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1 Aggressiveness as a component of fighting ability in pigs (*Sus scrofa*) using a game-
2 theoretical framework

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18

19 Understanding animal contests has benefited greatly from employing the concept of fighting
20 ability, termed resource-holding potential (RHP), with body size/weight typically used as a
21 proxy. However, victory does not always go to the larger/heavier contestant and the existing

22 RHP approach thereby fails to accurately predict contest outcome. Aggressiveness, typically
23 studied as a personality trait, might explain part of this discrepancy. We investigated whether
24 aggressiveness forms a component of RHP, examining effects on contest outcome, duration
25 and phases, plus physiological measures of costs (lactate and glucose). Furthermore, using
26 the correct theoretical framework, we provide the first study to investigate whether
27 individuals gather and use information on aggressiveness as part of an assessment strategy.
28 Pigs, *Sus scrofa*, were assessed for aggressiveness in resident–intruder tests whereby attack
29 latency reflects aggressiveness. Contests were then staged between size-matched animals
30 diverging in aggressiveness. Individuals with a short attack latency in the resident–intruder
31 test almost always initiated the first bite and fight in the subsequent contest. However,
32 aggressiveness had no direct effect on contest outcome, whereas bite initiation did lead to
33 winning in contests without an escalated fight. This indirect effect suggests that
34 aggressiveness is not a component of RHP, but rather reflects a signal of intent. Winner and
35 loser aggressiveness did not affect contest duration or its separate phases, suggesting
36 aggressiveness is not part of an assessment strategy. A greater asymmetry in aggressiveness
37 prolonged contest duration and the duration of displaying, which is in a direction contrary to
38 assessment models based on morphological traits. Blood lactate and glucose increased with
39 contest duration and peaked during escalated fights, highlighting the utility of physiological
40 measures as proxies for fight cost. Integrating personality traits into the study of contest
41 behaviour, as illustrated here, will enhance our understanding of the subtleties of agonistic
42 interactions.

43

44 **Keywords.** aggression, assessment, contest, personality, pig, resource-holding potential

45

46 The understanding of what determines the winner of animal contests has benefited greatly
47 from employing the concept of fighting ability, termed resource-holding potential (RHP)
48 (Parker, 1974). Victory tends to go to the larger or heavier contestant, who generally has a
49 greater ability to inflict injury, and therefore body size or weight is often used as a proxy for
50 RHP. However, it is not always the case that the larger contestant wins (e.g. Neat,
51 Huntingford, & Beveridge, 1998a). Rather, a range of factors will determine the overall
52 ability of an animal to win a fight. Existing studies have uncovered a number of RHP
53 correlates, in a variety of animal species (Arnott & Elwood, 2009a), demonstrating that
54 multiple traits influence fighting ability (e.g. Stuart-Fox, 2006). Despite this research effort,
55 problems persist in predicting contest winners, highlighting limitations of the existing RHP
56 approach. Relying on relatively consistent morphological traits to predict likelihood of
57 contest success fails to reflect changes in RHP caused by contextual factors that vary more
58 rapidly in time, such as fatigue and experience of recent wins or defeats (Elwood & Arnott,
59 2012; Hsu, Earley, & Wolf, 2006).

60 Empirical studies, across a range of species, have demonstrated consistent between-individual
61 differences in aggressiveness, characterized by its repeatability over time and across
62 situations (reviewed in Briffa, Sneddon, & Wilson, 2015). Aggression has been defined as
63 overt behaviour that is intended to inflict physical damage to another (reviewed in Nelson &
64 Trainor, 2007). In the context of animal contests, aggressiveness has recently been mentioned
65 as the propensity of an individual to use agonistic behaviour that could include initiating a
66 contest, escalating a contest and attacking an opponent (glossary of Briffa et al. 2015).

67 Intuitively, one might predict that a more aggressive individual may be more likely to win
68 against a less aggressive opponent. If so, aggressiveness would constitute an important
69 determinant of RHP. However, the importance of integrating animal personality within
70 existing contest theory has only recently been acknowledged (Briffa et al., 2015), with

71 aggressiveness generally having been overlooked. However, boldness has been studied in
72 contest settings in sea anemones, with boldness being correlated with aggressiveness (Rudin
73 & Briffa, 2012). Aggressiveness might account for part of the discrepancy with existing
74 studies in which, contrary to expectations, the contestant with apparently superior RHP does
75 not win. This gives rise to the need to examine whether aggressiveness, in terms of a
76 consistent behavioural response, is a component of RHP determining the overall chances of
77 victory in a contest. To date, only two studies have examined the effect of aggressiveness on
78 contest outcome, with Wilson, Grimmer, and Rosenthal (2013) finding that agonistic
79 behaviour during a contest predicts dominance during a feeding trial in sheepshead swordtail
80 fish, *Xiphophorus birchmanni*, while McEvoy, While, Sinn, and Wapstra (2013) found no
81 effect of aggressiveness, measured as a combined score of agonistic behaviour towards a
82 species model, on contest outcome in a social lizard species, *Egernia whitii*. In light of these
83 conflicting results there is clearly a need to better understand the role of aggressiveness in
84 animal contests.

