria, to identify the
32 optimum skin lesion trait for selection purposes. 1,146 pigs were mixed into new
33 social groups, and skin lesions were counted 24 hours (SL24h) and 3 weeks
34 (SL3wk) post-mixing, on the anterior, centre and posterior regions of the body. An
35 animal model was used to estimate genetic parameters for skin lesion traits and 14
36 aggressive behavioural traits. Estimated breeding values (EBVs) and phenotypic
37 values were scaled and standardized to allow direct comparison across multiple
38 traits. For each body region, individuals with SL24h and SL3wk EBVs in the least
39 aggressive 10% of the population and compared to the population mean to predict
40 the expected genetic and phenotypic response in aggressive behaviour to selection.
41 At mixing, selection for low anterior lesions was predicted to affect substantially more
42 behavioural traits of aggressiveness than lesions obtained on other body parts, with
43 EBVs between -0.21 and -1.17 SD below the population mean. Individuals with low
44 central SL24h EBVs also had low EBVs for aggressive traits (-0.33 to -0.55). Three
45 weeks later, individuals with high SL3wk EBVs had low EBVs for aggression at
46 mixing (between -0.24 and -0.53 SD below the population mean), although this was
47 predicted to affect fewer traits than selection against SL24h. These results suggest
48 that selection against anterior SL24h would result in the greatest genetic and
49 phenotypic reduction in aggressive behaviour recorded at mixing. Selection for
50 increased SL3wk was predicted to reduce aggression at mixing; however current

51 understanding about aggressive behaviour under stable social conditions is

52 insufficient to recommend using this trait for selection purposes.

53

54 **Keywords:** pigs, aggression, skin lesions, selection, genetics

55

56 **Implications**

57 Pigs fight to establish dominance when mixed into new social groups. This
58 aggressive behaviour affects growth and is a welfare concern. We estimated the
59 effect of selective breeding on aggressive behaviour, using the number of skin
60 lesions (scratches received) on different regions of the body to identify the least
61 aggressive individuals to breed from. The results suggest that selection for reduced
62 skin lesions at the front of the body at 24hrs post-mixing would result in the greatest
63 reduction in aggressive behaviour and is therefore the best selection criterion of all
64 analysed lesion traits to reduce aggressiveness at mixing.

65

66 **Introduction**

67 In indoor commercial farming systems pigs are housed in inflexible group sizes
68 under space-limited conditions. In order to create groups of a predetermined and
69 uniform size, growing pigs are often mixed with unfamiliar individuals throughout the
70 production cycle. Physical aggression usually occurs at mixing, which serves to
71 establish dominance relationships (Meese and Ewbank, 1973). Mixing induced
72 aggression has been associated with stress and injury (Mendl *et al.*, 1992),
73 suppressed immune responses (de Groot *et al.*, 2001), and reduced growth (Stookey
74 and Gonyou, 1994), carcass (Faucitano, 2001) and meat quality (D'Eath *et al.*,
75 2010). Although a number of practical interventions continue to be explored, an
76 under-explored solution to reduce aggression is via genetic selection. This study
77 aimed to examine the best trait to select upon in order to reduce aggressive
78 behaviour.

79

80 Phenotyping aggressive behaviour by direct observation or from video is highly
81 labour intensive; therefore skin lesions - which occur as a result of physical
82 aggression – may constitute valuable proxies for aggressive behaviour (Turner *et al.*,
83 2006; Guy *et al.*, 2009). Skin lesions are genetically and phenotypically correlated
84 with aggression and have been shown to have a significant heritable component
85 (h^2 : 0.08 to 0.43); therefore it is expected that selection against the quantity and body
86 location of skin lesions will result in a corresponding reduction in aggression (Turner
87 *et al.*, 2009; Desire *et al.*, 2015a).

88

89 Deciding how skin lesions should be used to select against aggression requires
90 understanding of the complex relationship between skin lesions and aggressive

91 behaviour. Skin lesions on one animal can be an indication of the behaviour of other
92 members of the social group (via an unreciprocated attack), as well as the individual
93 in question (via willing involvement in aggression). Failing to distinguish between the
94 underlying causes of lesions may lead to biased estimates of individual aggression.
95 On a phenotypic level, Turner *et al.* (2006) showed that skin lesions to the anterior
96 region of the body are strongly correlated with the proportion of time involved in
97 reciprocal aggression, whereas lesions to the rear of the body indicated a larger
98 proportion of time spent receiving non-reciprocal aggression.

99

100 Previous work suggests this relationship is partly under genetic regulation (Turner *et*
101 *al.*, 2009). In addition to measuring aggression performed immediately post-mixing,
102 skin lesions have been explored as a method of phenotyping aggression
103 experienced under socially stable conditions (several weeks post-mixing). Studies on
104 both on a phenotypic (Desire *et al.*, 2015a) and genetic (Turner *et al.*, 2009) level
105 have found that individuals involved in much aggression at mixing tend to have fewer
106 lesions several weeks later. These results suggest that avoidance of aggression
107 upon first mixing may be detrimental to the individual's long term welfare. Finally,
108 genetic variation and heritabilities of skin lesion traits differ between different body
109 regions and time points. In light of the above, it is important to carefully assess the
110 potential impact of selection for reduced aggression via skin lesion traits. Although
111 genetic correlations between skin lesion traits and some aggressive behavioural
112 traits have been previously published (Turner *et al.*, 2009) these correlations do not
113 give an indication of the magnitude of the expected response to selection. In
114 addition, the estimated genetic correlations among skin lesion and behaviour traits
115 are complex, often in conflict with one another, and associated with high errors of

116 estimation. This means that predicting the selection response based on genetic
117 correlations can be difficult. Due to time constraints, only one skin lesion trait is likely
118 to be recorded under practical conditions, therefore it is necessary to identify the
119 single best skin lesion trait for selection. The objective of this study was to identify
120 the optimum skin lesion trait for selection purposes, by determining the magnitude of
121 the reduction in aggressive behavioural traits at mixing, when using lesion numbers
122 recorded on different body regions at mixing and in the stable group as selection
123 criteria.

124 **Materials and methods**

125

126 *Animals and housing*

127 Data were collected from a commercial herd. Three individuals (average age 71
128 days, SD 4.5) taken from each of five litters were mixed to form a new social group
129 of 15 same sex, same breed individuals. Animals with all skin lesion and behavioural
130 phenotypes were included in the analyses, and the final dataset contained 1,146
131 individuals (698 purebred Yorkshire and 448 Yorkshire x Landrace) from 77 social
132 groups. Experimental animals were the progeny of 82 sires and 217 dams, and a 2-
133 generation pedigree was used (total 1,862 animals). Groups mixed on the same day
134 were classed as the same batch. At time of mixing, animals were approximately
135 matched for body weight in order to minimise variation between pen mates. Pigs
136 were weighed 24 hours following mixing. Animals were housed indoors in partially
137 slatted pens (30% slats, 70% solid flooring with light straw bedding) and were
138 provided with pelleted feed and water ad libitum.

139

140 *Skin lesion traits*

141 Fresh skin lesions were counted separately on the anterior (head, neck, forelegs and
142 shoulders), centre (flanks and back), and posterior (hind legs and rump) regions of
143 the body 24 hours post-mixing (SL24h). In order to ensure injuries inflicted prior to
144 mixing were not included in the analyses, lesions were also counted immediately
145 prior to mixing, and pre-mix lesion counts deducted from the post-mixing count.
146 Lesions were deemed to be fresh if they were a vivid red colour, bleeding or recently
147 scabbed. Lesions were counted in the same manner three weeks post-mixing
148 (SL3wk) as a measure of aggression under stable social conditions.

149

150 *Behavioural traits*

151 Animals were video recorded for 24 hours following mixing. The behavioural traits
152 used in this study were based on data recorded during these behavioural
153 observations. Each interaction was classed as either reciprocal aggression (RA) or
154 non-reciprocal aggression (NRA) as defined by Turner *et al.*, (2006). Behavioural
155 traits used in the analyses are defined in Table 1.

156

157 *Characteristics of the data*

158 Only aggressive behavioural traits that had been previously shown to be predictive of
159 skin lesion traits on a phenotypic level in the same population were chosen for
160 analysis (Desire *et al.*, 2015a). Skin lesion and aggressive behavioural traits showed
161 considerably skewed distributions (Supplementary Table S1), therefore a log
162 transformation ($y = \log_e + 1$) was used to approach the normal distribution.

163

164 *Statistical Analyses*

165 Univariate analyses were used to estimate genetic components and estimated
166 breeding values (EBVs) of all log transformed skin lesion and behavioural traits using
167 the following animal model:

168

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wc} + \mathbf{e}$$

169

170 where \mathbf{y} is the vector of records for skin lesions (SL24h and SL3wk) and aggressive
171 behaviour, and \mathbf{X} , \mathbf{Z} and \mathbf{W} are the incidence matrices of fixed effects, genetic
172 effects, and environmental (pen) effects, respectively. Vectors \mathbf{b} , \mathbf{a} , \mathbf{c} and \mathbf{e}
173 represent fixed effects, additive direct genetic effects, common environmental effects
174 (shared by all pigs in a pen), and residual error, respectively. Genetic line, sex, and

175 batch were included in all models as fixed categorical effects, while bodyweight at
176 time of mixing was fitted as a covariate. Age at time of mixing was included for
177 SL24h and aggressive behavioural traits. Bivariate analyses were used to estimate
178 genetic and group level correlations between skin lesion traits and aggressive
179 behavioural traits using the same fixed and random effects described for the
180 univariate analyses. Genetic analyses were performed using ASReml (Gilmour *et al.*,
181 2009).

