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Turner, SP; Nevison, IM; Desire, S; Camerlink, I; Roehe, R; Ison, SH; Farish, M; Jack, MC; D'Eath, RB

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1 **Aggressive behaviour at regrouping is a poor predictor of**
2 **chronic aggression in stable social groups**

3

4 **Simon P. Turner^{a,*}, Ian M. Nevison^b, Suzanne Desire^a, Irene Camerlink^a, Rainer Roehle^a, Sarah**
5 **H. Ison^{a,1}, Marianne Farish^a, Mhairi C. Jack^a and Richard B. D'Eath^a**

6

7 ^aAnimal and Veterinary Sciences Group, SRUC (Scotland's Rural College), Kings Buildings, West
8 Mains Road, Edinburgh, EH9 3JG, UK

9 ^bBiomathematics and Statistics Scotland, James Clerk Maxwell Building, Peter Guthrie Tait Road,
10 Edinburgh, EH9 3FD, UK

11 ¹Present address: Michigan State University, Anthony Hall, 474 S. Shaw Lane, East Lansing, MI
12 48824, USA

13

14 *Corresponding author

15 E-mail: simon.turner@sruc.ac.uk

16 Fax: +44 131 535 3121

17 Animal and Veterinary Sciences Group, SRUC (Scotland's Rural College), Kings Buildings, West
18 Mains Road, Edinburgh, EH9 3JG, UK

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20

21 **Abstract**

22 Commercial pigs globally are routinely mixed into new social groups. This results in regrouping
23 aggression predominantly during the first 24h which compromises welfare and productivity. Chronic
24 aggression persists thereafter and is also undesirable. Management strategies are needed that reduce
25 the costs of aggression in both of these contexts. Pigs vary greatly in aggressive behaviour and
26 numbers of skin lesions. This study examined how regrouping behaviour affects immediate and long-

27 term lesion counts with a specific focus on understanding the behaviour of pigs with few lesions in
28 both social contexts. Aggressive behaviour from 1163 growing pigs was observed for 24h post-
29 regrouping and fresh lesions were counted 24h and 3 weeks post-regrouping. Similarity between pigs
30 was calculated using all behavioural traits recorded during the 24h post-regrouping. Clusters of pigs
31 were formed using furthest neighbour clustering with a stopping rule of 80% similarity. Five clusters
32 of pigs representing 90% of the population (1047 pigs) were identified. For each regrouping
33 aggressive behaviour trait and for fresh lesion counts 24h post-regrouping the means differed
34 significantly ($P < 0.0001$) between clusters. The most extreme clusters were characterised by extremely
35 high or low levels of aggression with the other three clusters characterised by pigs that were
36 unaggressive losers, selectively aggressive or with long fights. Statistically significant ($P < 0.05$ –
37 $P < 0.001$) but numerically small differences between clusters were found in lesion count 3 weeks post-
38 regrouping. Pigs were separately categorised based upon their combination of lesion counts recorded
39 24h and 3 weeks post-regrouping. Pigs showing similar behaviour at regrouping displayed wide
40 ranging combinations of acute and chronic lesion outcomes. Pigs with particularly low lesion counts
41 at both regrouping and 3 weeks post-regrouping were found in all 5 clusters. Avoidance of aggressive
42 behaviour at regrouping resulted in few lesions at 24h but more lesions at 3 weeks. Increasing the
43 proportion of pigs in the population that receive few lesions from both regrouping and chronic
44 aggression may require management strategies that manipulate behaviour in both contexts. Long-term
45 costs of avoiding regrouping aggression, represented by lesion counts three weeks after re-grouping,
46 show that regrouping aggression may retain an important function in domesticated pigs and
47 potentially in other species.

48 **Keywords:** Aggression; pig; lesion; social; fighting; cluster analysis

49

50 **1. Introduction**

51

52 Aggressive behaviour is a component of the behavioural repertoire of both wild boar and
53 commercially managed pigs. The behaviours performed are similar in these two contexts but the
54 quantity is typically much increased under commercial production, particularly when unfamiliar
55 animals are suddenly introduced with minimal opportunity to withdraw (regrouping; Mendl, 1995).
56 Regrouping occurs several times in the life of most commercial pigs globally and the aggression
57 associated with this and subsequent chronic aggression in stable social groups can be damaging even
58 when resource needs for survival are fully met (e.g. Séguin et al., 2006; Turner et al., 2009).
59 Regrouping aggression has deleterious impacts on animal welfare and economic productivity and has
60 been the subject of much research to find a cost-effective method to reduce its expression. Less effort
61 has been placed on the consequences of, and methods to control chronic aggression in stable social
62 groups, although its welfare and economic impacts are likely to be significant (e.g. Tan et al., 1991).
63 Management or breeding approaches that reduce the costs of aggression in both of these contexts are
64 required.

65

66 The accumulation of skin lesions has been shown to reflect involvement in aggressive behaviour and
67 the location of the lesions on the body allow interpretation of whether their cause was reciprocated
68 fighting or non-reciprocated bullying (McGlone, 1985; Turner et al., 2006a). Furthermore, high
69 numbers of skin lesions are associated with heightened plasma cortisol and metabolites indicative of
70 muscle fatigue, a poorer growth rate, increased backfat depth, poorer food conversion efficiency,
71 poorer meat quality and lower reproductive output (Rundgren and Löfquist, 1989; Warris et al., 1998;
72 Turner et al., 2006b; Tönepöhl et al., 2013). As such, the reduction in skin lesions is an appropriate
73 target to easily measure the success of management change designed to control aggression. Large
74 phenotypic and genetic variation exists between individual pigs of the same breed managed
75 contemporaneously under the same conditions in the number of lesions received from regrouping
76 aggression and aggression in stable social groups (Turner et al., 2006a, 2009; Desire et al., 2015). The
77 phenotypic correlation between the number of lesions received in these two contexts is low (Turner et
78 al., 2009; Desire et al., 2015) and pigs therefore exist which have few lesions in both contexts, have
79 many lesions in both contexts or which have few in one context and many in the other.

