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## Complex contests and the influence of aggressiveness in pigs

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*Published in:*  
Animal Behaviour

*DOI:*  
[10.1016/j.anbehav.2016.08.021](https://doi.org/10.1016/j.anbehav.2016.08.021)

First published: 28/09/2016

*Document Version*  
Peer reviewed version

[Link to publication](#)

*Citation for published version (APA):*  
Camerlink, I., Arnott, G., Farish, M., & Turner, SP. (2016). Complex contests and the influence of aggressiveness in pigs. *Animal Behaviour*, 121, 71 - 78. Advance online publication. <https://doi.org/10.1016/j.anbehav.2016.08.021>

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# 1 Complex contests and the influence of aggressiveness in pigs

2

3 Animal contests vary greatly in behavioural tactics used and intensity reached, with some encounters  
4 resolved without physical contact while others escalate to damaging fighting. However, the reasons  
5 for such variation remains to be fully explained. Aggressiveness, in terms of a personality trait, offers  
6 a potentially important source of variation that has typically been overlooked. Therefore, we studied  
7 how aggressiveness as a personality trait influenced escalation between contestants matched for  
8 resource holding potential (RHP), using detailed observations of the contest behaviour, contest  
9 dynamics, and escalation levels. We predicted that winner and loser behaviour would differ depending  
10 on personality. This was tested by examining 52 dyadic contests between pigs (*Sus scrofa*).

11 Aggressiveness was assayed in resident-intruder tests prior to the contest. Contests were then staged  
12 between pigs matched for RHP in terms of body weight but differing in their aggressiveness. In 27%  
13 of the contests a winner emerged without escalated physical fighting, demonstrating that a fight is not  
14 a prerequisite between RHP-matched contestants. However, the duration of contests with or without  
15 fighting was the same. In contests without a fight, opponents spent more time on mutual investigation  
16 and non-contact displays such as parallel walking, which suggests that ritualized display may  
17 facilitate assessment and decision making. Winners low in aggressiveness invested more time in  
18 opponent investigation and display and showed substantially less aggression towards the loser after its  
19 retreat compared to aggressive winners. Aggressiveness influenced contest dynamics but did not  
20 predict the level of escalation. Prominent behavioural differences were found for the interaction  
21 between personality and outcome and we therefore recommend including this interaction in models  
22 where personality is considered. Analyses based on contest duration only would miss many of the  
23 subtleties which are shown here and we therefore encourage more detailed analyses of animal  
24 contests, irrespective of the level of contest escalation.

25

26 **Keywords.** Aggression, behaviour, contest, personality, pig

27

28 Animal contests are typically assessed through simple measures of contest duration and outcome  
29 (reviewed by Arnott & Elwood, 2009). However, a great deal of information may be lost using this  
30 approach alone, including differences in physiological state and motivation (e.g. Elwood, Wood,  
31 Gallagher, & Dick, 1998). For example, on some occasions, contestants spend time in low cost  
32 display behaviour after which the opponent with the lowest resource-holding potential (RHP, or  
33 fighting ability) withdraws. On other occasions contestants spend the same amount of time interacting  
34 but fight fiercely for that length of time, after which the opponent with the lowest RHP withdraws. In  
35 the traditional approach these contests would be rated the same whereas for the contestants there is a  
36 large difference in, amongst other things, physiological costs (Briffa & Sneddon, 2007). More detailed  
37 analysis of contests, for example inclusion of physiological measures or analysis by phases of  
38 escalation (e.g. Hsu, Lee, Chen, Yang & Cheng, 2008; Vieira & Peixoto, 2013; McGinley, Prenter, &  
39 Taylor, 2015), can deepen our understanding of contest behaviour (e.g. Jennings, 2014; Schnell,  
40 Smith, Hanlon, & Harcourt, 2015).

41 One situation in which a great deal of information may be lost is when confrontations are resolved  
42 without escalated aggression. Many species avoid escalation where possible and contests may  
43 naturally end without the occurrence of a fight or even before the opponents make contact (e.g.  
44 Bentley, Hull, Hardy, & Goubault, 2009). Here, dominance is settled through threat displays (e.g.  
45 Maynard-Smith & Price, 1973; primates: Judge & de Waal, 1993; pigs: Jensen, 1982). Theory  
46 predicts (e.g. the sequential assessment model, SAM) that contests ending at the display phase prior to  
47 escalated fighting will be of shorter duration (Parker & Rubenstein, 1981; Enquist & Leimar, 1983),  
48 while those between RHP-matched individuals will be escalated and of longer duration. However, this  
49 overlooks the potential importance of individual differences in behavioural tendencies that may  
50 influence escalation patterns (Briffa, Sneddon & Wilson, 2015; Camerlink, Turner, Farish, & Arnott,  
51 2015). Moreover, non-escalated contests are often excluded from analyses because they may count as  
52 missing values, for example when outcome criteria are based on the presence of a certain level of  
53 escalation. Yet, these contests may provide useful information on contest resolution (as for example in  
54 Rudin & Briffa, 2011), and their exclusion has been criticised (Elwood & Arnott, 2013). Neglecting

55 contests that do not perfectly fit into theoretical or statistical models may underestimate the  
56 importance of certain strategies such as conflict avoidance.

57 Firstly, contrary to current theory, we predict that within a population of RHP-matched individuals,  
58 some confrontations will be resolved without a fight and that these non-escalated contests will be of  
59 shorter duration. This will be tested using domestic pigs. In wild populations, pigs frequently show  
60 agonistic display towards each other but damaging aggression, including fights, between adults is rare  
61 (Mendl, 1995; Marchant-Forde & Marchant-Forde, 2005; D'Eath & Turner, 2009) and is  
62 predominantly limited to males during the mating season (Barette, 1986). In contrast, the routine  
63 mixing of groups of unfamiliar pigs in commercial husbandry results in long and injurious reciprocal  
64 fights irrespective of sex, which is a considerable welfare issue (Marchant-Forde & Marchant-Forde,  
65 2005). However, there are substantial individual differences in the amount of aggression (Turner et  
66 al., 2006), and this variation has been related to personality (e.g. Ruis et al., 2000).