182

183 As skin lesion and behavioural traits are measured on different scales, it is
184 impractical to directly compare genetic and phenotypic values across multiple traits.
185 Breeding values and untransformed phenotypic values were therefore scaled and
186 standardised, and expressed in terms of standard deviations from a population mean
187 of zero. Individuals were chosen for inclusion in each subsequent analysis based on
188 either SL24h EBVs in the lowest 10% of the population, or SL3wk EBVs in the
189 highest 10% of the population. This methodology was chosen as it allows the
190 selection response to be predicted based on the given data, rather than complex
191 genetic correlations that have a high level of estimation error, which might affect the
192 accuracy of predicted response using population genetics theory.

193 **Results**

194

195 *Heritabilities and common environmental effects*

196 Heritabilities estimated for skin lesion traits ranged from 0.11 to 0.43 (Table 2). A
197 substantially higher heritability was estimated for anterior SL3wk than anterior
198 SL24h. Heritabilities for behavioural traits ranged from 0.09 to 0.44 (Table 2). The
199 proportion of variance attributed to common environmental effects was generally
200 lower than estimated heritabilities for skin lesion and behavioural traits ($c^2 = 0.06$ to
201 0.15), except for posterior SL24h, average fight duration, and duration of time spent
202 receiving NRA.

203

204 *Genetic and pen level correlations between skin lesion and behaviour traits*

205 *Genetic correlations.* Where significant, genetic correlations between anterior SL24h
206 and aggressive behavioural traits were positive (Table 3). The proportion of fights
207 won was negatively correlated with central and posterior SL24h, while the duration of
208 NRA received, and the number of pen mates that NRA was received from were
209 positively correlated with these traits (Table 3). Genetic correlations between anterior
210 SL3wk and aggressive behavioural traits were generally negative (Table 4), except
211 duration of NRA received and number of pen mates that NRA was received from.
212 Positive correlations were found between central SL3wk and duration of NRA
213 received, and number of pen mates that NRA was received from (Table 4). No
214 significant genetic correlations were found between posterior SL3wk and aggressive
215 behavioural traits (Table 4).

216

217 *Pen level correlations.* Most pen level correlations between skin lesions and
218 aggressive traits did not significantly differ from zero. Those that did were mainly
219 positive for SL24h (Table 3). Statistically significant negative pen level correlations
220 were found between posterior SL24h and the number of reciprocal fights involved
221 with, and duration of NRA received (-0.08, SE 0.03; Table 3). Negative pen level
222 correlations were found between all SL3wk traits and the number of pigs attacked by
223 (RA), and between anterior or central SL3wk and the duration of NRA received
224 (Table 4).

225

226 *Low EBVs for SL24h*

227 *Associations with SL24h.* Individuals with low EBVs for anterior, central or posterior
228 SL24h had low EBVs (-0.69 SD and -1.89 SD; (Figure 1 [a, c, e]) and phenotypic
229 values (-0.38 SD to -0.94 SD; Figure 2 [a, c, e]) for all skin lesion traits at mixing

230

231 *Associations with SL3wk.* Individuals with low EBVs for SL24h had low EBVs for
232 SL3wk (-0.15 SD to -0.41 SD (Figure 1 [a, c, e])). Phenotypically, individuals with low
233 EBVs for SL24h did not differ significantly in the number of SL3wk in comparison to
234 the population as a whole (-0.05 SD to 0.07 SD; Figure 2 [a, c, e]).

235

236 *Associations with aggressive behaviour.* Individuals with low EBVs for anterior
237 SL24h also had low EBVs for all aggressive behavioural traits (-0.21 to -1.17 SD;
238 Figure 3 [a]). Other than proportion of fights won, duration of NRA initiated, and
239 number of pen mates attacked (NRA), individuals with low EBVs for central SL24h
240 had significantly lower EBVs for aggressive behavioural traits (-0.28 to -0.51 SD),
241 compared to the population average. Individuals with low EBVs for posterior SL24h

242 had EBVs that were significantly lower than the population mean for duration of NRA
243 received (-0.74 SD); duration of RA received (-0.41 SD); number of pigs attacked by
244 (RA) (-0.27 SD); total number of RA received (-0.27 SD), and higher than the
245 population average for proportion of fights won (0.45 SD) and duration of RA
246 initiated (0.19 SD; Figure 3 [e]).

247

248 Phenotypic values for individuals with low EBVs for anterior, central and posterior
249 SL24h largely mirrored those observed on the genetic level (Figure 4 [a, c, e]).
250 Individuals with low EBVs for anterior SL24h received non-reciprocal attacks for
251 11.55 seconds less than the population mean (Supplementary Table S2).

252

253 *High EBVs for SL3wk*

254 *Associations with SL24h.* Individuals with high EBVs for SL3wk did not differ
255 significantly from the population mean for anterior SL24h EBVs but had higher than
256 average EBVs for central and posterior SL24h (0.19 to 0.42 SD; Figure 1 [b, d, f]).
257 On a phenotypic level, only central SL24h significantly differed from the population
258 mean in individuals with low EBVs for central SL3wk (0.25 SD ; Figure 2 [d]). No
259 other significant associations were found between SL24h and SL3wk at the
260 phenotypic level(Figure 2 [b, d, f]).

261

262 *Associations with SL3wk.* Individuals with high SL3wk EBVs had high EBVs for all
263 other skin lesion traits at this time point (0.91 to 1.69 SD; Figure 1 [b, d, f]). These
264 individuals also had high skin lesion numbers on a phenotypic level compared to the
265 population mean (0.52 to 1.45 SD; Figure 2 [b, d, f]).

266

267 *Response on aggressive behaviour.* Except for the duration of NRA received, high
268 EBVs for anterior SL3wk corresponded with low EBVs for all aggressive behavioural
269 traits (-0.37 to -0.54 SD; Figure 3 [b]). The same trends were also observed for high
270 central SL3wk EBVs (-0.30 to -0.53 SD; Figure 3[d]). Individuals with high EBVs for
271 posterior SL3wk had low mean EBVs for all behavioural traits (-0.28 to -0.46 SD),
272 except for proportion of fights won and duration of NRA received, which did not
273 significantly differ from zero (Figure 3 [f]).

274

275 Phenotypic values for individuals with low EBVs for anterior, central and posterior
276 SL24h largely mirrored those observed on the genetic level (Figure 4 [b, d, f]).
277 Individuals with low EBVs for anterior SL3wk were involved in 2.39 fewer reciprocal
278 interactions than the population mean (Supplementary Table S3).

279

280 **Discussion**

281

282 *Heritabilities*

283 Heritabilities for skin lesion traits were of a low to moderate magnitude. These
284 estimates differed from those reported by Turner *et al.* (2009) for the same
285 population, as only those animals with behavioural data available were used in this
286 analysis. Heritabilities for SL3wk were higher than SL24h, which is likely to be due to
287 lower environmental variance 3 weeks post-mixing compared to 24 hours post-
288 mixing. The lowest heritability estimated for behavioural traits was for receipt of NRA.
289 Receipt of NRA results from the behaviour of other individuals in a pen, and not the
290 individual itself, which may explain why direct genetic effects account for so little of
291 the genetic variation in this trait. The highest heritabilities were estimated for traits
292 related to RA. During engagement in RA, the individual animal is actively involved in
293 the event, choosing to either attack or respond to an attack, which may explain why
294 these traits showed the highest heritabilities.

295

296 Social genetic effects describe genetic variation due to interactions between pen-
297 mates (Bijma and Wade, 2008). It is likely that social genetic effects contribute
298 significantly to mixing-related aggression in pigs. Ideally, both direct and social
299 genetic effects would be considered when assessing the genetic basis of aggression
300 in pigs, however these effects are difficult to estimate, optimally requiring several
301 hundred groups composed of few families (Bijma, 2010). It was therefore not
302 possible to include social effects in this study, however common environmental
303 effects were included in the genetic model to approximate social effects. Common
304 environmental effects had a low influence on the number of skin lesions and

305 involvement in aggression. As expected, traits that related to behaviour of other
306 group members, for example the receipt of NRA, tended to have higher common
307 environmental effects.

308

309 *Expected response following selection for reduced SL24h*

310

311 Consistent with the strength and direction of genetic correlations published
312 previously (Turner *et al.*, 2009), individuals with low SL24h EBVs had significantly
313 lower genetic and phenotypic values for SL24h to all body regions compared to the
314 population as a whole. The results suggest that selection for anterior SL24h would
315 have the lowest effect on posterior SL24h and vice versa. This is likely to be
316 because lesions to these body regions reflect involvement in opposing behaviours.
317 On a genetic level, there was generally a positive association between SL24h and
318 SL3wk, in that individuals with low SL24h EBVs had slightly reduced EBVs for
319 SL3wk compared to the whole population, and vice versa. However, this relationship
320 was not universally observed on a phenotypic level.