80

81 Large differences also exist between pigs in the expression of the underlying aggressive behavioural
82 traits (e.g. Erhard et al., 1997; Turner et al., 2006a). Tönepöhl et al. (2013) and Desire et al. (2015)
83 have shown that aggressive behavioural strategies performed at regrouping affect the accumulation of
84 lesions at regrouping, but are also associated with the number of fresh lesions pigs continue to receive
85 many weeks post-regrouping. The association between aggressive behavioural strategy at regrouping
86 and long-term lesion number appears to be mostly independent of fight success and is present at both
87 the pig and pen levels (Desire et al., 2015). However, at present it is unclear what aggressive strategy
88 or strategies are played by pigs which accrue few lesions from both acute regrouping aggression and
89 subsequent chronic aggression in stable social groups. This study seeks to characterise the aggressive
90 behaviour of such pigs during the 24 hours following regrouping when aggressive social interactions
91 are most frequent and intense. Pigs which receive few lesions under both regrouping and stable social
92 contexts might be regarded as possessing phenotypes that would be the optimum target of
93 management interventions designed to control aggression. This study therefore aims to provide the
94 basic knowledge, currently lacking, of the behavioural strategies performed by these pigs during the
95 regrouping period which may inform the management approaches that will favour the proliferation of
96 these desirable phenotypes.

97

98

99 **2. Methods**

100

101 **2.1. Ethical statement**

102 The study was carried out in strict accordance with the recommendations in the European Guidelines
103 for accommodation and care of animals. The protocol was approved by the SRUC Ethical Review
104 Committee. End points were in place to prevent injury exceeding levels seen on other commercial
105 animals housed contemporaneously on the same farm. Endpoints determined that if an animal reached

106 this point they would be housed in a hospital pen and veterinary advice sought. No animal was
107 hospitalised or required veterinary treatment due to aggression during the course of the study.

108

109 **2.2. Animals and housing**

110 The subjects were 1163 grower stage pigs (701 purebred Yorkshire and 462 crossbred Yorkshire x
111 Landrace; 357 males, 119 castrates and 687 females) born and managed in 14 batches on a Swedish
112 commercial farm. Pigs were housed in littermate groups without regrouping until 70.5 (SD 4.3) days
113 of age and 27.6 (SD 5.6) kg bodyweight when they were regrouped into new groups of 15 using the
114 protocol described below. The pens into which the pigs were mixed had a floor space allowance of
115 0.85 m²/pig (29% slats; 71% lightly bedded solid flooring). This space allowance is considerably
116 more generous than that required by the European Union Council Directive 2008/120/EC (0.30 m² per
117 20-30kg pig) which increased the opportunity to avoid aggressive encounters if pigs wished. *Ad*
118 *libitum* dry pelleted food was provided from a single space feeder and *ad libitum* water was available
119 from a nipple drinker. The mean ambient temperature was 19.4 (SD 2.9) °C.

120

121 **2.3. Regrouping and lesion counting**

122 Single sex and single-breed groups of 15 were formed by mixing three pigs from each of five
123 littermate groups. As far as possible, pigs of a similar body weight were regrouped together.
124 Immediately before regrouping, the sex, breed, litter details, pre-regrouping lesion count, and identity
125 were recorded for each pig. After 24 h, the animals were weighed, and a post-regrouping lesion count
126 was recorded from which the pre-regrouping lesion count was subtracted. The number of fresh lesions
127 estimated to be within 24 hours old (fresh blood, bright red in colour or with recent and continuous
128 scabs) was counted by a single observer throughout. Separate lesions were counted when two injuries
129 were orientated in the same direction but separated by an approximate distance of at least 5mm of
130 undamaged skin. Lesions were superficial and therefore severity was not recorded. Lesions to the
131 front (head, neck, shoulders, and front legs), middle (flanks and back), or rear (rump, hind legs, and

132 tail) of the body were recorded separately. Around 3 weeks after regrouping at 89.8 (SD 5.2) days of
133 age, lesions were again counted on one occasion.

134

135 **2.4. Behavioural recording**

136 Pigs were video recorded for 24 hours post-regrouping and were individually identifiable by spray
137 paint marks applied to their backs immediately before regrouping. The frequency and duration of
138 reciprocal and non-reciprocal aggression were recorded together with the identity of the initiator and
139 winner where these were clear. Reciprocal aggression was defined as a fight that lasted for more than
140 one second where both pigs were involved in pushing, head knocking or biting (Turner et al., 2006a).
141 Two severities of reciprocal aggression were separately recorded; escalated reciprocal aggression
142 included bites delivered at a rate of at least one bite every 3 seconds while non-escalated reciprocal
143 aggression included bites delivered at a slower rate, head knocks and pushes. The initiator of
144 reciprocal aggression was recorded as the pig which delivered the first bite. Fight success was
145 recorded when a pig pursued a retreating animal over a distance of at least 1 m and did not receive
146 renewed damaging aggression from the loser for at least 3 seconds. Non-reciprocal aggression
147 involved the delivery of escalated aggression with no retaliation from the receiver. Non-reciprocal
148 aggression could occur as a unique event independent of a reciprocal fight, as a component of a
149 reciprocal fight, or at the end of a reciprocal fight as the loser retreated. Three observers extracted
150 these data from the videos. Analysis of three 1 hour samples of data showed a significant degree of
151 inter-observer association (mean $r = 0.83$, $P < 0.001$). A large number of quantitative behavioural
152 traits ($n=31$) were derived from these data to characterise a pig's involvement in, and its tendency to
153 initiate and win aggression. These were used to study the behavioural strategies of pigs with
154 contrasting lesion count outcomes. Table 1 lists the 10 traits most informative in characterising the
155 behaviour of the pigs and the rationale for selecting these 10 is explained below.