67 Secondly, we hypothesize that variation in contest behaviour (such as ritualized display, non-  
68 damaging aggression, and damaging aggression) and contest intensity will be influenced by the  
69 personality of the contestants. A personality trait is “a specific aspect of a behavioural  
70 repertoire that can be quantified and that shows between-individual variation and within-individual  
71 consistency” (Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013, p. 467). Personality is related  
72 to many behavioural and physiological characteristics (e.g. Stamps & Groothuis, 2010), including the  
73 response that an individual shows when faced with an opponent and its subsequent likelihood of  
74 winning (e.g. Colléter & Brown, 2011; Melotti, Oostindjer, Bolhuis, Held, & Mendl, 2011). As such,  
75 personality has recently been suggested as a component of RHP (reviewed by Briffa et al., 2015).

76 Aggression is one personality trait which can have an important role in contest behaviour. In pigs,  
77 aggressiveness is commonly assessed in the resident-intruder test; a test which has demonstrated  
78 considerable variation between individuals and a moderate repeatability within individuals (Erhard &  
79 Mendl, 1997; D'Eath, 2004). We previously showed that aggressiveness as a personality trait,  
80 measured with the resident-intruder test, influenced the initiation of agonistic behaviour during a  
81 subsequent contest, although evidence that it formed a component of RHP was lacking, as  
82 aggressiveness did not have a significant effect on the outcome or contest duration when an escalated

83 fight occurred (Camerlink et al., 2015). Existing contest theory (e.g. SAM, Enquist & Leimar, 1983)  
84 predicts encounters between RHP-matched contestants will be maximally escalated. However, this  
85 overlooks the potentially important role of variation in aggressive personality and therefore we predict  
86 that variation in this personality trait will result in variation in escalation level, even between RHP-  
87 matched contestants.

88 Our objective is to investigate how aggressiveness, assayed as a personality trait, of the winner and  
89 loser affects contest behaviour and escalation. To achieve this, contests were analysed for the  
90 dynamics and durations of all specific agonistic behaviours. We predict that 1) contrary to existing  
91 theory, only a proportion of contests between RHP-matched individuals will escalate to fighting and  
92 that these will be of a shorter duration; 2) variation in aggressiveness as a personality trait will result  
93 in variation in escalation level, even between RHP-matched contestants; and 3) winners and losers  
94 that differ in aggressiveness will show differences in their expression of contest behaviour. These  
95 predictions were studied using 104 size-matched pigs. In addition we provide a detailed analysis of  
96 contest dynamics to outline how certain behaviours provoke escalation.

97

## 98 **METHODS**

99 The study was approved by SRUC's Animal Ethics Committee and the UK Government Home Office  
100 legislation ensuring compliance with EC Directive 86/609/EEC for animal experiments and adhered  
101 to the ASAB guidelines. A full description of ethical considerations and methods has been detailed  
102 previously in Camerlink et al. (2015) and are summarised below.

103

### 104 *Animals and housing*

105 A total of 114 young male and female pigs ((Large White×Landrace) × American Hampshire) from  
106 17 litter groups were studied at 9 wk of age at the research farm (Easter Howgate, UK). Animals were  
107 studied over three consecutive batches from April to October 2014. Piglets were kept with their sow  
108 in conventional farrowing crates up to 4 wk of age. Thereafter the sow was removed and the piglets  
109 remained in the crate for two more weeks. Males were not castrated and the tail and teeth were kept  
110 intact. At 6 wk of age pigs were moved to the experimental facilities where they were kept with their

111 siblings in a pen measuring 1.9×5.8 m (~1.0-1.1 m<sup>2</sup> / animal). Pens had a solid floor with straw  
112 bedding (~5 kg) and were cleaned daily and provided with fresh straw. Water and pelleted feed was  
113 available *ad libitum*. From two weeks prior to testing all pigs were gradually (over six occasions)  
114 habituated to the various test situations to reduce the possibility of fear responses during the tests.

115

#### 116 *Resident-intruder test*

117 The resident-intruder (RI) test is an established test in behaviour research that is undertaken to obtain  
118 a quantifiable measure of individual aggressiveness which is consistent over time (pigs: D'Eath &  
119 Pickup, 2002). The RI test was carried out twice for each pig at 9 wk of age. An individual "resident"  
120 pig was kept in a separate part of its home pen for the duration of the test (max 10 min). Then, an  
121 approximately 20% smaller and unfamiliar "intruder" pig was introduced into the same compartment  
122 (i.e. the resident's home pen). Under these conditions, the resident typically attacks the inferior  
123 intruder within a short period of time. The latency until the first attack was recorded. If the resident  
124 did not attack within 5 min after initial contact then the test was ended and the latency time was set at  
125 300 s. For all pigs the test was repeated the following day with a different intruder. Residents were  
126 thus tested twice for their aggressiveness. Pigs were used as either a resident or intruder but never  
127 both. Intruders were used a maximum of 3 times. Test results of the second day were moderately  
128 correlated with the results of the first day ( $r_s = 0.58$ ;  $P < 0.001$ ). Similar correlations between test days  
129 have been reported previously for this test ( $r_s = 0.55 - 0.73$ , Erhard & Mendl, 1997). The attack  
130 latencies of both test days were summed to obtain a single value of aggressiveness. Values could  
131 range between 0 – 600 sec, with lower values reflecting a more aggressive response.