321

322 If the aim of using skin lesions for selection purposes were to simply reduce lesion
323 numbers, central or anterior SL24h should be used. However, the main goal of any
324 breeding program incorporating skin lesions would be to reduce aggression,
325 preferably on both a short and long term basis; therefore the results suggest that
326 selection against anterior SL24h would have the greatest effect on aggressive
327 behaviour. Associations between EBVs in the bottom or top 10% of skin lesion traits
328 with aggressive traits were generally in accordance with genetic correlations
329 between the same traits. The results suggest that selecting individuals based on low

330 anterior SL24h would result in the greatest reduction in mean EBVs for behavioural
331 traits relating to RA. Reciprocal contests make up the majority of time spent engaged
332 in physical aggression and carry the biggest risk of injury, therefore reducing this
333 behaviour is highly desirable. A slightly greater reduction in receipt of RA was
334 predicted, in comparison to initiation of RA, suggesting that the recipient of an attack
335 may be more likely to become injured than the initiator. This may be because the
336 initiator is more likely to win a contest, inflicting more damage in the process
337 (Stukenborg *et al.*, 2011).

338

339 The possible role of social genetic effects on social aggression was mentioned
340 above. Where there is a negative correlation between direct and social genetic
341 effects, selection based on direct breeding values alone can result in an undesirable
342 result (for example, selecting for reduced SL24h could theoretically result in
343 increased aggression; Ellen *et al.*, 2014). Previous studies suggest a positive
344 correlation between direct and social effects for aggressive behaviour, meaning that
345 animals with a low genetic propensity to become involved in aggression also have a
346 low chance of being attacked (Wilson *et al.*, 2011; Alemu *et al.*, 2014). Negative
347 correlations between social and direct effects have been found for dominance traits
348 (Wilson *et al.*, 2009; Sartori and Mantovani, 2012) however social effects accounted
349 for little of the variation in these studies. If a positive correlation exists between social
350 and direct effects for aggressive traits, combined selection for social and direct EBVs
351 for SL24h may reduce aggressive behaviour to a greater degree than our results
352 suggest.

353

354 Individuals with low EBVs for anterior SL24h had EBVs that were close to the
355 population mean for the proportion of fights won. This suggests that selection for low
356 anterior SL24h would not result in a strong selection for individuals that win a high
357 proportion of fights. It is likely that the low genetic correlation between anterior
358 SL24h and proportion of fights won is due to the fact that proportion of fights won is
359 independent from the duration of time spent engaged in aggression. For example, an
360 individual with very high fight success may have spent little time engaged in
361 aggression (receiving few lesions in the process), or much time engaged in
362 aggression (receiving many lesions). Likewise, the same can be true for animals
363 with a low fight success rate. Because of this relationship, individuals with low
364 anterior SL24h EBVs were involved in low levels of aggression, but contained
365 individuals with both high and low EBVs for proportion of fights won. These results
366 may address the criticism that selection for low lesions may simply result in selection
367 for meek animals, as it would seem that some dominant individuals are able to
368 convey social rank with very little aggression, possibly via behavioural cues, or short,
369 decisive fights.

370

371 Genetic correlations indicate that high fight success and low receipt of non-reciprocal
372 attacks are associated with few lesions to the central and posterior regions of the
373 body. These correlations alone would suggest that selection against either of these
374 traits could result in selection for highly dominant individuals. The results of the
375 analysis performed in this study suggest that selection for low central SL24h EBVs
376 would result in a reduction of several other behaviours, including initiation of
377 reciprocal fighting. This suggests that individuals with low EBVs for central SL24h
378 have a low propensity to be involved in both reciprocal and NRA. In contrast to

379 genetic correlations, traits likely to be related to dominance were not predicted to be
380 affected by selection for low central SL24h. This conflict seems to suggest that
381 central lesions are an ambiguous proxy measure of aggression, as they appear to
382 capture both aggressive and unaggressive individuals. In contrast, individuals with
383 low posterior SL24h had high values for proportion of fights won and duration of RA
384 initiated, and a decrease in all traits relating to the amount of aggression received.
385 This suggests that selecting against posterior SL24h would result in selection for
386 dominance related behaviours. Correlations between central or posterior SL24h and
387 aggressive traits presented in this study sometimes conflicted with those previously
388 calculated by Turner *et al.* (2008) using similar phenotyping methods. However, the
389 strength and direction of genetic correlations between anterior SL24h and behaviour
390 traits were similar between the two populations, providing further evidence that
391 anterior SL24h is the best trait overall for reducing aggression at mixing.

392

393 *Expected response following selection for increased SL3wk*

394 Due to lower and opposing genetic correlations between aggressive traits at mixing
395 and SL3wk, selection for increased SL3wk was predicted to reduce mean levels of
396 aggressive behaviour to a lesser extent than selection for low anterior SL24h.
397 Despite this, aggressive EBVs and phenotypes were still significantly lower than the
398 population mean in individuals with high EBVs for SL3wk. Selecting for increased
399 anterior or central SL3wk is expected to change mean EBVs for all aggressive traits
400 to a similar degree. Most behavioural EBVs were lower than the population as a
401 whole in this cohort; suggesting selection for increased lesions under stable social
402 conditions would result in a reduction in aggressive behaviour at mixing.

403

404 In accordance with genetic correlations, individuals with high EBVs for central SL3wk
405 had significantly higher EBVs for the duration of NRA received, which conflicts with
406 the aim of reducing aggression via selection. However, selection for increased
407 central SL24h is predicted to result in a higher proportion of unaggressive animals in
408 subsequent generations, and a lower proportion of aggressive animals. It would
409 therefore also be expected that duration of NRA received would actually decrease in
410 subsequent populations, despite positive genetic correlations between skin lesions
411 and this behavioural trait. Similarly, it is expected that the number of skin lesions
412 would also reduce under stable conditions, despite selecting for increased lesions at
413 this time, as this would ultimately reduce the amount of aggression experienced by
414 subordinate animals as hypothesised above. From a behavioural perspective, the
415 results suggest there would be little difference between using anterior or central
416 SL3wk for selection purposes.

417

418 Aggression is most intense upon first mixing and it is behaviour at this time point that
419 has been the focus of most research. It is worth considering the implications of
420 aggression under stable social conditions as, once mixed, animals are often housed
421 for several weeks or months within these groups. Practically, counting skin lesions
422 on larger, older animals in a socially stable environment is less time consuming than
423 counting lesions on younger animals, as there are fewer lesions, the animals are
424 more settled and tend to show less avoidance of an observer present in the pen.
425 Furthermore, heritability estimates of skin lesion numbers under stable social
426 conditions have been found to be of a higher magnitude to those inflicted under
427 newly mixed conditions, possibly due to less environmental noise, (Turner *et al.*,

428 2009; Desire *et al.*, 2015b), potentially increasing the response to selection for these
429 traits.

430

431 At present, it is still not well understood how lesions three weeks post-mixing are
432 related to longer-term aggressive behaviour. No study has yet looked at long-term
433 aggressive behaviour in sufficient detail to allow for thorough investigation into the
434 genetic and phenotypic relationships between skin lesion traits and aggression under
435 stable and unstable social conditions. Lower correlations between behaviour at
436 mixing and SL3wk suggests that individuals with the most lesions at three weeks
437 may not always be the least aggressive individuals at this time point. Without
438 behavioural information it is unknown what factors contribute to aggression under
439 stable social conditions, and under what circumstances individuals engage in
440 aggression. For example, lesions received under stable social conditions may be the
441 result of attacks by dominant individuals or reciprocal fighting between subordinate
442 individuals, perhaps partly due to unstable or ambiguous dominance hierarchies.
443 Genetic correlations between SL24h, SL3wk and aggressive behaviour at mixing
444 provide a conflicting narrative. Positive genetic correlations between SL24h and
445 SL3wk (Turner *et al.*, 2009; Desire *et al.* 2015b) suggest individuals that receive
446 many lesions at mixing go on to receive many lesions under stable social conditions,
447 whereas negative correlations between most behavioural traits at mixing and SL3wk
448 suggest that on the whole, animals that are aggressive at mixing go on to have fewer
449 lesions 3 weeks later. Direct behavioural observations on animals under stable social
450 conditions are required to explore this further. Until long-term aggressive behaviour
451 is better understood, skin lesions recorded under stable social conditions only
452 provide information on the aggression performed by a group as a whole and not the

453 individual in question. In contrast, the relationship between skin lesions at mixing and
454 aggressive behaviour is well established. In particular, anterior SL24h are highly
455 correlated with RA, meaning that skin lesions on this body region result from the
456 actions of the individual in question. When anterior SL24h are used as a phenotype,
457 it is a good proxy measure of an individual's behaviour, rather than other animals in
458 the social group. Moreover, although mixing aggression has been studied for several
459 decades, the damaging effects of long-term aggression have not been quantified. It
460 should be noted that in this study skin lesion numbers recorded immediately prior to
461 mixing were subtracted from those counted 24 hours later, to ensure only those
462 lesions resulting from mixing aggression were included in the analysis. This
463 methodology effectively doubles the amount of labour required to record SL24h,
464 however correlations between raw anterior lesion numbers recorded 24 hours post-
465 mixing and lesion numbers adjusted for pre-mix counts were very high (0.95; $P <$
466 0.001) suggesting that recording skin lesions prior to mixing is not necessary.