156 **Table 1.** Mean expression of behavioural traits in each of the five clusters.

	Cluster 1 (n=195 pigs)	Cluster 2 (n=199 pigs)	Cluster 3 (n=168 pigs)	Cluster 4 (n=330 pigs)	Cluster 5 (n=155 pigs)	SED	F statistic	Population mean (n=1047 pigs)	Population SEM
	‘Selectively aggressive’	‘Unaggressive losers’	‘Aggression avoiders’	‘Persistent aggressors’	‘Extreme aggressors’				
Sum of aggression									
Total duration of escalated RA ¹	5.39 (218.2)	4.87 (129.3)	1.12 (2.1)	6.18 (482.0)	6.75 (853.1)	0.09	1145	5.05 (155.0)	0.06
Total duration of RA ²	5.59 (266.7)	5.13 (168.0)	1.23 (2.4)	6.56 (705.3)	7.18 (1311.9)	0.09	1135	5.35 (209.6)	0.07
Total frequency of RA	2.00 (6.4)	1.51 (3.5)	0.36 (0.4)	2.42 (10.2)	2.98 (18.7)	0.04	1108	1.92 (5.8)	0.03
Total duration of all interactions ³	5.95 (382.8)	5.37 (213.9)	3.30 (26.1)	6.70 (811.4)	7.31 (1494.2)	0.07	1037	5.85 (346.2)	0.05
Total frequency of all interactions	2.72 (14.2)	2.03 (6.6)	1.48 (3.4)	2.97 (18.5)	3.51 (32.4)	0.04	691	2.58 (12.2)	0.02
Initiation and receipt of aggression									
Frequency of initiated RA	1.35 (2.9)	0.66 (0.9)	0.09 (0.1)	1.74 (4.7)	2.42 (10.2)	0.05	734	1.30 (2.7)	0.03
Total frequency of all initiated interactions	1.93 (5.9)	0.93 (1.5)	0.35 (0.4)	2.28 (8.8)	2.98 (18.7)	0.05	732	1.75 (4.8)	0.03
Duration of received RA	4.76 (115.7) ^a	4.72 (111.2) ^a	0.94 (1.6)	5.72 (303.9)	6.29 (538.2)	0.10	717	4.67 (105.7)	0.06

Duration of escalated RA received	4.53 (91.8) ^a	4.46 (85.5) ^a	0.87 (1.4)	5.34 (207.5)	5.86 (349.7)	0.10	697	4.38 (78.8)	0.06
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Outcome of aggression

Duration of RA lost	3.79 (43.3)	4.56 (94.6)	0.58 (0.8)	5.51 (246.2)	5.84 (342.8)	0.11	700	4.26 (69.8)	0.06
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157 Only the 10 traits with the highest F statistic are shown. Values presented are the natural logarithm of means (back-transformed means in parentheses). SED
 158 and SEM are estimated for log_e transformed data. Within a row, all pairwise comparisons between clusters were significant at between p<0.05 and p<0.001
 159 unless shown by the same superscripts. All durations were measured in seconds.

160 ¹RA = reciprocal aggression

161 ²Unless explicitly stated otherwise, 'RA' is the sum of escalated and non-escalated reciprocal aggression.

162 ³All interactions' included reciprocal and non-reciprocal aggression given and received.

163

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168 **2.5. Statistical analysis**

169 **2.5.1. Cluster analysis of behavioural strategies at regrouping**

170 All lesion count traits and several of the behavioural traits showed positively skewed distributions and
171 a log transformation $Y = \log_e(1 + \text{observation})$ was used as appropriate to reduce the skewness and to
172 satisfy the assumption of normality. A similarity matrix comparing every pig with each other was
173 computed using all 31 behavioural traits and based on the squared Euclidean distance metric, which
174 removes the effects of scale, thus making each behavioural variable comparable. A hierarchical
175 cluster analysis (Genstat, 15th Edition, VSN International Ltd, UK) was undertaken. Cluster formation
176 was based on the furthest neighbour criterion and a stopping rule of 80% similarity. Pen identity was
177 not accounted for in the construction of the clusters as pen effects have previously been found to
178 account for only a small proportion of the variance in skin lesions and aggressive behaviour in the
179 same sample of pigs (0.04 to 0.13; Turner et al., 2009).