85 In addition to influencing fight outcome, correlates of RHP provide animals with a means to
86 gather information about the fighting ability of the opponent. Fighting is energetically costly
87 and also bears the risk of injury or death (e.g. Briffa & Elwood, 2005; Glass & Huntingford,
88 1988; Kelly & Godin, 2001). Selection should therefore favour individuals that make
89 appropriate decisions based on assessment of the costs and benefits of fighting (Maynard-
90 Smith & Parker, 1976; Parker, 1974; Parker & Rubenstein, 1981), although such assessment
91 does not always occur (Elwood & Arnott 2012; Mesterton-Gibbons & Heap 2014). There are
92 two classes of theoretical models of animal contests that differ in their assumptions about the
93 information-gathering abilities of contestants (reviewed by Arnott & Elwood, 2009a; Elwood
94 & Arnott, 2012). The first type, termed self-assessment, assumes that each contestant has
95 knowledge of its own RHP, but gathers no information about the opponent (e.g. ‘war of

96 attrition without assessment', Mesterton-Gibbons, Marden, & Dugatkin, 1996; 'energetic war
97 of attrition', Payne & Pagel, 1996, 1997; 'cumulative assessment model' (CAM), Payne
98 1998). In these models, two animals compete up to a particular threshold at which point one
99 gives up. Opponents each accrue costs (e.g. energy expenditure and injury) in line with their
100 individual RHP, meaning that the inferior opponent will typically reach its threshold sooner
101 and give up. In CAM costs also accrue due to the actions of the opponent, with superior
102 opponents being better at inflicting costs. The second type, termed mutual assessment (e.g.
103 'sequential assessment model', Enquist & Leimar, 1983), involves individuals gathering
104 information concerning relative fighting ability, typically interpreted as gathering information
105 about an opponent's RHP and comparing this against their own ability. This need not be a
106 cognitively demanding task (see Elwood & Arnott, 2013; Fawcett & Mowles, 2013 for
107 discussion of this topic), yet it can be difficult to discriminate from other forms of assessment
108 (Briffa & Elwood 2009). Mutual assessment has the advantage that the weaker contestant can
109 terminate the contest as soon as it perceives it is inferior to an opponent and likely to lose,
110 thus minimizing fight costs for both itself and the winner. However, assessing an opponent
111 may be difficult and costly, and basing decisions on individual thresholds (self-assessment) to
112 determine the degree of escalation and contest winner may be a more economical option
113 under certain circumstances (see Mesterton-Gibbons & Heap, 2014 for relative costs of
114 mutual and self-assessment). This may account for mounting recent empirical evidence of
115 self-assessment (e.g. Brandt & Swallow, 2009; Copeland, Levay, Sivaraman, Beebe-Fugloni,
116 & Earley, 2011; Rudin & Briffa, 2011; Tanner & Jackson, 2011; Martinez-Cotrina,
117 Bohorquez-Alonso, & Molina-Borja, 2014; Tsai, Barrows, & Weiss, 2014).

118 Since the publication of a review paper that provided a framework to accurately discriminate
119 between alternative assessment strategies (Arnott & Elwood, 2009a), there have been a
120 number of empirical papers in a range of species examining RHP assessment strategies (e.g.

121 Garcia et al., 2012; Jennings, Elwood, Carlin, Hayden, & Gammell, 2012; Kasumovic,
122 Mason, Andrade, & Elias, 2011; Lopes Junior & Cardoso Peixoto, 2013; McGinley, Prenter,
123 & Taylor, 2015; Painting & Holwell, 2014; Palaoro, Dalosto, Costa, & Santos, 2014;
124 Reichert & Gerhardt, 2011; Yasuda, Takeshita, & Wada, 2012). However, these studies have
125 focused on morphological traits related to RHP. None have considered the prospect that
126 behavioural asymmetries in aggressiveness between contestants could be subject to the same
127 assessment strategies as more traditional RHP measures. The aggressiveness displayed by an
128 opponent provides a source of socially acquired public information (sensu Dall, Giraldeau,
129 Olsson, McNamara, & Stephens, 2005) that may enable an animal to adjust its response (e.g.
130 Hyman & Hughes, 2006). Such information could be particularly valuable if it reveals honest
131 information regarding behavioural consistency, thereby predicting future behaviour. Previous
132 work suggested that animals may be capable of comparing their aggressiveness to that of an
133 opponent (pigs, *Sus scrofa*: Erhard, Mendl, & Ashley, 1997), but this was not studied in
134 dyadic contests, nor was the correct theoretical approach to discriminate between different
135 assessment strategies used (Arnott & Elwood, 2009a; Taylor & Elwood, 2003).