467

468 This study provides evidence that significant reductions in social aggression could be
469 achieved via selection for skin lesions. Much of the variation in skin lesion numbers
470 is attributed to environmental factors, and previous research has demonstrated that
471 variation in management systems can affect the phenotypic expression of
472 aggression (Arey and Edwards, 1998), however information regarding how
473 environmental factors affect the genetic expression of these traits is limited. Although
474 previous studies have found phenotypic correlations between skin lesions and
475 aggression (Stukenborg *et al.*, 2011; Tönepöhl *et al.*, 2013; Turner *et al.*, 2006) few
476 studies have estimated genetic correlations across traits. Results from populations
477 housed under different management systems suggest anterior SL24h is a reliable

478 measure of social aggression in growing pigs (Turner *et al.*, 2008; Turner *et al.*,
479 2009). In practice, selection for skin lesions would be incorporated into a selection
480 index tailored to a wider breeding goal. Therefore, further research is required to
481 estimate the genetic correlation with other traits in the breeding goal and derive the
482 marginal economic and non-economic value of skin lesions to allow these traits to be
483 weighted within a multi-trait commercial index.

484

485 *Conclusion*

486 Results suggest that selection against anterior SL24h would have the greatest effect
487 on behaviour at mixing, both on a genetic and phenotypic level. The results also
488 suggest that anterior SL24h are a more accurate representation of the behaviour of
489 separate individuals, as opposed to other skin lesion traits which may be more
490 representative of the behaviour of others in the pen. There is also evidence that
491 selection for increased SL3wk would have the favourable effect of reducing
492 aggressive behaviour at mixing, although to a lesser degree than selection against
493 anterior SL24h. Although there are several advantages to using skin lesions
494 recorded under stable social conditions to phenotype individuals for selection
495 purposes, more research into the relationship between aggressive behaviour at
496 mixing and aggression under stable social conditions is needed. In conclusion, with
497 the evidence currently available, anterior SL24h would be the preferable trait for
498 genetic selection, as it has the potential to significantly reduce levels of aggression
499 observed in the first 24 hours post-mixing, and also reduce the genetic trend in
500 longer-term aggression (three weeks post-mixing).

501

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509

510

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579

580 **Tables**

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

Trait	Description
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
Number of RA involved with	Total number of reciprocal fights the focal pig was involved with, regardless of which pig initiated the attack
Proportion of fights won	Proportion of all reciprocal fights which the focal pig won
Average duration RA & NRA involved (s)	Average duration (in seconds) of all aggressive encounters in which the focal pig was involved
Duration of RA/NRA initiated (s)	Duration of time (in seconds) spent in aggression in which the focal pig was the initiator
Duration of RA/NRA received (s)	Duration of time (in seconds) spent in aggression in which the focal pig was the recipient of the attack
Number of pen mates attacked (RA/NRA)	The number of pen mates the focal pig attacked
Number of pen mates attacked by (RA/NRA)	The number of pen mates the focal pig was attacked by
Pen mates interacted with	Total number of pen mates with which the focal pig had any aggressive interactions

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586 **Table 2** Heritabilities (h^2), phenotypic proportions of pen variances (c^2), phenotypic (σ^2p), and genetic (σ^2a) variances for skin lesion traits
 587 recorded on pigs 24 hours post-mixing (SL24h) and 3 weeks post-mixing (SL3wk) and aggressive behavioural traits

588

	Trait	h^2	c^2	σ^2p	σ^2a
SL24h	Anterior	0.13 (0.05)	0.06 (0.02)	1.14	0.15
	Central	0.21 (0.06)	0.10 (0.03)	1.22	0.25
	Posterior	0.12 (0.05)	0.14 (0.03)	0.87	0.11
SL3wk	Anterior	0.43 (0.08)	0.03 (0.02)	0.31	0.13
	Central	0.39 (0.08)	0.06 (0.02)	0.35	0.13
	Posterior	0.11 (0.05)	0.07 (0.02)	0.44	0.05
Behaviour	Number of RA involved with	0.44 (0.08)	0.07 (0.02)	0.82	0.36
	Proportion of fights won	0.34 (0.08)	0.01 (0.02)	0.04	0.01
	Average duration of NA and NRA involved (s)	0.14 (0.05)	0.15 (0.03)	0.38	0.05
	Duration NRA initiated (s)	0.33 (0.07)	0.03 (0.02)	3.42	1.12
	Duration NRA received (s)	0.09 (0.04)	0.13 (0.03)	1.82	0.16
	Duration of RA initiated (s)	0.35 (0.08)	0.01 (0.02)	5.44	1.92
	Duration RA received (s)	0.28 (0.07)	0.06 (0.02)	2.08	0.58
	Number of pen mates attacked (RA)	0.40 (0.08)	0.04 (0.02)	0.48	0.19
	Number of pen mates attacked by (RA)	0.33 (0.07)	0.07 (0.02)	0.40	0.13
	Number of pen mates attacked (NRA)	0.31 (0.07)	0.02 (0.02)	0.57	0.18
	Number of pen mates attacked by (NRA)	0.11 (0.05)	0.19 (0.04)	0.43	0.05
	Number of attacks initiated (RA)	0.42 (0.08)	0.03 (0.02)	0.72	0.30
	Number of attacked received (RA)	0.32 (0.07)	0.07 (0.02)	0.61	0.20
	Number of pen mates interacted with	0.37 (0.08)	0.09 (0.03)	0.24	0.09

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590 RA = reciprocal aggression; NRA = non-reciprocal aggression

591 **Table 3** Genetic (r_G) and pen level (r_C) correlations¹ between anterior, central and posterior skin lesion traits recorded on pigs 24 hours post-
592 mixing (SL24h), with aggressive behavioural traits recorded 24 hours following mixing (standard errors presented in parentheses)

	Anterior SL24h		Central SL24h		Posterior SL24h	
	r_G	r_C	r_G	r_C	r_G	r_C
Number of RA involved with	0.78 (0.10)	0.42 (0.21)	-0.02 (0.19)	-0.41 (0.23)	-0.11 (0.22)	-0.47 (0.21)
Proportion of fights won	0.24 (0.22)	0.01 (0.56)	-0.49 (0.18)	-0.46 (0.56)	-0.52 (0.21)	-0.48 (0.48)
Average duration of NA and NRA involved (s)	0.66 (0.18)	0.14 (0.22)	-0.17 (0.26)	-0.11 (0.20)	-0.36 (0.27)	-0.15 (0.19)
Duration of NRA initiated (s)	0.56 (0.17)	0.10 (0.36)	-0.21 (0.22)	0.01 (0.32)	-0.19 (0.23)	-0.02 (0.30)
Duration of NRA received (s)	0.34 (0.29)	0.17 (0.03)	0.54 (0.24)	-0.07 (0.04)	0.67 (0.28)	-0.08 (0.03)
Duration of RA initiated (s)	0.72 (0.12)	0.38 (0.39)	-0.10 (0.20)	-0.34 (0.43)	-0.32 (0.22)	-0.47 (0.40)
Duration of RA received (s)	0.77 (0.12)	0.51 (0.20)	0.10 (0.21)	-0.12 (0.25)	0.06 (0.24)	-0.02 (0.23)
Number of pen mates focal pig attacked (RA)	0.75 (0.12)	0.21 (0.03)	-0.07 (0.20)	0.23 (0.03)	-0.30 (0.22)	0.22 (0.03)
Number of pigs attacked by (RA)	0.84 (0.10)	0.50 (0.02)	0.08 (0.20)	0.19 (0.03)	0.16 (0.22)	0.11 (0.03)
Number of pen mates attacked (NRA)	0.59 (0.17)	0.17 (0.38)	-0.15 (0.22)	0.00 (0.35)	-0.07 (0.23)	0.03 (0.33)
Number of pen mates attacked by (NRA)	0.21 (0.29)	0.18 (0.21)	0.54 (0.22)	0.28 (0.18)	0.67 (0.26)	0.30 (0.16)
Number of attacks initiated (RA)	0.73 (0.12)	0.51 (0.27)	-0.05 (0.20)	-0.35 (0.31)	-0.28 (0.22)	-0.53 (0.28)
Number of attacks received (RA)	0.85 (0.10)	0.58 (0.18)	0.09 (0.20)	-0.39 (0.23)	0.12 (0.23)	-0.40 (0.21)
Number of pen mates interacted with	0.69 (0.13)	0.30 (0.22)	-0.01 (0.20)	-0.16 (0.22)	0.00 (0.22)	-0.05 (0.21)

593 ¹ Bold font signifies correlation significantly different from 0

594 RA = reciprocal aggression; NRA = non-reciprocal aggression

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598 Table 4: Genetic (r_G) and pen level (r_C) correlations¹ between anterior, central and posterior skin lesion traits recorded on pigs 3 weeks post-
 599 mixing (SL3wk), with aggressive behavioural traits recorded 24 hours following mixing (standard errors presented in parentheses)