132

#### 133 *Contest*

134 Contests were staged in a neutral arena between pairs of unfamiliar pigs at 10 wk of age. Opponents  
135 were of similar body weight (<5% difference, i.e. matching RHP, with weight a validated measure of  
136 RHP in pigs; Andersen et al., 2000; Jensen & Yngvesson, 1998; Rushen, 1987) and differing in their  
137 aggressiveness as reflected in the attack latency of the RI test. Body weight ranged from 24 – 48 kg  
138 (mean  $34 \pm 0.5$  kg) and the summed attack latency ranged from 27 – 600 s (mean  $257 \pm 17$  s). To

139 ensure a balanced difference in aggressiveness, animals were for the purpose of opponent matching  
140 categorized into ‘low aggressive’ (summed attack latency of  $\geq 360$  s), ‘intermediate’ (121 – 359 s),  
141 and ‘high aggressive’ ( $\leq 122$  s). The range in attack latency that defined the bounds of these  
142 categories was derived from examination of the distribution of attack latencies as a continuous  
143 variable within the population. This resulted in weight-matched pigs from high against low  
144 aggressiveness ( $N = 16$ ), high-intermediate ( $N = 19$ ), and low-intermediate ( $N = 17$ ). Sexes were  
145 matched randomly which resulted in 15 male-male contests; 12 female-female contests; and 25 male-  
146 female contests. The arena was 2.9×3.8 m with a solid floor covered with a light bedding of wood  
147 shavings. Opponents entered the arena simultaneously from opposite sides. The time was started from  
148 the moment both had entered the arena and was stopped when a clear winner was apparent, when an  
149 animal reached an end-point due to a fear response or mounting, or otherwise after 30 min. A winner  
150 was recorded when one pig retreated after having received an aggressive act and failed to retaliate  
151 within 2 min after retreat. The contest was recorded by a Canon Legria HF52 camera located close to  
152 the ceiling. Five contests were excluded because they had to be stopped due to an end-point before an  
153 outcome was reached (four were ended due to a fear response or mounting; one contest reached the  
154 maximum time without a winner). This resulted in 52 contests (104 pigs of which 55 were males and  
155 49 females). Ending the contest prematurely prevented any injury other than superficial skin lesions  
156 due to receiving bites. Videos were observed for the duration and frequency of behaviours and the  
157 sequence in which they occurred. Observations were taken by one observer using The Observer XT  
158 11.5 (Noldus Information Technology, The Netherlands). The detailed ethogram of behaviours is  
159 given in Table 1. For analysis of the contest escalation, four levels were distinguished based on the  
160 intensity of the behaviours. These levels were I. display (non-damaging contact and low/medium  
161 intensity display); II. pushing (non-damaging high intensity display); III. biting (damaging  
162 low/medium intensity); and IV. fighting (damaging high intensity).

163

#### 164 *Data analysis*

165 Data were analysed with SAS version 9.3 (SAS Institute Inc., Cary, NC, USA) using mixed models  
166 (MIXED Procedure). Response variables were the proportion of contest time spent on a behaviour

167 (see Table 1 for behaviours analysed), the number of bites, contest duration, and aggressiveness in  
168 attack latency (all continuous data). Residuals of the response variables were assessed for the  
169 normality of their distribution (UNIVARIATE Procedure, Shapiro-Wilk statistics) and outliers  
170 (Studentized residuals). Model assumptions were tested using the REG (regression) Procedure;  
171 variables were tested for multicollinearity (VIF option), homoscedasticity (White test; SPEC option),  
172 and independence (Durbin-Watson coefficient; DW option). To obtain normality of the residuals,  
173 contest duration (in seconds) was log transformed; the behaviours investigation, nose wrestling,  
174 parallel walking, pushing, fighting and bullying (analysed in proportion of contest time) were arcsine  
175 square root transformed; and the number of bites (frequency) was square root transformed.

176 The mixed models had outcome status (winner or loser) as a repeated statement and contest as  
177 experimental unit (SAS syntax: repeated outcome / subject= contest) to account for dependence  
178 between opponents (as described by Briffa & Elwood, 2010). This specifies that the two opponents  
179 within a contest (i.e. the winner and loser) are not independent of each other. The random effects were  
180 batch (group of pigs at the same age) and litter (i.e. sibling group; 17 groups). The estimated random  
181 effects were normally distributed (EBLUPs extracted from the mixed models were assessed  
182 graphically and by Shapiro-Wilk statistic). The SAS default covariance structure (variance  
183 component) showed the best fit based on the lowest Akaike information criterion (AIC) and Bayesian  
184 information criterion (BIC) values compared to other covariance structures.

185 When behaviour was the response variable, the fixed factors that were included were attack latency,  
186 contest outcome (winner/loser), the interaction between attack latency and contest outcome, body  
187 weight, and sex (male/female). Fixed effects were stepwise removed from the models based on the  
188 evaluation of the goodness of fit, choosing the model with the lowest AIC and BIC.

189 The relationship between escalation level (4 levels) and contest duration, aggressiveness, and body  
190 weight was analysed with the continuous variables as response variable and escalation level as fixed  
191 class effect in order to allow for the complexity of the repeated and random model structure (of which  
192 the options are limited in a model with multinomial distribution) and to enable extraction of the  
193 LSmeans per category. The same method was applied for fight occurrence (1/0).

194 Data are presented as least square means (LSmeans) with standard errors.



195

196 *Analysis of contest dynamics*

197 Contest dynamics were analysed through sequential analysis using The Observer XT 11.5 (Noldus  
198 Information Technology, The Netherlands). Frequencies and probabilities of transitions between  
199 behaviours were extracted with the State Lag Sequential Analysis for lag -1 and lag 1, which captures  
200 the behaviour preceding and following the behaviour of interest respectively. Data are presented in a  
201 transition map where the radius of each circle reflects either the frequency or duration of occurrence  
202 of each behaviour as a percentage of the total frequency or duration of the whole contest, and the  
203 widths of the arrows indicate the probability of the transition from one behaviour to the next in the  
204 direction from tail to head of the arrow.

205

206 **RESULTS**

207

208 *Contest dynamics and phases of escalation*

209 Contests lasted on average  $339 \pm 19$  s (i.e. 5 ½ min.; range 119 – 1041 s). Contests typically  
210 progressed through incremental phases of intensity showing a linear escalation pattern (Figure 1). The  
211 contest dynamics, however, were more complex with transitions between phases of varying intensity  
212 (Figure 2). Lower-intensity behaviour could reoccur during higher escalation phases. For example,  
213 within contests there were on average 2.5 fights (range 0 – 22), which shows that between fights  
214 contestants paused and performed other behaviours.

215 The level of escalation was first assessed by four levels of intensity indicating the maximum intensity  
216 that a contestant had shown during the contest, which was either display, pushing, biting, or fighting.