180

181 Pigs within a cluster necessarily shared similar behavioural expression on average across all traits, but
182 cluster analysis cannot illustrate where clusters statistically differ in expression of each individual
183 behavioural trait. To estimate how the expression of each of the 31 behavioural traits differed between
184 the clusters, cluster means for each of the traits were compared by fitting linear mixed models using
185 the residual maximum likelihood (REML) algorithm. Cluster identity was fitted as a fixed effect
186 while the random effects part of the model reflected the hierarchical structure of pigs nested within
187 pens, nested within batches of pens. Only the 10 traits with the highest F statistic indicating greatest
188 deviation between clusters are shown in Table 1. With few exceptions, all pair-wise comparisons of
189 clusters differed at a highly statistically significant level ($P < 0.001$) with respect to all of the 31
190 behavioural traits. As a result, a second approach was used to identify the key behavioural traits that
191 characterised each cluster by finding those traits expressed with greatest similarity by members of a
192 cluster. The total variance of all standardised behavioural traits within a cluster was summed and the
193 variance of each individual behaviour was then expressed as a proportion of the total variance of that

194 cluster. As pigs within a cluster shared similar behavioural profiles, those behaviours that accounted
195 for the lowest proportion of the total variance had, by definition, played the largest role in clustering
196 the pigs together. The five traits determined on that basis to be most influential in grouping pigs into
197 each cluster are shown in Fig. 1. The remaining 13 traits not described in either Table 1 or Fig. 1 were
198 less informative in characterising the clusters and will not be considered further (three describing total
199 involvement in aggression; seven describing the initiation and receipt of aggression and three
200 describing the outcome of aggression, including whether the winner was ambiguous or clear).
201 Differences between clusters in skin lesion count and body weight were investigated in the same
202 manner by fitting mixed models as for the 31 behavioural traits.

203

204 **2.5.2. Association between regrouping behaviour and short and long-term** 205 **skin lesions**

206 A principal aim of the study was to understand how aggressive behavioural strategies performed at
207 regrouping resulted in contrasting skin lesion outcomes when the two contexts of regrouping and the
208 stable social group situation were taken together. To investigate this, pigs were categorised by
209 simultaneous reference to their lesion counts at regrouping and at 3 weeks post-regrouping relative to
210 the population distribution for these traits. Categorising pigs by reference to both regrouping and
211 stable group lesion counts allowed examination of both the immediate and long-term effects of
212 different behavioural strategies performed at regrouping. Specifically, the population was divided into
213 four categories based on quartiles of regrouping lesion counts and then further categorised based on
214 quartiles of stable group lesion counts. In total therefore, 16 categories were formed ranging from
215 pigs with the lowest quartile regrouping and lowest quartile stable group lesion counts through to pigs
216 with the highest quartile regrouping and highest quartile stable group lesion counts. This
217 categorisation was performed separately for lesions to the front of the body which primarily result
218 from reciprocal fighting (Turner et al. 2006a) and for the total lesion count (sum of lesions to the
219 front, middle and rear of the body). Chi square analyses were then used to determine whether
220 behavioural clusters contained a higher or lower number of pigs from different lesion count categories

221 than expected. The Chi square analyses used expected values based on all 16 categories but were
222 performed only for the four most extreme combinations of regrouping and stable group lesion counts
223 (lowest quartile – lowest quartile (LL); highest quartile – highest quartile (HH); lowest quartile –
224 highest quartile (LH) and highest quartile – lowest quartile (HL) for regrouping and stable group
225 lesion counts respectively). This allowed a focus on understanding how pigs with comparable lesion
226 counts at one time point (e.g. lowest quartile at regrouping) diverged to an extreme degree at the other
227 time point (e.g. lowest vs. highest quartile stable group lesion count). Two behavioural clusters with
228 expected values of fewer than five pigs in any of the lesion count categories were excluded from the
229 Chi square analyses. Significant deviations from expected numbers of pigs were identified by
230 inspection of residuals after adjustment by the method of Haberman (1973) to have a mean of 0 and
231 standard deviation of 1. Residuals greater than 2.0 were taken as evidence of a statistically significant
232 difference from expected values at $P < 0.05$.

233

234

235 **3. Results**

236

237 **3.1. Characteristics of behavioural clusters**

238 Seven behavioural clusters were identified by the cluster analysis but two were removed from further
239 analysis. These two clusters contained 34 and 82 animals in total which was regarded as insufficient
240 to study extreme combinations of regrouping and stable group lesion counts. The number of animals
241 in the remaining clusters is shown in Table 1. No significant differences between clusters were found
242 in body weight at regrouping (ranging from 27.0 SE 0.41 (cluster 3) to 28.4 SE 0.37 kg (cluster 5),
243 $P > 0.1$). Highly statistically significant differences were apparent between all clusters in the amount
244 that each of the quantitative behavioural traits was expressed. Table 1 shows cluster means for the 10
245 behavioural traits that showed greatest difference in expression between the clusters. Out of a total of
246 310 possible pair-wise comparisons between clusters in expression of the 31 behavioural traits, all

247 apart from six were statistically significant at $p < 0.05$ and nine at $p < 0.001$. For the suites of
248 behavioural traits in Table 1 describing the sum of aggressive interactions or tendency to initiate
249 aggression, differences were apparent between each of the clusters in the order 3<2<1<4<5.

250

251 Fig. 1 summarises the five quantitative behavioural traits that accounted for the lowest proportion of
252 the total variance in behaviour in each cluster. These parameters played the largest role in categorising
253 pigs together into a common cluster by virtue of similar behavioural expression. Traits associated
254 specifically with involvement in non-reciprocal aggression were less influential in clustering pigs
255 together than those associated specifically with reciprocal aggression. Three traits describing
256 involvement in non-reciprocal aggression (number of pigs attacked, frequency of non-reciprocal
257 aggression given and the sum of that given and received) were included in the cluster analysis, but
258 none accounted for a low proportion of the total behavioural variance in any cluster. There was much
259 overlap between clusters in the behavioural traits that were instrumental in clustering pigs together.
260 For example, the total durations of reciprocal aggression and escalated reciprocal aggression both
261 proved important in forming four of the five clusters as shown by the low proportion of total
262 behavioural variance attributable to these traits. Clustering of pigs into Clusters 2 and 3 was based
263 upon a more unique set of behavioural traits that focussed more specifically on the outcome of fights
264 rather than the total quantity of fights.