	Anterior SL3wk		Central SL3wk		Posterior SL3wk	
	r_G	r_C	r_G	r_C	r_G	r_C
Number of RA involved with	-0.34 (0.14)	-0.13 (0.31)	-0.30 (0.15)	-0.39 (0.23)	-0.31 (0.22)	-0.04 (0.26)
Proportion of fights won	-0.49 (0.14)	-0.35 (0.80)	-0.45 (0.15)	-0.79 (0.63)	-0.30 (0.23)	-0.29 (0.67)
Average duration of NA and NRA involved (s)	-0.19 (0.20)	-0.17 (0.27)	-0.30 (0.20)	-0.13 (0.22)	-0.30 (0.28)	-0.14 (0.22)
Duration of NRA initiated (s)	-0.38 (0.15)	-0.22 (0.41)	-0.33 (0.16)	-0.34 (0.33)	-0.28 (0.24)	-0.45 (0.34)
Duration of NRA received (s)	0.51 (0.22)	-0.16 (0.04)	0.66 (0.19)	-0.18 (0.04)	0.14 (0.34)	-0.06 (0.03)
Duration of RA initiated (s)	-0.36 (0.15)	0.05 (0.54)	-0.21 (0.16)	-0.44 (0.43)	-0.35 (0.23)	0.11 (0.45)
Duration of RA received (s)	-0.20 (0.17)	-0.31 (0.31)	-0.25 (0.17)	-0.29 (0.25)	-0.15 (0.25)	-0.17 (0.26)
Number of pen mates focal pig attacked (RA)	-0.33 (0.15)	0.05 (0.03)	-0.21 (0.16)	0.08 (0.04)	-0.33 (0.23)	-0.02 (0.03)
Number of pigs attacked by (RA)	-0.33 (0.15)	-0.15 (0.04)	-0.39 (0.15)	-0.18 (0.04)	-0.26 (0.24)	-0.08 (0.03)
Number of pen mates attacked (NRA)	-0.31 (0.16)	-0.18 (0.45)	-0.30 (0.16)	-0.32 (0.36)	-0.21 (0.25)	-0.41 (0.38)
Number of pen mates attacked by (NRA)	0.47 (0.20)	0.14 (0.25)	0.58 (0.18)	-0.12 (0.21)	0.22 (0.32)	-0.09 (0.21)
Number of attacks initiated (RA)	-0.33 (0.15)	-0.23 (0.39)	-0.20 (0.16)	-0.52 (0.30)	-0.25 (0.23)	-0.05 (0.34)
Number of attacks received (RA)	-0.32 (0.16)	-0.22 (0.31)	-0.42 (0.15)	-0.40 (0.23)	-0.32 (0.24)	-0.05 (0.26)
Number of pen mates interacted with	-0.37 (0.15)	-0.11 (0.30)	-0.20 (0.16)	-0.32 (0.23)	-0.28 (0.23)	-0.27 (0.24)

600 ¹ Bold font signifies correlation significantly different from 0

601 RA = reciprocal aggression; NRA = non-reciprocal aggression

602 **Figure captions**

603 **Figure 1** Mean estimated breeding values (EBVs) for skin lesion traits of pigs with EBVs in
604 the lowest 10% for either anterior (a), central (c) or posterior (e) skin lesions recorded 24
605 hours post-mixing (SL24h), or highest 10% EBVs for anterior (b), central (d) or posterior (f)
606 skin lesions recorded 3 weeks post-mixing (SL3wk). Skin lesion trait that selection was
607 based on is indicated above each panel and shaded black.

608 **Figure 2** Mean phenotypic values for skin lesion traits of pigs with EBVs in the lowest 10%
609 for either anterior (a), central (c) or posterior (e) skin lesions recorded 24 hours post-mixing
610 (SL24h), or highest 10% EBVs for anterior (b), central (d) or posterior (f) skin lesions
611 recorded 3 weeks post-mixing (SL3wk). Skin lesion trait that selection was based on is
612 indicated above each panel and shaded black.

613 **Figure 3** Mean estimated breeding values (EBVs) for aggressive behavioural traits of pigs
614 with EBVs in the lowest 10% for either anterior (a), central (c) or posterior (e) skin lesions
615 recorded 24 hours post-mixing (SL24h), or highest 10% EBVs for anterior (b), central (d) or
616 posterior (f) skin lesions recorded 3 weeks post-mixing (SL3wk). Skin lesion trait that
617 selection is based on is indicated beneath each panel. Numbers on horizontal axes
618 correspond with the following behavioural traits: 1 - number of RA involved with; 2 -
619 proportion of fights won; 3 - average duration of RA and NRA involved (s); 4 - duration of
620 NRA initiated (s); 5 - duration of NRA received (s); 6 - duration of RA initiated (s); 7 -
621 duration of RA received (s); 8 - number of pen mates focal pig attacked (RA); 9 - number of
622 pigs attacked by (RA); 10 - number of pen mates attacked (NRA); 11 - number of pen mates
623 attacked by (NRA); 12 - total RA initiated; 13 - total RA received; 14 - number of pen mates
624 interacted with. RA = reciprocal aggression; NRA = non-reciprocal aggression.

625 **Figure 4** Mean phenotypic values for aggressive behavioural traits of pigs with EBVs in the
626 lowest 10% for either anterior (a), central (c) or posterior (e) skin lesions recorded 24 hours

627 post-mixing (SL24h), or highest 10% EBVs for anterior (b), central (d) or posterior (f) skin
628 lesions recorded 3 weeks post-mixing (SL3wk). Skin lesion trait that selection is based on is
629 indicated beneath each panel. Numbers on horizontal axes correspond with the following
630 behavioural traits: 1 - number of RA involved with; 2 - proportion of fights won; 3 - average
631 duration of RA and NRA involved (s); 4 - duration of NRA initiated (s); 5 - duration of NRA
632 received (s); 6 - duration of RA initiated (s); 7 - duration of RA received (s); 8 - number of
633 pen mates focal pig attacked (RA); 9 - number of pigs attacked by (RA); 10 - number of pen
634 mates attacked (NRA); 11 - number of pen mates attacked by (NRA); 12 - total RA initiated;
635 13 - total RA received; 14 - number of pen mates interacted with. RA = reciprocal
636 aggression; NRA = non-reciprocal aggression.

637

Supplementary Table S1 Characteristics of skin lesion traits recorded on pigs 24h post-mixing (SL24h) and 3 weeks post-mixing (SL3wk) and behavioural data for all animals included in the statistical analysis

<i>Trait</i>	Original scale					Transformed scale		
	<i>N</i>	<i>Min-Max</i>	<i>Mean (SD)</i>	<i>SK</i>	<i>K</i>	<i>Mean (SD)</i>	<i>SK</i>	<i>K</i>
Anterior SL24h	1146	0 - 99	19.07 (17.35)	1.37	2.27	2.58 (1.07)	-0.90	0.43
Central SL24h	1146	0 - 100	10.82 (12.03)	1.43	6.03	2.06 (1.1)	-0.64	-0.52
Posterior SL24h	1146	0 - 41	3.69 (8.30)	-0.73	4.08	1.36 (1.02)	-0.12	-1.30
Anterior SL3wk	1146	0 - 63	10.40 (5.62)	1.59	8.89	2.3 (0.56)	-1.15	2.66
Central SL3wk	1146	0 - 40	10.36 (5.93)	1.03	1.90	2.28 (0.6)	-0.92	1.54
Posterior SL3wk	1146	0 - 30	4.53 (3.49)	1.16	2.92	1.49 (0.71)	-0.52	-0.34
Number of RA involved with	1146	0 - 56	8.43 (7.16)	1.37	3.04	1.91 (0.9)	-0.60	-0.35
Proportion of fights won	1047	0 - 1	0.30 (0.25)	0.54	-0.27	0.25 (0.19)	0.20	-0.85
Average duration NA and NRA involved (s)	1138	1 - 250	42.70 (27.97)	2.03	8.24	3.59 (0.64)	-0.39	0.46
Duration NRA initiated (s)	1146	0 - 996	41.71 (68.81)	4.64	40.72	2.53 (1.82)	-0.19	-1.27
Duration NRA received (s)	1146	0 - 444	41.47 (46.53)	2.88	13.9	3.12 (1.34)	-0.88	0.36
Duration of RA initiated (s)	1146	0 - 2394	289.8 (366.2)	2.07	5.30	4.3 (2.34)	-0.88	-0.53
Duration RA received (s)	1146	0 - 2997	329.6 (353)	2.08	6.62	5.1 (1.45)	-1.08	1.45
Number of pen mates attacked (RA)	1146	0 - 11	2.86 (2.32)	0.65	-0.20	1.14 (0.69)	-0.40	-0.94
Number of pen mates attacked by (RA)	1146	0 - 9	2.86 (2.06)	0.40	-0.52	1.18 (0.63)	-0.59	-0.66
Number of pen mates attacked (NRA)	1146	0 - 14	2.57 (2.69)	1.32	1.54	1.00 (0.75)	0.06	-1.10
Number of pen mates attacked by (NRA)	1146	0 - 9	2.57 (1.67)	0.61	0.1	1.26 (0.45)	-1.64	2.39
Number of attacks initiated (RA)	1146	0 - 36	4.23 (4.30)	1.75	4.97	1.32 (0.85)	-0.14	-0.89
Number of attacked received (RA)	1146	0 - 25	4.20 (3.78)	1.44	3.04	1.37 (0.79)	-0.32	-0.72
Number of pen mates interacted with	1146	0 - 14	6.69 (3.06)	0.02	-0.66	1.94 (0.49)	-1.13	1.48

RA = reciprocal aggression; NRA = non-reciprocal aggression; SK = skewness; K = kurtosis

Supplementary Table S2 Comparison of lesion traits and aggressive behavioural traits for all pigs and pigs in the lowest 10th percentile of EBVs for anterior skin lesions recorded 24 hours post mixing (SL24h). Raw mean values for all pigs, mean phenotypic differences (in SD) between all pigs and selected pigs, and expected mean change (in trait units) after selection for SL24h.