217 The level of escalation did not influence the contest duration (Table 2;  $F_{3,84} = 1.39$ ;  $P = 0.25$ ).

218 Contestants who engaged in mutual fighting (escalation level 4) were on average heavier than pigs  
219 who only pushed or bit the opponent (Table 2;  $F_{3,82} = 2.82$ ;  $P = 0.04$ ). Contestants that bit the

220 opponent (level 3) were on average more aggressive than opponents whose maximum level of

221 aggression was pushing (level 2), but animals from escalation level 3 did not differ from level 1 or 4

222 (Table 2;  $F_{3,84} = 2.41$ ;  $P = 0.07$ ). Escalation level 1 and 2 included only few individuals ( $N = 3$  and 9,

223 respectively) and therefore contests were also analysed by the occurrence of a fight as a binary trait  
224 (i.e. the absence or presence of a mutual fight).  
225 Out of the 52 contests, 38 contests (73%) included mutual fights and in 14 contests (27%) no fight  
226 occurred but a clear winner was still apparent. Contests with a fight did not significantly differ in  
227 duration from contests without a fight (with fight  $337 \pm 19$  s; without fight  $345 \pm 50$  s;  $F_{1,86} = 0.76$ ;  $P$   
228  $= 0.39$ ). Contests were more likely to escalate into a fight when contestants were heavier (fight  $35.1 \pm$   
229  $2$  kg; no fight  $33 \pm 2$  kg;  $F_{1,84} = 5.5$ ;  $P = 0.02$ ) but the fight occurrence was unrelated to the  
230 contestants' aggressiveness as measured in the RI test (in attack latency; fight  $253 \pm 25$  s; no fight  $264$   
231  $\pm 36$ ;  $F_{1,86} = 0.09$ ;  $P = 0.77$ ). The behavioural profile of the contests with a fight significantly differed  
232 from the contests without a fight (Figure 1; Table 3). In contests which reached an outcome without  
233 fighting a greater percentage of the total contest time was spent on parallel walking. Less time was  
234 spent in the 'heads up' posture and there was less pushing. In these contests without a fight the winner  
235 spent 15% more time bullying the loser than in contests with a fight.

236

#### 237 *Aggressiveness as a personality trait affecting contest behaviour*

238 Aggressiveness as a personality trait significantly altered the behaviour of winners and losers,  
239 although numerical differences in the duration and frequency of behaviours were mostly small. More  
240 aggressive individuals (short attack latency in the resident-intruder test) bit their opponent in the  
241 contest more frequently than individuals which were assessed as less aggressive (long attack latency  
242 in RI test) ( $b = -0.02$  bites / s increase in attack latency;  $F_{1,82} = 5.94$ ;  $P = 0.02$ ; Figure 3). Winners  
243 delivered on average 13 bites more than losers (winners  $18 \pm 2$  bites; losers  $5 \pm 2$  bites;  $F_{1,82} = 34.7$ ;  $P$   
244  $<0.001$ ).

245 The most profound effects were observed for the interaction between aggressiveness and contest  
246 outcome. Winners which showed little aggression in the resident-intruder test spent more time during  
247 the contest on non-damaging opponent investigation (Figure 4a; interaction aggressiveness  $\times$  outcome  
248  $F_{1,83} = 5.91$ ;  $P = 0.02$ ), more parallel walking (Figure 4b;  $F_{1,84} = 6.10$ ;  $P = 0.02$ ) and tended to spend a  
249 greater amount of time on non-agonistic behaviours such as walking, standing and exploring the

250 environment ( $b = -0.04 \pm 0.02$  % / s increase of attack latency in losers, with winners set to 0;  $F_{1,80} =$   
251 3.73;  $P = 0.06$ ). The most prominent difference was seen after the contest outcome was established.  
252 After the retreat of the loser, winners with an aggressive personality (short attack latency) spent up to  
253 75% of the contest time on bullying behaviour (unilateral biting and chasing by the winner towards  
254 the loser), whereas less aggressive winners showed almost no bullying behaviour towards the losers  
255 (Figure 4c; aggressiveness  $\times$  outcome  $F_{1,83} = 12.60$ ;  $P < 0.01$ ). Moreover, losers which were assessed  
256 pre-contest as being less aggressive (long attack latency RI test) received more bullying than  
257 aggressive losers.

258 The behaviours 'heads up', nose wrestling, shoulder-to-shoulder, pushing, and mutual fighting (means  
259 provided in Table 3) were unaffected by the aggressiveness of the opponents, did not differ between  
260 winners and losers, and were not influenced by the interaction between aggressiveness and contest  
261 outcome (all  $P > 0.10$ ). Heavier opponents spent less time in nose wrestling ( $b = -0.20 \pm 0.1\%$  of time  
262 / kg;  $F_{1,81} = 12.23$ ;  $P < 0.001$ ) but were more engaged in the energetically costly pushing behaviour ( $b$   
263  $= 0.62 \pm 0.3\%$  of time / kg;  $F_{1,82} = 7.37$ ;  $P < 0.01$ ). Sex differences were (at this age) only found for  
264 pushing, with males spending considerably more time on this behaviour (males  $9.0 \pm 2\%$  of time,  
265 females  $5.0 \pm 2\%$ ;  $F_{1,82} = 7.73$ ;  $P < 0.01$ ).

266

## 267 **DISCUSSION**

268 Here we show that although the duration between contests may be the same, the content of the  
269 contests can differ greatly with regard to behaviour. This was most profoundly shown by the presence  
270 or absence of an escalated mutual fight during a contest even though the total contest duration until  
271 retreat by the loser was the same. The occurrence or not of a fight has profound effects on the  
272 energetic costs and the risk of injury. This implies that within contests of the same duration the  
273 specific behavioural interactions can determine completely different levels of severity.

274 Aggressiveness as a personality trait did not influence the occurrence of a fight or its outcome (as  
275 shown in Camerlink et al., 2015). However, aggressiveness resulted in behavioural differences when  
276 it came to the experience of victory or defeat whereby aggressive winners directed substantially more  
277 damaging aggression towards the loser after retreat as compared to unaggressive winners.

278

279 *To fight or not to fight*

280 The main difference between contests was the occurrence of a fight or the absence thereof whereas in  
281 both situations a clear winner and loser were present. This confirms that RHP-matched pigs can settle  
282 dominance relationships without needing to fight. This finding contrasts contest theory (e.g. SAM,  
283 Enquist & Leimar, 1983), as does the finding that contest duration did not differ between escalated  
284 and non-escalated contests.