265

266 [INSERT FIGURE 1 HERE]

267

268 Fig. 2 plots the duration involved in reciprocal aggression that a pig won against the duration of
269 reciprocal aggression that the pig lost for animals in each of the five behavioural clusters. At the
270 extremes of behavioural expression, pigs in Cluster 3 largely avoided engagement in reciprocal
271 aggression (hereafter ‘aggression avoiders’), whilst those in Cluster 5 engaged in a median of 22
272 minutes (interquartile range 16.7 - 29.7) of this behaviour (‘extreme aggressors’). Inspection of Table
273 1 and Fig. 2 would suggest that pigs in Cluster 2 were less successful in winning reciprocal aggression
274 than those in other clusters (‘unaggressive losers’). Pigs in Cluster 1 (‘selectively aggressive’) showed

275 an amount of aggression similar to the population mean, but were more successful than pigs in other
276 clusters apart from the extreme aggressors (Cluster 5). Lastly, Cluster 4 was characterised by
277 aggressive pigs which fought for a shorter total duration than pigs in the ‘extreme aggressor’ cluster
278 (5) but had fights of similar mean duration (‘persistent aggressors’).

279

280 [INSERT FIGURE 2 HERE]

281

282 A large number of significant differences were estimated in lesion counts at regrouping between the
283 clusters of pigs. At regrouping, the pigs in the ‘aggression avoider’ cluster (3) accrued the lowest total
284 number of lesions (mean 8.0), whilst those in the ‘extreme aggressor’ cluster (5) gained the highest
285 number (mean 46.5); $p < 0.001$; Table 2). This pattern was also apparent for the front, middle and rear
286 body regions. Fewer significant differences in lesion counts 3 weeks post-regrouping were found
287 between behavioural clusters. Pigs in the ‘aggression avoider’ cluster (3) had a greater total lesion
288 count (26.3) than those in any other cluster (20.8 – 22.8; $P < 0.05$). Furthermore, pigs in this cluster
289 also had significantly more stable group lesions specifically to the front and the middle of the body
290 than pigs in most of the other clusters ($P < 0.05$), although numerical differences were small.

291 **Table 2.** Mean skin lesion counts for pigs in each of the five clusters.

	Cluster 1 (n=195 pigs) 'Selectively aggressive'	Cluster 2 (n=199 pigs) 'Unaggressive losers'	Cluster 3 (n=168 pigs) 'Aggression avoiders'	Cluster 4 (n=330 pigs) 'Persistent aggressors'	Cluster 5 (n=155 pigs) 'Extreme aggressors'	SED	F	Significance	Population mean (n=1047 pigs)	Population SEM
Lesions at regrouping										
Front	2.59 (12.3)	2.27 (8.7)	1.52 (3.6)	2.94 (17.9)	3.39 (28.7)	0.10	105.2	P<0.001	2.59 (12.3)	0.03
Middle	2.11 (7.3) ^a	1.90 (5.7)	1.59 (3.9)	2.26 (8.6) ^a	2.56 (11.9)	0.10	22.9	P<0.001	2.10 (7.2)	0.03
Rear	1.47 (3.4) ^{ab}	1.33 (2.8) ^{ac}	1.15 (2.2) ^c	1.57 (3.8) ^{bd}	1.71 (4.5) ^d	0.09	9.6	P<0.001	1.44 (3.2)	0.03
Total	3.11 (21.4)	2.88 (16.8)	2.20 (8.0)	3.42 (29.6)	3.86 (46.5)	0.12	60.6	P<0.001	3.12 (21.7)	0.04
Stable group lesions										
Front	2.31 (9.1) ^{ab}	2.31 (9.1) ^{abc}	2.48 (10.9) ^c	2.26 (8.6) ^a	2.28 (8.8) ^{ab}	0.06	5.0	P<0.001	2.31 (9.1)	0.02
Middle	2.26 (8.6) ^{abc}	2.35 (9.5) ^{ad}	2.46 (10.7) ^d	2.22 (8.2) ^{be}	2.20 (8.0) ^{ce}	0.07	6.5	P<0.001	2.28 (8.8)	0.02
Rear	1.50 (3.5) ^a	1.55 (3.7) ^a	1.53 (3.6) ^a	1.44 (3.2) ^a	1.53 (3.6) ^a	0.08	1.2	P=0.31	1.48 (3.4)	0.02
Total	3.13 (21.9) ^a	3.17 (22.8) ^a	3.30 (26.1)	3.08 (20.8) ^a	3.10 (21.2) ^a	0.06	5.1	P<0.001	3.13 (21.9)	0.02

292 Values presented are the natural logarithm of means (back-transformed means in parentheses). Within a row, all pairwise comparisons between clusters were
 293 significant at between p<0.05 and p<0.001 unless shown by the same superscripts. SED and SEM are estimated for log_e transformed data.