	Trait	Raw mean of all pigs	Mean difference between all and selected pigs in SD (SE) ¹	Expected change after selection ²
SL24h	Anterior (<u>selection trait</u>)	19.07	-0.91 (0.03)	-15.85
	Central	10.82	-0.61 (0.05)	-7.35
	Posterior	3.69	-0.43 (0.07)	-3.60
SL3wk	Anterior	10.40	-0.06 (0.08)	-0.34
	Central	10.36	0.07 (0.10)	0.43
	Posterior	4.53	0.00 (0.07)	0.01
Behaviour	Number of RA involved with	8.43	-0.63 (0.06)	-4.51
	Proportion of fights won	0.30	-0.06 (0.14)	-0.01
	Average duration of NA and NRA involved (s)	42.70	-0.53 (0.06)	-14.76
	Duration of NRA initiated (s)	41.71	-0.24 (0.06)	-16.29
	Duration of NRA received (s)	41.47	-0.25 (0.07)	-11.55
	Duration of RA initiated (s)	289.80	-0.44 (0.06)	-160.42
	Duration of RA received (s)	329.60	-0.62 (0.05)	-217.42
	Number of pen mates attacked (RA)	2.86	-0.57 (0.08)	-1.32
	Number of pigs attacked by (RA)	2.86	-0.74 (0.07)	-1.52
	Number of pen mates attacked (NRA)	2.57	-0.28 (0.09)	-0.76
	Number of pen mates attacked by (NRA)	2.57	-0.44 (0.11)	-0.73
	Total RA initiated	4.23	-0.47 (0.07)	-2.03
	Total RA received	4.20	-0.66 (0.06)	-2.48
	Number of pen mates interacted with	6.69	-0.60 (0.09)	-1.83

SL24h = skin lesions recorded 24 hours post-mixing; SL3wk = skin lesions recorded 3 weeks post-mixing ; RA = reciprocal aggression; NRA = non-reciprocal aggression

¹ Bold font signifies change significantly different from 0

² Untransformed phenotypes were scaled and standardised ([see Table S1](#)) and the corresponding change in SD after selection based on breeding values was used to calculate the expected change in aggressive behaviour.

Supplementary Table S3 Comparison of lesion traits and aggressive behavioural traits for all pigs and pigs in the highest 10th percentile of EBVs for anterior skin lesions recorded 3 weeks post mixing (SL3wk). Raw mean values for all pigs, mean phenotypic differences (in SD) between all pigs and selected pigs, and expected mean change (in trait units) after selection for SL3wk

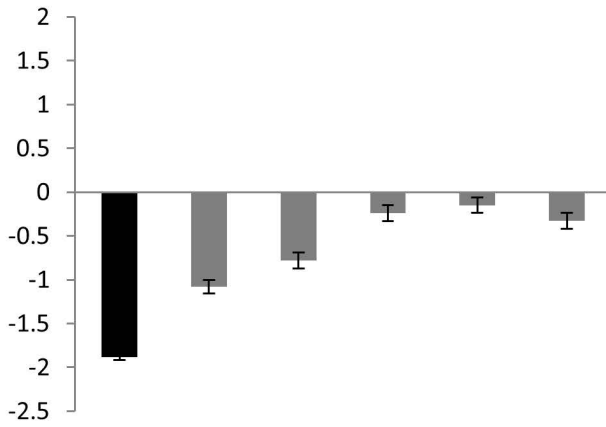
Trait		<u>Raw mean of all pigs</u>	<u>Mean difference between all and selected pigs in SD (SE)¹</u>	<u>Expected change after selection²</u>
SL24h	Anterior	19.07	-0.04 (0.08)	-0.76
	Central	10.82	0.21 (0.11)	2.58
	Posterior	3.69	0.22 (0.11)	1.79
SL3wk	Anterior (<u>selection trait</u>)	10.40	1.42 (0.13)	7.95
	Central	10.36	1.00 (0.12)	5.91
	Posterior	4.53	0.52 (0.12)	1.82
Behaviour	Number of RA involved with	8.43	-0.33 (0.08)	-2.39
	Proportion of fights won	0.30	-0.31 (0.09)	-0.08
	Average duration of NA and NRA involved (s)	42.70	-0.19 (0.07)	-5.30
	Duration of NRA initiated (s)	41.71	-0.13 (0.08)	-8.72
	Duration of NRA received (s)	41.47	-0.10 (0.07)	-4.50
	Duration of RA initiated (s)	289.80	-0.30 (0.07)	-108.12
	Duration of RA received (s)	329.60	-0.28 (0.07)	-98.06
	Number of pen mates focal pig attacked (RA)	2.86	-0.35 (0.09)	-0.81
	Number of pigs attacked by (RA)	2.86	-0.35 (0.08)	-0.71
	Number of pen mates attacked (NRA)	2.57	-0.28 (0.08)	-0.75
	Number of pen mates attacked by (NRA)	2.57	0.1 (0.09)	0.17
	Total RA initiated	4.23	-0.29 (0.08)	-1.25
	Total RA received	4.20	-0.3 (0.07)	-1.14
	Number of pen mates interacted with	6.69	-0.39 (0.09)	-1.19

SL24h = skin lesions recorded 24 hours post-mixing; SL3wk = skin lesions recorded 3 weeks post-mixing; RA = reciprocal aggression; NRA = non-reciprocal aggression

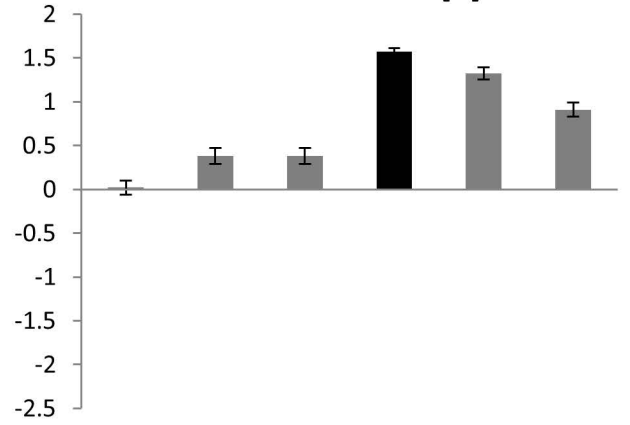
¹ Bold font signifies change significantly different from 0

| ² Untransformed phenotypes were scaled and standardised ([see Table S1](#)) and the corresponding change in SD after selection based on breeding values was used to calculate the expected change in aggressive behaviour.

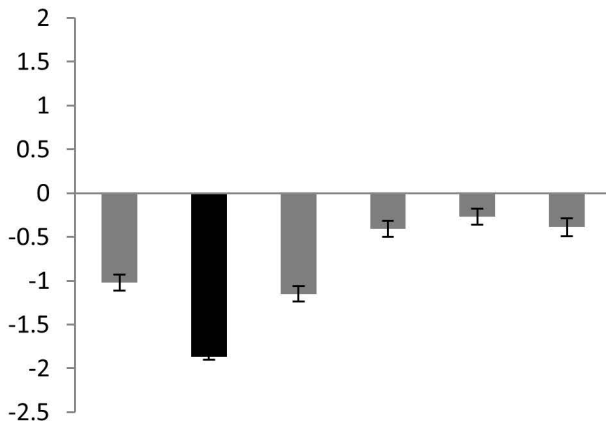
Anterior SL24h [a]



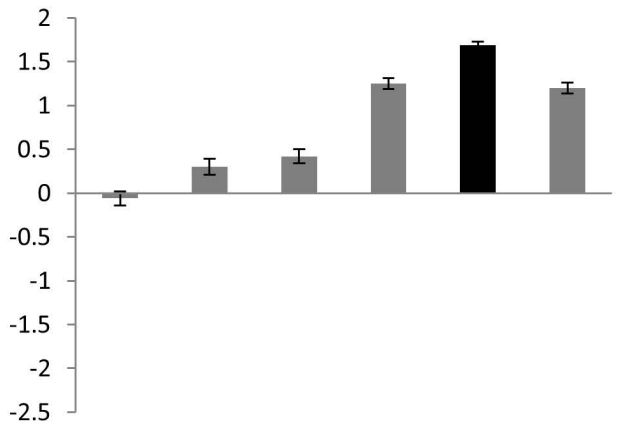
Anterior SL3wk [b]