285 The absence of a fight in some contests, together with an increase in parallel walking, a form of  
286 ritualized display, suggests that some form of assessment was made at a pre-fight phase (Mendl &  
287 Erhard, 1997; Arnott & Elwood, 2009). Display behaviour such as parallel walking has been studied  
288 in deer (Jennings & Gammell, 2013), where it has been suggested to aid opponent assessment (Clutton-  
289 Brock, Albon, Gibson, & Guinness, 1979; Jennings & Gammell, 2013). Contestants that invest more  
290 time in investigation and display may obtain more accurate information and consequently be better  
291 able to assess their opponent, resulting in a decision to avoid fighting. Conversely, animals with a low  
292 motivation to fight will be unwilling to escalate the contest and may therefore be expected to engage  
293 in longer periods of display prior to disengagement. It is possible that both of these mechanisms have  
294 a role in explaining the greater investment in display in contests that ended without a fight.

295 Contests in which the opponents avoid fighting or physical contact may occur frequently (e.g. Bentley  
296 et al., 2009; Rudin & Briffa, 2011). In analyses these contests are often ignored because the read-out  
297 parameters such as winning or losing may be absent or too subtle to fulfil the criteria. Elwood and  
298 Arnott (2013) previously discussed the issue of differing conclusions depending on whether  
299 researchers considered all contests or restricted analyses to escalated fights only. They advocated that  
300 in terms of furthering our understanding of animal contest behaviour, valuable information is lost if  
301 analyses are restricted to fights only. The decision to avoid fighting can be a strategy in itself  
302 (Maynard-Smith & Price, 1973; Parker & Rubenstein, 1981) and this should be taken into account  
303 when analysing animal contests, in particular when conclusions about assessment strategies are made.  
304 The present findings reiterate the importance of studying contest behaviour in addition to the

305 traditional measures of contest duration and outcome before conclusions are drawn about the  
306 assessment ability of animals.

307

308 *Effect of aggressiveness as a personality trait on contest behaviour*

309 Personality is increasingly investigated as a potential component of RHP (Briffa et al., 2015). The  
310 detailed analysis of the behavioural repertoire during a contest shows that aggressiveness as a  
311 personality trait had important influences on the content of the contest, with differing consequences  
312 for the cost of fighting. Previously we showed that aggressiveness as a personality trait did not  
313 influence the duration or outcome of the contest, but that aggressiveness provided an honest signal of  
314 intent as it predicted willingness to initiate aggression in a contest (Camerlink et al., 2015). The  
315 current study shows the added benefit of detailed behavioural observations in addition to traditional  
316 measures of animal contests.

317 Interactions between outcome and aggressiveness in our statistical models revealed that winners  
318 which had a long attack latency in the resident-intruder test, indicating low aggressiveness, invested  
319 more time in non-damaging opponent investigation, parallel walking and non-agonistic behaviours  
320 such as walking and exploration of the environment. These behaviours are less likely to escalate into  
321 damaging aggression, as was reflected in the analysis of contest dynamics, which suggests that more  
322 aggressive winners were taking more risks with their behaviour. Previously, we showed that pigs with  
323 a more aggressive personality were more likely to initiate aggression, especially bites, during the  
324 contest (Camerlink et al., 2015). Here we show that initiation of such behaviour has a high probability  
325 of transitioning into a fight. Moreover, after victory high aggressive winners continued to exert  
326 aggressive behaviour on the loser whereas low aggressive winners did not. This is in line with  
327 previous work showing that high aggressive pigs are more persistent in their aggressive behaviour  
328 (D'Eath, 2002). Together these results provide a consistent image that more aggressive personalities  
329 are more willing to engage in fighting, shown through a willingness to attack and through persistent  
330 aggressiveness. This is in line with other studies on personality, whereby animals with a proactive  
331 coping style are more bold and rigid in their aggressive behaviour (Koolhaas et al., 1999; Briffa et al.,  
332 2015; pigs: Bolhuis, Schouten, Schrama, & Wiegant, 2005; Melotti et al., 2011). Rudin and Briffa

333 (2012) also reported interactions between personality (boldness) and contest outcome in sea  
334 anemones, whereby losers were less bold than winners. The profound behavioural differences related  
335 to the interaction between personality and outcome in the current study would suggest that, where  
336 possible, researchers should try to incorporate these factors into their setup and analyses. Mendl and  
337 Erhard (1997) suggested that pigs differing in their aggressiveness as a personality trait may apply  
338 different contest assessment strategies, and this is the focus of another study that we have conducted.

339

#### 340 *Securing the outcome with bullying behaviour*

341 Winners with a more aggressive personality showed substantially more bullying behaviour upon  
342 winning than unaggressive winners, who showed hardly any bullying behaviour. This has previously  
343 been observed in groups of fighting pigs as well (D'Eath, 2002). Bullying is typically performed by  
344 the dominant individual after the subordinate individual has retreated, and involves the dominant  
345 animal chasing and biting the subordinate which attempts to flee (Melotti et al., 2011). Bullying is  
346 more often observed in less decisive fights (Jensen, 1994) which suggest that the outcome may be less  
347 clear when fights involve an aggressive animal, or that more aggressive winners have a stronger urge  
348 to reaffirm the outcome, which again may relate to potential differences in assessment ability (Mendl  
349 & Erhard, 1997).

350 Bullying behaviour was also considerably higher in contests without a fight as compared to contests  
351 with a fight. Fighting is energetically costly, and in contests where no fight took place the winner may  
352 have retained more energy to chase the loser whereas the loser may have retained more energy to flee  
353 (see Camerlink et al., 2015 for the physiological costs of these fights). If the loser retained energy by  
354 avoiding a fight this could also increase the chance that it would attempt to retaliate, which the winner  
355 could aim to avoid by chasing the loser. Energy expenditure and reaffirmation may thus be  
356 intertwined. It could be the case that similar amounts of bullying occur between contests with and  
357 without a fight at a later stage when contestants have regained energy.