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3.2. Composition of clusters with respect to combinations of regrouping and stable lesion counts

3.2.1. Lesions to the front of the body

For simplicity, only pigs falling into the upper or lower quartile lesion categories at both regrouping and at 3 weeks post-regrouping are described below (lowest-lowest (LL, n=85 pigs); lowest-highest (LH, n=64); highest-lowest (HL, n=71); highest-highest (HH, n=75) for regrouping and stable group lesion counts respectively). For lesions to the front of the body, the lowest lesion count quartile at regrouping ranged from 0-7 lesions and the highest ranged from 27-99 lesions. At 3 weeks post-regrouping, the lowest front lesion count quartile ranged from 0-7 and the highest from 13-63. Each of the five behavioural clusters contained pigs from all four of the lesion categories (Fig. 3) with the exception of the ‘aggression avoider’ cluster (3) which contained no pigs classified as HL or HH. Significantly more LL pigs were found in the ‘unaggressive loser’ and ‘aggression avoider’ clusters (2 and 3) and fewer in the ‘persistent aggressor’ and ‘extreme aggressor’ clusters (4 and 5) than expected by chance ($p < 0.05$; Table 3). The same distribution was found for LH pigs except there was no statistical evidence that they were under- or over-represented in the ‘unaggressive loser’ cluster (2). In contrast, HL pigs were under-represented in the ‘selectively aggressive’, ‘unaggressive loser’ and ‘aggression avoider’ clusters (1, 2 and 3) and over-represented in the ‘persistent aggressor’ and ‘extreme aggressor’ clusters (4 and 5). Lastly, HH pigs were under-represented in the ‘aggression avoider’ cluster (3) and over-represented in the ‘extreme aggressor’ cluster (5).

[INSERT FIGURE 3 HERE]

319 **Table 3.** Residuals of the number of pigs in each behavioural cluster according to lesion counts on the
 320 front of the body.

Cluster	Front lesion count quartile class			
	LL ¹	LH	HL	HH
1: 'Selectively aggressive'	0.63	-0.30	-2.59	-1.53
2: 'Unaggressive losers'	2.55	-0.05	-3.29	-1.60
3: 'Aggression avoiders'	3.81	8.69	-3.81	-3.93
4: 'Persistent aggressors'	-3.11	-4.21	3.07	1.64
5: 'Extreme aggressors'	-3.37	-3.07	6.40	5.36

321 Positive residuals greater than 2.0 or negative residuals greater than -2.0 (in bold) were taken as
 322 evidence of a greater or lesser number of pigs respectively within a cluster than expected at p<0.05.
 323 The actual number of pigs with each lesion outcome present in each cluster is shown in Fig. 3.

324 ¹Acronyms refer to lowest (L) and highest (H) quartile lesion count at regrouping (first letter) and in
 325 stable social groups (second letter). For example, LL indicates lowest quartile regrouping and lowest
 326 quartile stable group lesions.

327

328

329 **3.2.2. Total count of lesions to the whole body**

330 As above, only data on pigs categorised into the lesion count quartiles LL (n=66), LH (n=63), HL
 331 (n=62) and HH (n=75) are described below. For the total lesion count on the body (sum of front,
 332 middle and rear lesions), the lowest lesion count quartile at regrouping ranged from 0-13 lesions and
 333 the highest ranged from 49-199. At 3 weeks post-regrouping, the lowest total lesion count quartile
 334 ranged from 0-16 and the highest from 33-115. Pigs from LL, LH, HL and HH lesion categories were
 335 present in all five of the behavioural clusters with the exception of HL pigs which were absent from
 336 the 'aggression avoider' cluster (3). The representation of these four lesion categories in the clusters
 337 (Table 4) was similar to that described above (and shown in Fig. 3) when pigs were categorised
 338 according to lesions to the front of the body. Specifically, LL and LH pigs were both over-

339 represented in the ‘aggression avoider’ cluster (3) and under-represented in the ‘persistent aggressor’
 340 and ‘extreme aggressor’ clusters (4 and 5). HL pigs were under-represented in the ‘unaggressive
 341 loser’ and ‘aggression avoider’ clusters (2 and 3) and over-represented in the ‘persistent aggressor’
 342 and ‘extreme aggressor’ clusters (4 and 5). Lastly, HH pigs were under-represented in the ‘aggression
 343 avoider’ cluster (3) and over-represented in the ‘extreme aggressor’ cluster (5).

344

345

346 **Table 4.** Residuals of the number of pigs in each behavioural cluster according to lesion counts to the
 347 whole of the body (sum front, middle and rear regions).

348

Cluster	Total lesion count quartile class			
	LL	LH	HL	HH
1: ‘Selectively aggressive’	1.21	-0.24	-1.19	0.32
2: ‘Unaggressive losers’	1.77	0.67	-2.93	-1.61
3: ‘Aggression avoiders’	2.57	6.33	-3.54	-2.30
4: ‘Persistent aggressors’	-2.14	-3.32	2.38	-0.16
5: ‘Extreme aggressors’	-3.14	-2.68	5.09	4.01

349 Positive residuals greater than 2.0 or negative residuals greater than -2.0 (in bold) were taken as
 350 evidence of a greater or lesser number of pigs respectively within a cluster than expected at $p < 0.05$.

351 ¹Acronyms refer to lowest (L) and highest (H) quartile lesion count at regrouping (first letter) and in
 352 stable social groups (second letter). For example, LL indicates lowest quartile regrouping and lowest
 353 quartile stable group lesions.