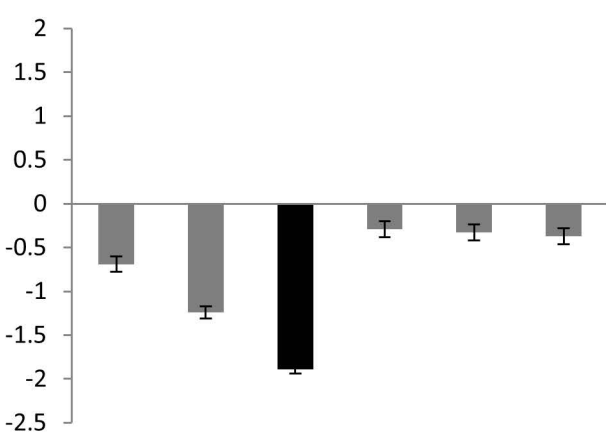
Central SL24h [c]



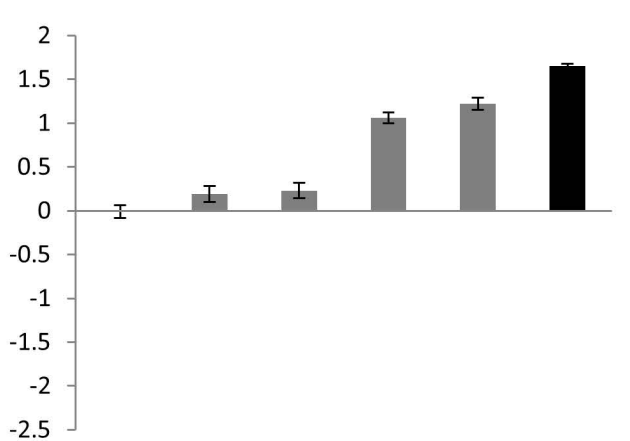
Central SL3wk [d]



Posterior SL24h [e]



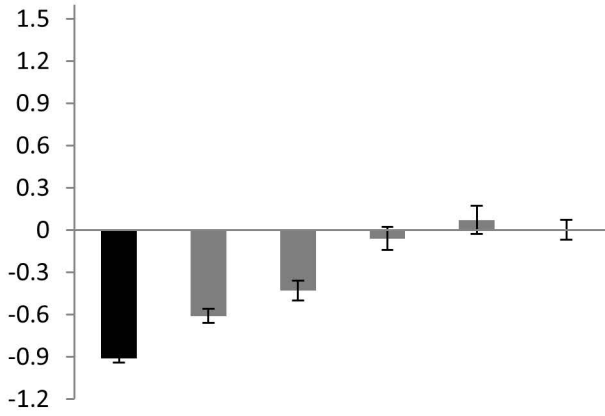
Posterior SL3wk [f]



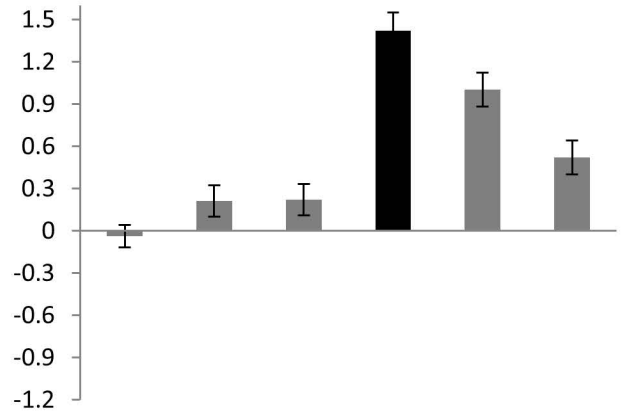
Anterior SL24h
 Central SL24h
 Posterior SL24h
 Anterior SL3wk
 Central SL3wk
 Posterior SL3wk

Anterior SL24h
 Central SL24h
 Posterior SL24h
 Anterior SL3wk
 Central SL3wk
 Posterior SL3wk

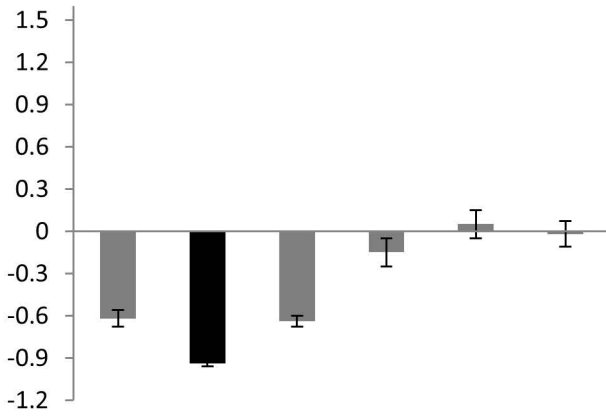
Anterior SL24h [a]



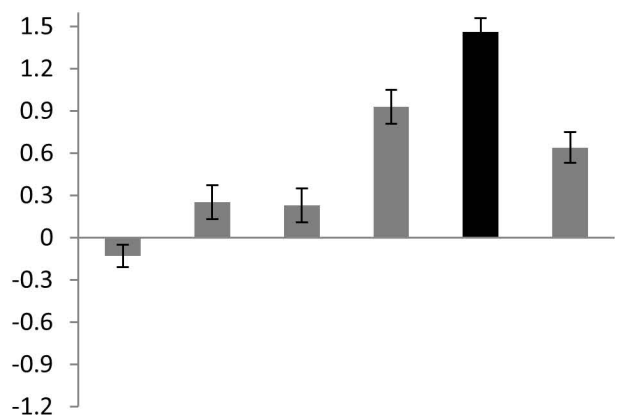
Anterior SL3wk [b]



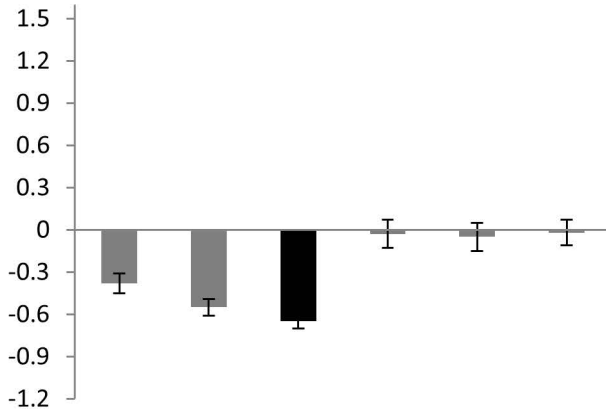
Central SL24h [c]



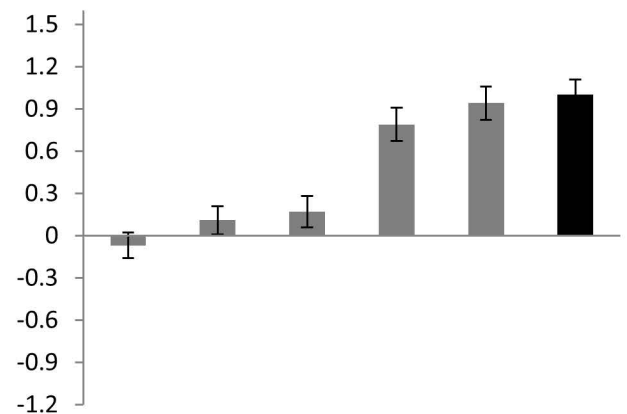
Central SL3wk [d]



Posterior SL24h [e]



Posterior SL3wk [f]