358

#### 359 **CONCLUSION**

360 Contrary to predictions from contest theory, a substantial percentage of RHP-matched contests were  
361 settled without a fight. However, the duration of contests with and without fighting did not differ.  
362 These results highlight that RHP-matched contestants can solve conflicts by avoiding escalated  
363 damaging behaviour, and these contests should be studied rather than disregarded when investigating  
364 questions of assessment ability and aggressive strategies. Bullying behaviour just after the retreat of  
365 the loser, which was strongly related to aggressiveness, suggests that contestants employ different  
366 tactics to determine contest outcome. Given the important influence of personality on contest  
367 dynamics, we recommend that, where possible, this be considered in future studies of animal contests.

368

### 369 **ACKNOWLEDGEMENTS**

370 This research was funded by the Biotechnology and Biological Sciences Research Council (BBSRC).  
371 SRUC receives financial support from the Scottish Government Strategic Research Programme. We  
372 thank Miguel Soley for his assistance with the sequential analyses.

373

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468 determinants of fighting ability in arthropod contests. *Functional Ecology*, 27(2), 305-313.

469

470 **TABLES**471 **Table 1.** Ethogram of the major behaviours recorded during the contest\*.

Behaviour	Description
Investigation	Sniff or light touch to body of opponent with nose without force
Heads up	Display; Both have nose lifted high up in the air, either parallel or frontal
Nose wrestling	Both firmly press the side of their nose against the side of the nose of the other
Parallel walk	Display; Opponents walk simultaneously with the shoulders aligned
Shoulder-to-shoulder	Display; Standing or moving with the shoulder against the shoulder of the opponent without putting significant pressure on the shoulder
Pushing	Head/shoulder used to move opponent aside with pressure
Unilateral bite	Opens its mouth and delivers a bite which contacts the opponent
Mutual fight (fight)	Aggressive act, e.g. biting and pushing, which is retaliated with an aggressive act within 5 s. Continues until one retreats or until other behaviour is performed for at least 3 s.
Bullying	Unilateral pursuit including chasing, biting, or attempted biting
Withdrawal	Not retaliating to an aggressive act within 10 s after receipt. Includes a head tilt movement whereby the animal turns away its head from the opponent
Non-agonistic	Walking, standing, exploring the arena, lying, defecating, urinating or mounting (both front legs are over the back, rear, side or head of the opponent)

472 \* Contest refers to the total time that two opponents were in the contest arena.

473

474 **Table 2.** Levels of escalation (I – IV) in contests between size-matched opponents.

	I. Display ( <i>N</i> = 3)	II. Push ( <i>N</i> = 9)	III. Bite ( <i>N</i> = 16)	IV. Fight ( <i>N</i> = 76)	<i>P</i> -value
Contest duration (s)	202 ± 113	333 ± 56	399 ± 63	341 ± 33	0.25
Body weight (kg)	36.7 ± 3 <sup>ab</sup>	32.6 ± 3 <sup>a</sup>	32.5 ± 3 <sup>a</sup>	35.1 ± 2 <sup>b</sup>	0.04
Attack latency (s)	328 ± 100 <sup>ab</sup>	320 ± 46 <sup>a</sup>	166 ± 53 <sup>b</sup>	255 ± 20 <sup>ab</sup>	0.07

475 The *P*-value refers to the difference between the four levels of escalation. *N* shows the number of pigs  
 476 by their maximum level of escalation.

477 <sup>a,b</sup> Values lacking a common superscript letter differ by *P* <0.05.

478

479 **Table 3.** Average time budgets in percentage of contest time for contests with and without a fight.

Behaviour	Average (range)	Fight ( <i>N</i> = 37)	No fight ( <i>N</i> = 15)	<i>P</i> -value
Investigation	4.3 ± 0.4 (0-22.3)	3.8 ± 1.0	5.8 ± 1.2	0.15
Heads up	2.4 ± 0.3 (0-10.2)	2.8 ± 0.3	1.2 ± 0.5	<b>&lt;0.01</b>
Parallel walking	3.0 ± 0.3 (0-10.9)	2.6 ± 0.4	4.3 ± 0.6	<b>&lt;0.01</b>
Nose wrestling	3.2 ± 0.3 (0-13.1)	2.9 ± 0.7	3.7 ± 0.8	0.12
Shoulder to shoulder	13.8 ± 0.9 (0-32.6)	14.0 ± 2.2	12.5 ± 2.6	0.42
Pushing	7.1 ± 1.1 (0-53.1)	8.6 ± 1.2	3.1 ± 2.0	<b>0.03</b>
Unilateral biting (n bites)	11.6 ± 1.3 (0-66)	12.8 ± 2.0	8.0 ± 2.9	<b>0.10</b>
Mutual fighting	10.7 ± 1.0 (0-39.0)	14.9 ± 1.8	0.0 ± 0	.
Bullying	12.5 ± 1.8 (0-74.7)	8.2 ± 2.6	23.4 ± 3.6	<b>&lt;0.001</b>
Non-agonistic	43.0 ± 1.8 (5.4-87.7)	42.3 ± 3.0	46.0 ± 4.1	0.36

480

481 **FIGURE CAPTIONS**

482

483 **Figure 1.** Average latency (with standard error bars) after entering the arena at which the first  
484 occurrence of the behaviour listed on the x-axis was observed, displayed for contests with and without  
485 a fight.

486

487 **Figure 2.** Transition map of behaviours during dyadic contests. The circle radius indicates the relative  
488 duration or frequency of occurrence (durations of <3 sec or frequencies of on average <1 have the  
489 same radius). The colour groups the behaviours into overarching categories of intensity (from white  
490 (non-damaging investigation) to dark grey (damaging behaviour)). Arrow widths indicate the  
491 probability of the transitions. Transitions with a probability <0.10 are not displayed.