354

355

356 4. Discussion

357

358 **4.1. Characteristics of behavioural clusters**

359 The five clusters of pigs were formed using 31 traits describing their aggressive behaviour at
360 regrouping. The clusters differed significantly in the quantity with which they expressed all 31 traits.
361 The large sample size probably facilitated the identification of statistically significant differences
362 between clusters, but inspection of the cluster means suggests that the differences were numerically
363 large and probably biologically meaningful. This suggests that no single trait, or small number of
364 traits, were responsible for characterising the behavioural profile of the different clusters. The
365 behavioural traits were identified that explained the lowest proportion of the total behavioural
366 variance within a cluster and were therefore expressed with greatest similarity by cluster members.
367 The identified traits showed large amounts of overlap between clusters. From this, it appears that
368 behavioural strategies of individual pigs are more easily clustered on the basis of the quantity rather
369 than the quality of aggressive behaviour. Beyond this generalisation it was evident that the most
370 aggressive clusters ('persistent aggressor' and 'extreme aggressor'; clusters 4 and 5) were formed due
371 to similarities between their members in the total duration of aggressive behaviour performed,
372 particularly reciprocal aggression. The least aggressive clusters of pigs ('unaggressive losers' and
373 'aggression avoiders'; clusters 2 and 3) were formed based on slightly different sets of quantitative
374 behavioural traits associated with fight outcomes as well as the quantity of aggression *per se*. Pigs in
375 the 'unaggressive loser' cluster (2) were the least successful in winning reciprocal aggression
376 encounters whilst pigs in the 'aggression avoider' cluster (3) largely avoided all forms of aggression
377 and consequently neither won nor lost fights. Evidence of pigs which successfully avoid regrouping
378 aggression has also been presented by Camerlink et al. (2014) who reported that these pigs appear to
379 show other alterations in their response to regrouping (greater sociality evidenced by closer spatial
380 integration and more non-damaging social nosing).

381

382 **4.2. Implications of behavioural strategies for skin lesions**

383 Although highly significant differences in lesion counts at regrouping were apparent between clusters
384 of pigs, fewer differences between clusters were present 3 weeks post-regrouping. Where statistically

385 significant differences between clusters in lesion counts were identified 3 weeks post-regrouping, the
386 numerical differences were slight. This suggests that the aggressive strategy played at regrouping has
387 discernible but only small effects on skin lesions 3 weeks post-regrouping. This is largely in
388 agreement with the results of Tönepöhl et al. (2013) who found evidence that some but not all aspects
389 of aggressive behaviour of sows at regrouping affected lesion counts 10 weeks later and that these
390 effects were restricted to lesions on the front of the body. Furthermore, no significant differences were
391 found between clusters of pigs in the current study in the number of lesions specifically to the rear of
392 the body at 3 weeks post-regrouping. The rump usually receives lesions during non-reciprocated
393 bullying typical of defeat and submission (Turner et al., 2006a). The absence of an effect of
394 aggressive behavioural strategy on these lesions suggests that receipt of chronic on-going bullying 3
395 weeks post-regrouping was not affected by the behaviour of pigs at regrouping, even where pigs
396 avoided contests associated with the establishment of dominance relationships ('aggression avoiders';
397 cluster 3) or tended to lose these ('unaggressive losers'; cluster 2).

398

399 Several suggestions may be offered to explain the minor role played by regrouping aggression in
400 determining long-term lesion outcomes. Although regrouping aggression is key to the establishment
401 of social relationships between unfamiliar pigs, it is probable that the major determinant of fresh
402 lesions received under stable social conditions is the proximate long-term aggressive strategy of pigs
403 played in the weeks following regrouping. This will be partially determined by the need to compete
404 for resources, although in the current study the floor space allowance was generous and the feeder and
405 drinker provision complied with guidelines to industry (e.g. the feeder provision was close to that
406 required by the higher welfare RSPCA Freedom Food scheme and drinker provision met the
407 requirements of the UK Defra Code of Recommendations for the Welfare of Pigs). Differences in
408 ability of individual pigs to dynamically adapt their aggressive behavioural strategy based on fight
409 experience have been reported (Bolhuis et al., 2005) and may also explain why pigs which show
410 similar behaviour at regrouping can subsequently diverge greatly in the number of lesions shown
411 under stable social conditions. Aggressive behaviour performed in groups of stable composition
412 refines and maintains previously established social relationships and is often provoked during

413 competition for limited resources (Hagelsø Giersing and Studnitz, 1996). Other non-aggressive social
414 behaviours, such as appeasement and social grooming, may also be influential in the long-term
415 maintenance of these relationships (Camerlink et al., 2014) and may play a role in determining the
416 number of lesions resulting from chronic aggression. Lastly, this study has quantified engagement in
417 aggressive behaviour without regard to the identity of the opponent. The use of more sophisticated
418 analytical methods such as social network analysis (e.g. Wey et al., 2008; Makagon et al., 2012;
419 Büttner et al., 2015) to produce new quantitative measurements for each animal summarising their
420 interactions in a complex social network could provide new insight that would help to understand the
421 behaviour of pigs that are successful in avoiding lesions from both regrouping and chronic aggression
422 (LL pigs).

423

424 Regrouping aggression does not appear to cluster into discrete, identifiable behavioural strategies
425 responsible for specific combinations of lesion outcomes across social contests. For example, the
426 aggressive behavioural strategy performed at regrouping does not explain the cause of the marked
427 divergence of LL from LH pigs. The present analysis has examined the behaviours associated with
428 specific combinations of lesions from these two contests with a focus on pigs with uniformly low or
429 high lesions across the two time points (LL, HH) or those that transitioned from one extreme to the
430 other (LH, HL). The data indicate that most behavioural clusters contained pigs with all of these
431 lesion outcomes despite sharing greater than 80% similarity in behavioural profile in the 24 hours
432 following regrouping. These patterns were apparent for the total number of lesions to the entire body
433 and to those located on the front region alone which is the usual target of bites during reciprocal
434 aggression (Turner et al., 2006a).

435

436 However, differences between clusters in the relative abundance of pigs with each lesion outcome
437 were apparent. For lesions to the front of the body, the least aggressive cluster ('aggression avoiders';
438 cluster 3) contained more LL pigs than expected by chance and no HL or HH pigs. The number of LH
439 pigs was much greater than that expected by chance suggesting that the strategy of avoiding
440 regrouping aggression was associated with the receipt of many lesions 3 weeks post-regrouping.