Anterior SL24h

Central SL24h

Posterior SL24h

Anterior SL3wk

Central SL3wk

Posterior SL3wk

Anterior SL24h

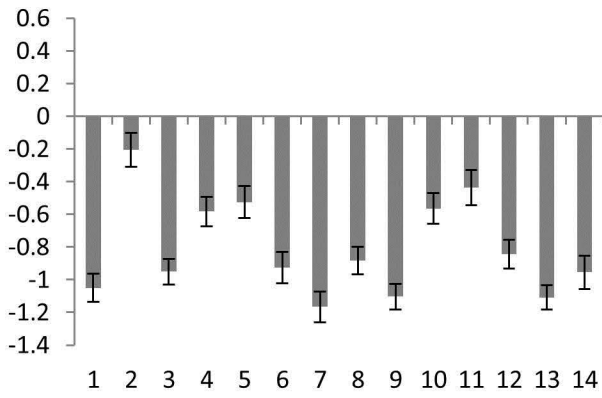
Central SL24h

Posterior SL24h

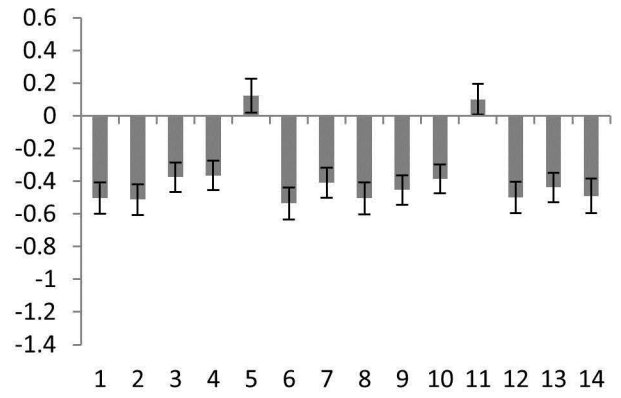
Anterior SL3wk

Central SL3wk

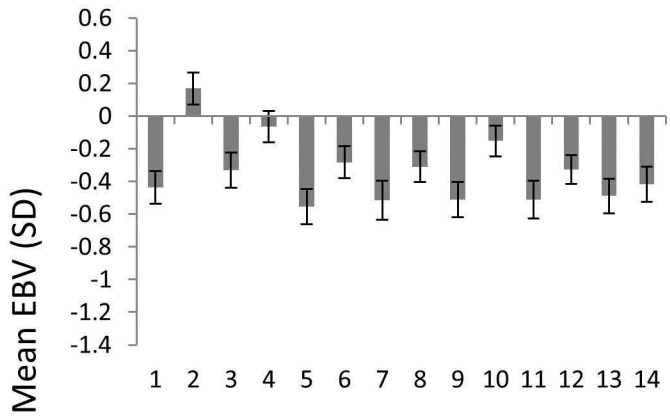
Posterior SL3wk



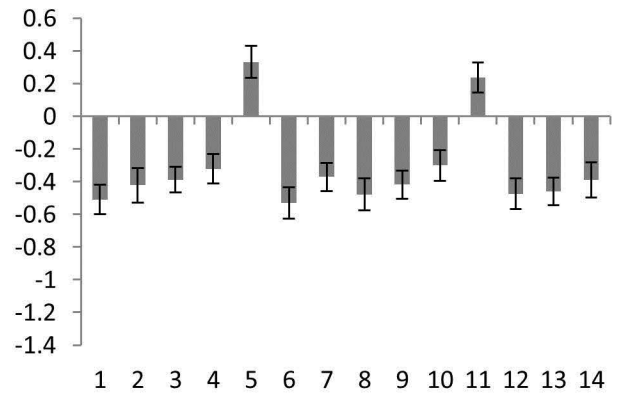
Anterior SL24h [a]



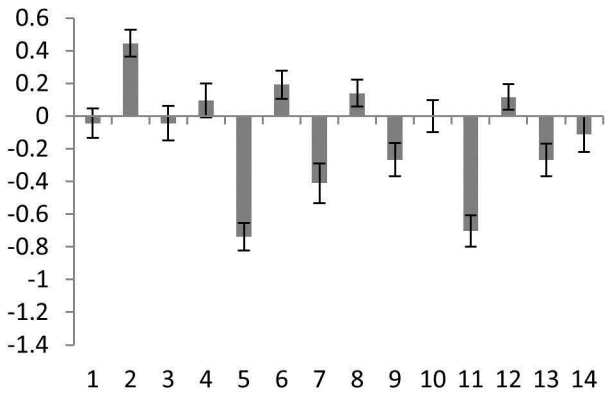
Anterior SL3wk [b]



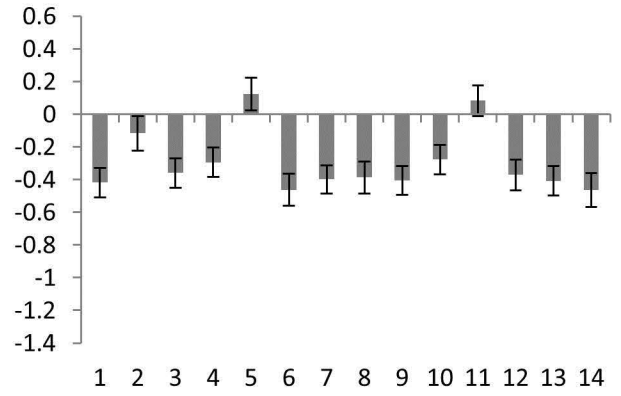
Central SL24h [c]



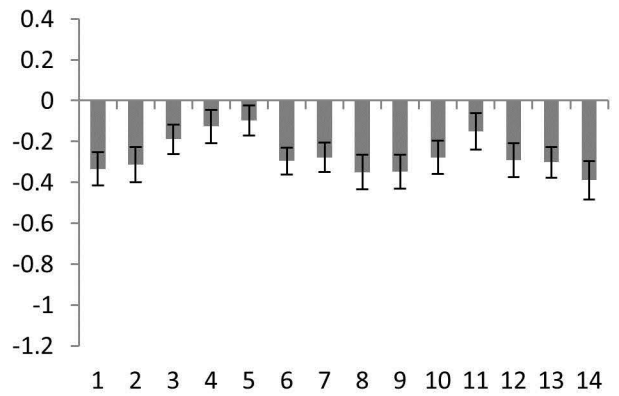
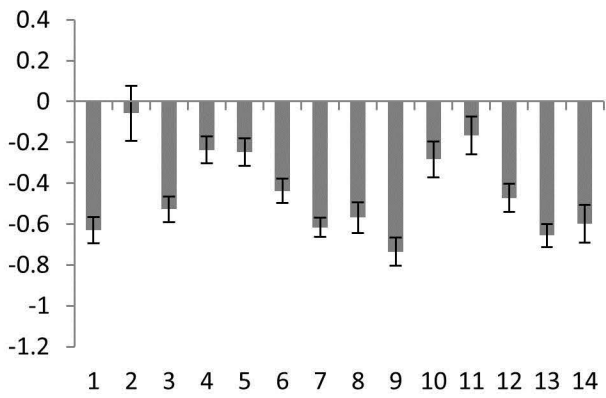
Central SL3wk [d]



Posterior SL24h [e]

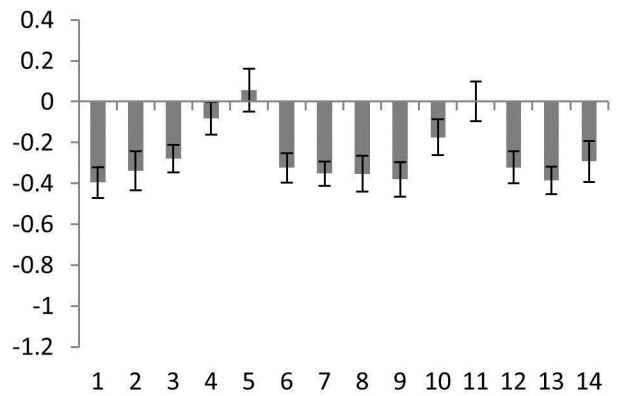
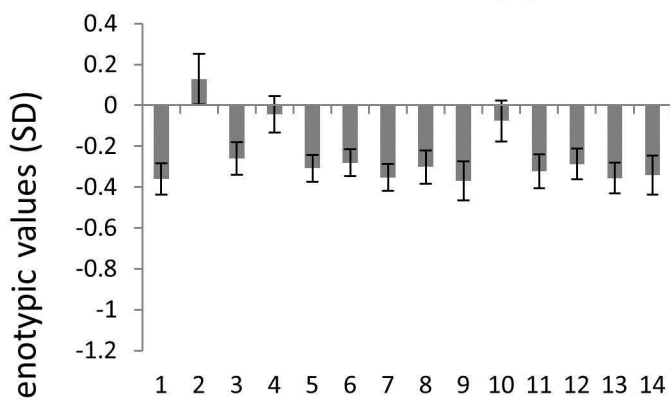


Posterior SL3wk [f]



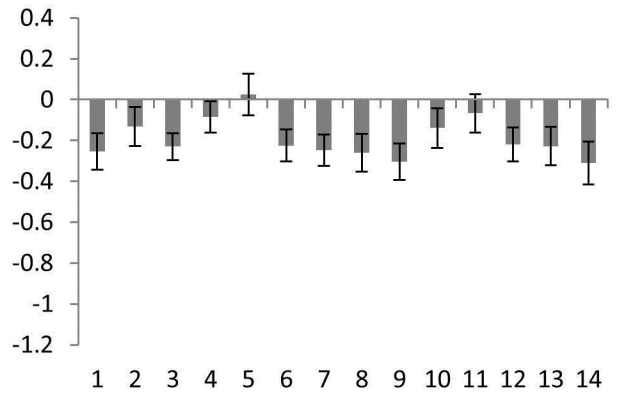
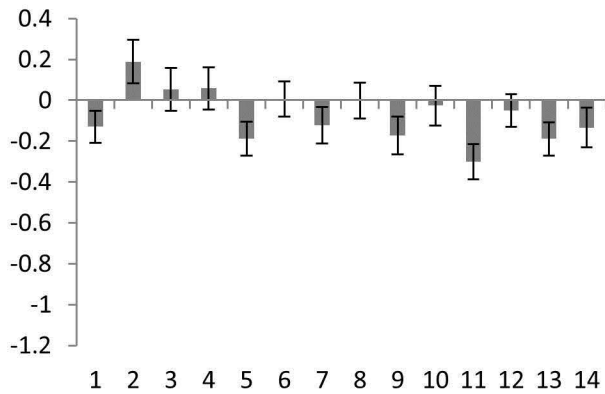
Anterior SL24h [a]

Anterior SL3wk [b]



Central SL24h [c]

Central SL3wk [d]



Posterior SL24h [e]

Posterior SL3wk [f]