492

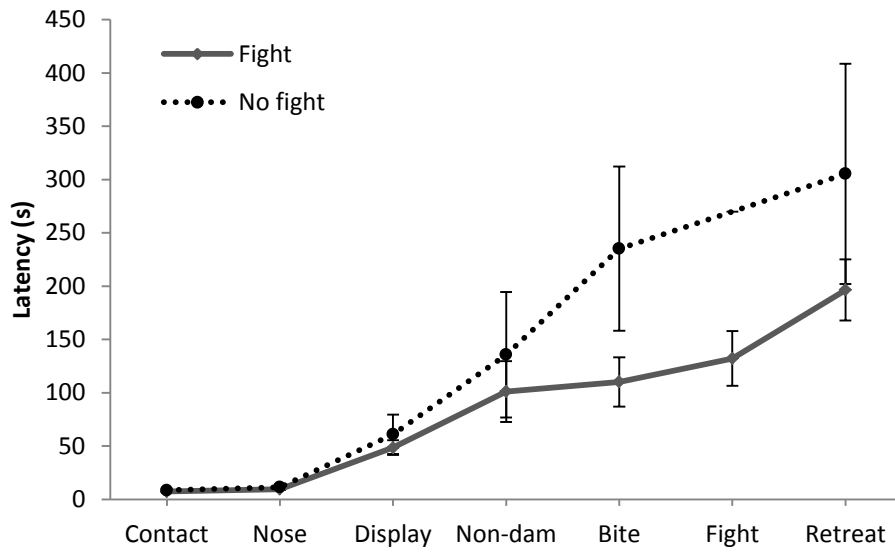
493 **Figure 3.** Number of unilateral bites (delivered outside fights) by winners and losers differing in  
494 aggressiveness reflected in attack latency. Winners are depicted in black circles and a solid trend line  
495 whereas losers are depicted in open circles and a dashed trend line.

496

497 **Figure 4 a – c.** The percentage of contest time spent on non-damaging investigation, parallel walking  
498 and bullying behaviour by winners and losers differing in aggressiveness as reflected by attack  
499 latency. A shorter attack latency reflects greater aggressiveness. Winners are depicted in black circles  
500 and a solid trend line whereas losers are depicted in open circles and a dashed trend line. The  
501 percentage of bullying for winners indicates the amount of time spent in chasing the loser whereas for  
502 the losers it means the time spent fleeing from the attacks of the winner.