441 Lesions to the front of the body tend to result from engagement in reciprocal fighting rather than
442 receipt of bullying (Turner et al., 2006a). As a result, these LH pigs that were unaggressive at
443 regrouping appear to have shown significant amounts of reciprocal aggression in the following weeks.
444 Evidence from rats suggests that experience of fighting, even when this leads to defeat, can reduce the
445 amount of aggression received by animals when they subsequently meet unfamiliar individuals
446 (Lehner et al., 2011). This, together with the current data, may indicate that there is a long-term cost
447 to avoiding aggression. The most aggressive cluster ('extreme aggressors'; cluster 5) contained fewer
448 LL pigs than expected and more HL and HH pigs. As a cluster, these pigs were the most successful at
449 winning encounters at regrouping compared to pigs in other clusters (except the 'selectively
450 aggressive' cluster (1)) and, as such, may be expected to have attained the highest dominance rank. If
451 this is the case, it is perhaps unsurprising that this cluster contained many HL pigs. However, it is
452 interesting that it also contained a disproportionately high number of HH pigs which continued to
453 receive many fresh lesions to the front of the body 3 weeks post-regrouping, long after dominance
454 relationships should have been formed. Potentially these pigs received many challenges to their high
455 dominance position requiring frequent reciprocal aggression or they were simply more aggressive
456 pigs as a result of genetic and lifetime experiential effects. The patterns described above were very
457 similar for the total lesion count.

458

459

460 **4.3. Implications for management**

461 Reducing aggression at regrouping and in stable social groups implies a proliferation of LL pigs in the
462 population. As all behavioural clusters contained LL pigs, favouring the production of LL pigs
463 through management or breeding is unlikely to eliminate from the population any aggressive strategy
464 identified in this study. The only aggressive behavioural strategy which was associated with a greater
465 likelihood of an LL outcome was that displayed by the 'aggression avoider' cluster (3), characterised
466 by the total avoidance of reciprocal aggression at regrouping. However, this strategy also resulted in
467 many LH pigs and a total lesion count 3 weeks post-regrouping that was significantly higher than for

468 any other cluster. It has been suggested previously (Mendl and Erhard, 1997; Turner et al., 2010) that
469 an unwillingness to fight may result from high levels of fear and therefore measures of affective state
470 of pigs of different aggressive strategy, and lesion outcomes would be particularly valuable in guiding
471 effort to better control aggression and improve welfare. To understand how injuries at regrouping and
472 in later stable groups compare in their effects on welfare it would also be beneficial to identify any
473 difference in severity of lesions at these two time points, as well as the number of lesions as here.

474

475 Management strategies which focus solely on minimisation of aggressive behaviour at regrouping
476 appear unlikely to benefit the number of lesions pigs receive in the longer-term. The simultaneous
477 reduction in aggression in these two social contexts is likely to require the direct and simultaneous
478 targeting of lesion count at both time points through appropriate management change. The phenotypic
479 correlation between lesion counts at regrouping and 3 weeks post-regrouping is significant but low
480 (Turner et al., 2009; Desire et al., 2015). However, larger genetic correlations have been estimated
481 between lesion counts in these two contexts (Turner et al., 2009). This suggests that management
482 change and breeding to reduce aggression in one social context (regrouping or stable social groups)
483 will have different impacts on the other context. Unlike management change, selective breeding for a
484 low lesion count in only one context may achieve a simultaneous reduction in lesions in the other
485 context without requiring the recording of lesion counts in both situations.

486

487 **5. Conclusions**

488 Aggressive behaviour at regrouping and subsequently under conditions of stable group composition
489 are affected by different motivational drivers (Hagelsø Giersing and Studnitz, 1996), despite sharing
490 some commonality in genetic determination illustrated by their genetic correlation. Aggression in
491 both contexts is unlikely to respond simultaneously to a management intervention made under only
492 one of these contexts. Practical and economic constraints limit opportunities to reduce lesions from
493 aggressive behaviour. At present it is unknown how a reduction in the high number of lesions
494 received over a short period at regrouping would compare in welfare and economic impacts to a

495 reduction in the lower number of lesions received over a longer period in stable social groups. Work
496 to understand where effort is best targeted to maximise welfare and economic gains would be
497 beneficial. Evidence that avoidance of regrouping aggression results in a higher number of lesions
498 from chronic aggression whose location indicates involvement in reciprocated aggression shows that
499 regrouping aggression may retain a function in domestic pigs. This may have implications for other
500 species where regrouping aggression occurs and effort is made to reduce its expression.

501

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508

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587

588 **Fig. 1.** Percentage of total behavioural variance explained by quantitative behavioural traits for each
589 of the five clusters (C1-C5) of pigs. For clarity, only the five behavioural traits per cluster are shown
590 that accounted for the lowest percentage of the total behavioural variance as these contributed most to
591 clustering pigs together based on similarity of behavioural expression. RA = reciprocal aggression.

592

593 **Fig. 2.** Distribution of pigs from each of the five behavioural clusters with respect to the duration of
594 reciprocal aggression won (sec; X axis) and the duration of reciprocal aggression lost (sec; Y axis).

595

596 **Fig. 3.** The number of pigs from each behavioural cluster that displayed extreme combinations of
597 lesion counts to the front of the body at regrouping and 3 weeks post-regrouping (stable group).
598 Acronyms refer to lowest (L) and highest (H) quartile lesion count at regrouping (first letter) and in
599 stable social groups (second letter). For example, LL indicates lowest quartile regrouping and lowest
600 quartile stable group lesions.

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