503

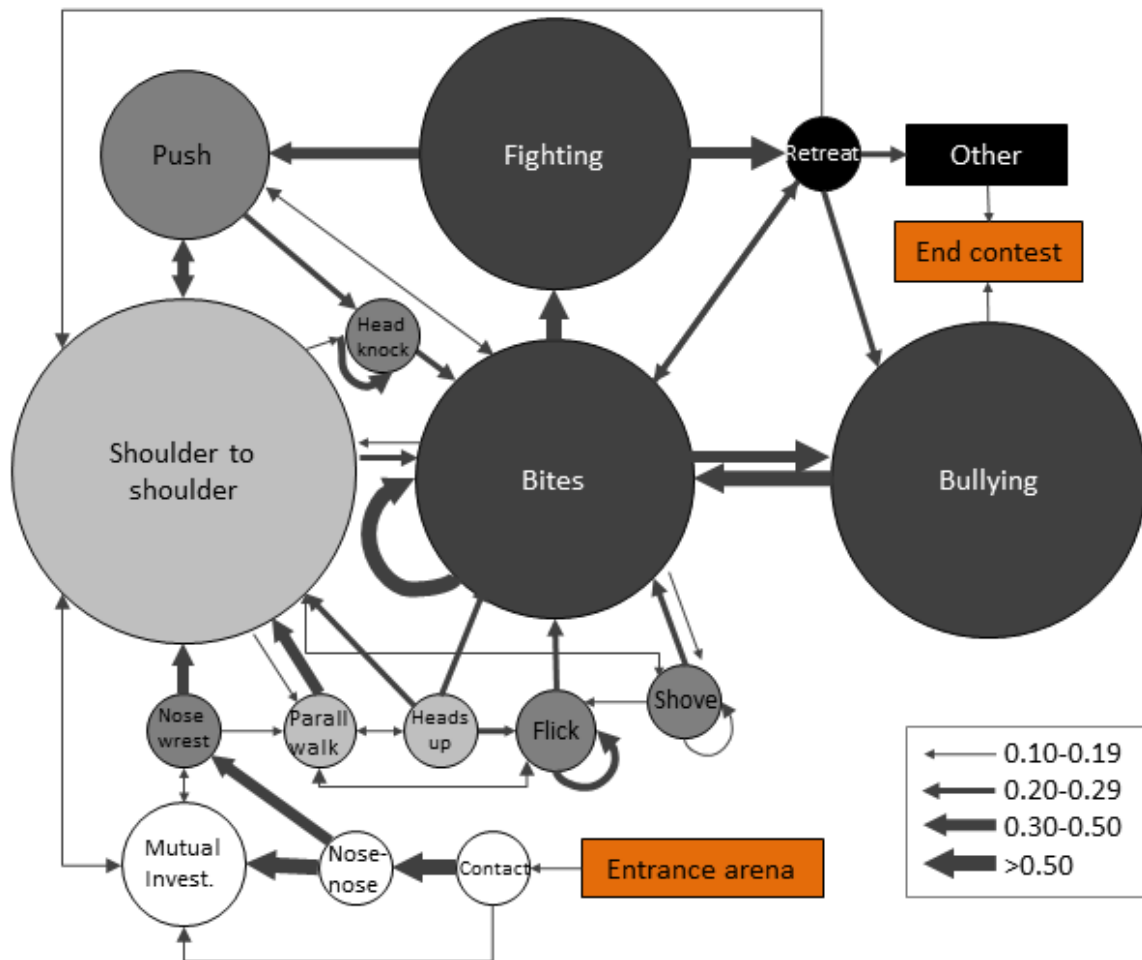
504 **Figure 1**



505

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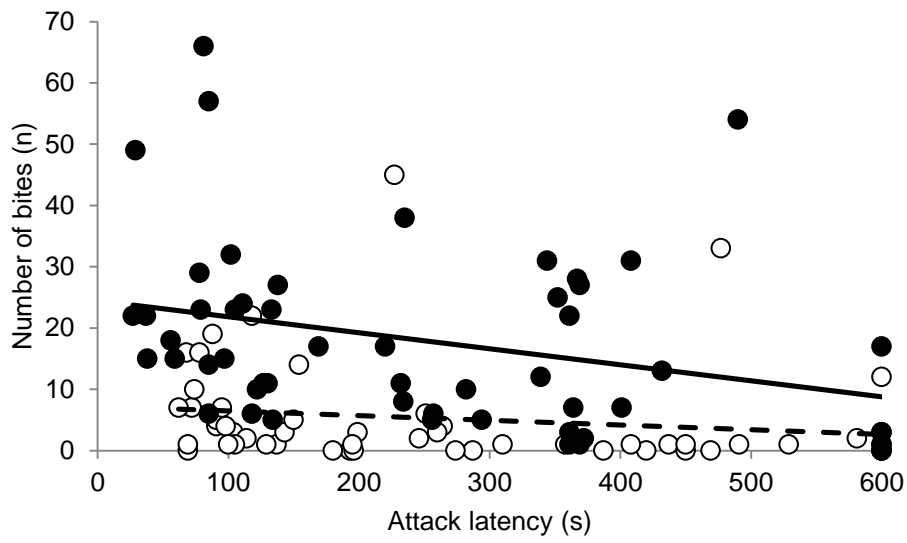
507 **Figure 2**



508

509 **Figure 3**

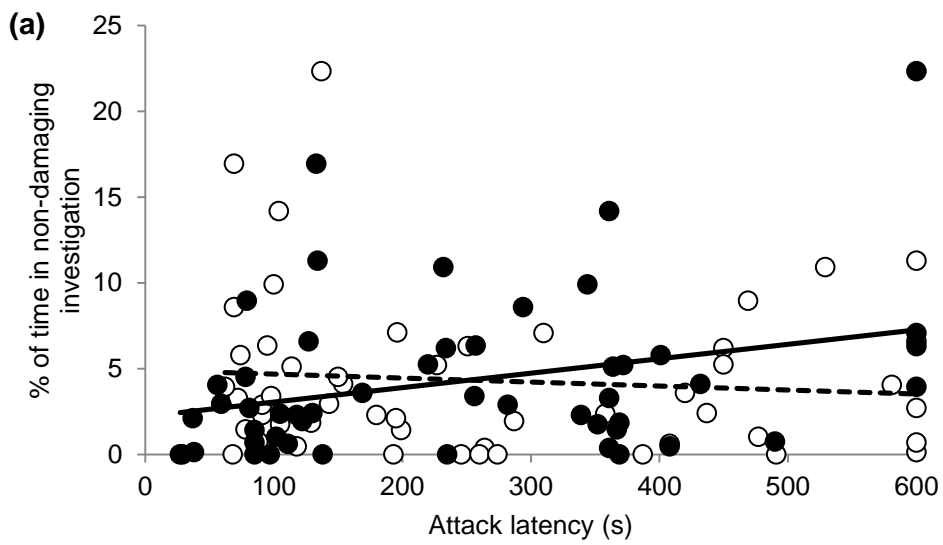
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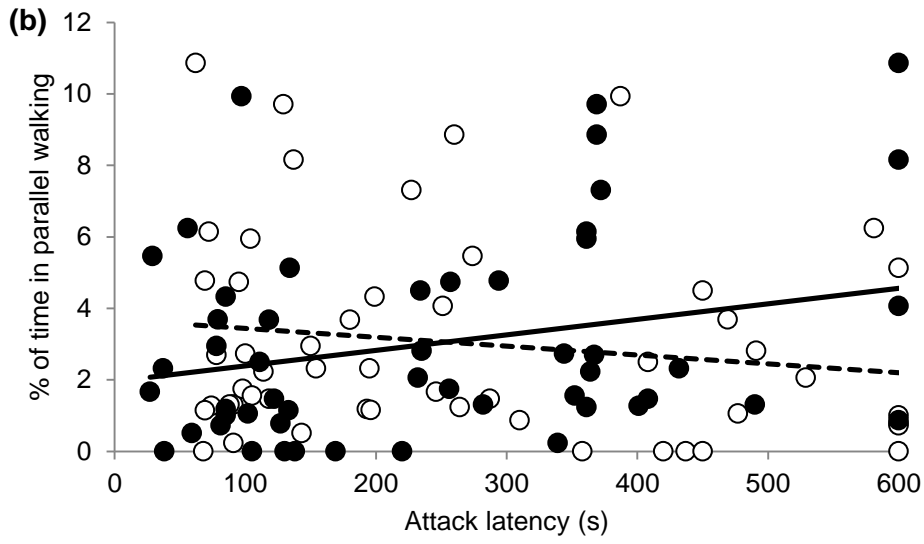
513 **Figure 4 a – c**



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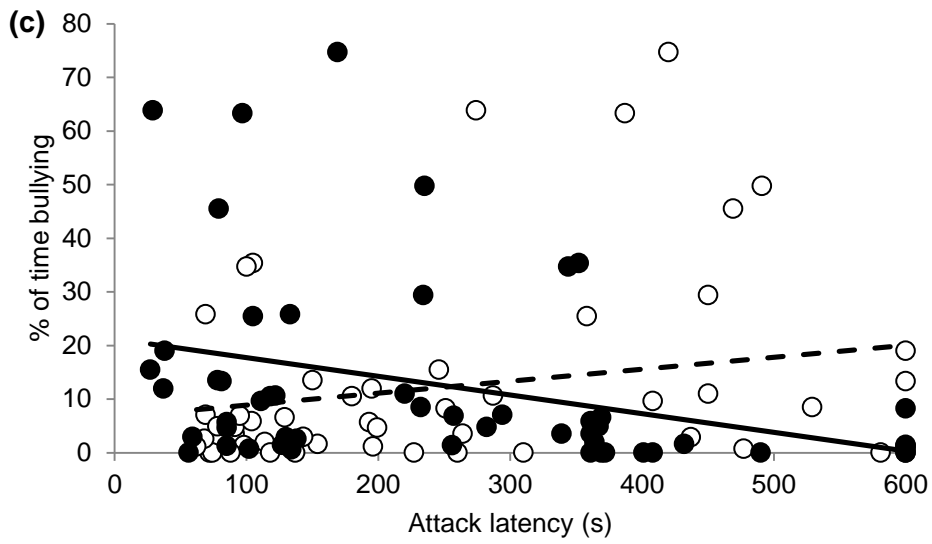
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