136 Here we outline a framework to examine whether aggressiveness is a component of RHP and
137 whether or not it forms a part of the assessment strategy (either self- or mutual assessment)
138 used in the decision-making process of contesting animals. To test for assessment we
139 examined the relationship between winner and loser aggressiveness and contest duration,
140 using the framework advocated to discriminate between assessment strategies when using
141 traditional RHP measures (Taylor & Elwood, 2003, reviewed in detail by Arnott & Elwood,
142 2009a). Furthermore, we also examined the duration of display phases and escalated fighting
143 to indicate whether the assessment strategy may switch from one contest phase to another
144 (e.g. Hsu, Lee, Chen, Yang, & Cheng, 2008). Pigs provide a useful model system to test the
145 outlined predictions. In commercial pig production, aggressive behaviour is a problem and

146 has therefore been researched for a number of decades, generating a vast amount of
147 knowledge including the behavioural pattern occurring during contests (McGlone, 1985;
148 Rushen & Pajor, 1987). The social structure of domestic pigs is based on a dominance
149 hierarchy formed through aggressive interactions (Meese & Ewbank, 1972), making them an
150 ideal study system to investigate the influence of aggressiveness. While there is considerable
151 descriptive work on pig aggression, the information-gathering and decision-making processes
152 used by pigs to resolve aggressive encounters are poorly understood. As such, theoretical
153 models developed to study contests offer a useful framework to better understand aggressive
154 encounters between unfamiliar pigs.

155 In this study we assayed individual differences in aggressiveness, using the established
156 resident–intruder (RI) test (Erhard & Mendl, 1997), which provides a measure of
157 aggressiveness that is consistent over time (D’Eath, 2004; Clark & D’Eath, 2013). The
158 resultant measure of attack latency provides an unambiguous, quantifiable measure of
159 aggression in a format that can be interpreted within an RHP framework. Contests were then
160 staged between pigs that varied in their level of aggressiveness, while matched for other
161 traditional measures of RHP (body weight, Rushen, 1987). We also examined the effects of
162 aggressiveness on contest behaviour, including the duration of display phases and escalated
163 fighting. This is important because studies that only focus on changes in outcome without
164 considering changes in fight cost may fail to find an effect where one actually exists (Arnott
165 & Elwood, 2007). In other words, manipulating aggressiveness may alter the behaviour of
166 contestants in a fight but without being sufficiently influential to affect outcome. The
167 traditional measure of contest cost, namely contest duration, has been criticized as providing
168 only a poor proxy for actual fight cost (e.g. McGinley et al., 2015). Therefore, in addition to
169 using measures of duration, we also quantified the physiological costs of fighting in terms of
170 lactate accumulation and glucose levels as has previously been advocated (e.g. Prenter,

171 Elwood, & Taylor, 2006). Based on previous studies we expected that lactate and glucose
172 would increase along with the contest duration (Briffa & Sneddon, 2007), whereby the loser
173 would have higher lactate and lower glucose values than the winner (Briffa & Elwood, 2005;
174 Schuett & Grober, 2000). Our experimental approach also enabled us to employ the correct
175 framework (Arnott & Elwood, 2009a) to examine whether individuals gather and use
176 information on aggressiveness as part of the contest decision-making process. Using this set-
177 up we tested the prediction that if aggressiveness is a component of RHP, then the more
178 aggressive individual should win.

179

180 **METHODS**

181 *Ethical note*

182 This study was carried out in accordance with the recommendation in the European
183 Guidelines for accommodation and care of animals, UK Government DEFRA animal welfare
184 codes, and adhered to the ASAB/ABS guidelines. The work was approved by SRUC's
185 Animal Ethics Committee (no. ED AE 21-2014) and the UK Government Home Office
186 legislation (Project licence PPL60/4330) under the Animals Scientific Procedures Act 1986
187 and was conducted in constant collaboration with SRUC's veterinary surgeon. Contests were
188 ended immediately when a clear outcome of winner and loser was apparent, or otherwise
189 after 30 min if no clear outcome could be identified. Four contests were ended because of a
190 fear response or repeated mounting behaviour of one of the pigs. Ending the contest
191 prematurely prevented any injury other than skin lesions from bites.

192

193 *Animals and housing*

194 A total of 114 young male and female pigs (Large White×Landrace sow × American
195 Hampshire boar) were studied. They originated from 17 litter groups, which were born in
196 three batches at the SRUC pig research farm. They were raised in conventional farrowing
197 crates. Males were not castrated and the tail and teeth were kept intact. Piglets were weaned
198 from the sow when they were 4 weeks of age and were studied at 9 weeks of age. After
199 weaning they were kept in the same litter groups in a pen measuring 1.9×5.8 m, allowing ca.
200 1.0–1.1 m² per pig. Pens had a solid floor which was covered with approximately 5 kg of
201 long straw. Pens were cleaned daily and provided with ca. 3.5 kg of fresh straw. Pigs had ad
202 libitum access to water and pelleted commercial feed.

203

204 *Habituation*

205 To reduce the possibility of fear responses in the test situation, pigs were habituated to the
206 study by being gradually exposed (over six occasions) to being alone for a few minutes and to
207 being handled in a weigh crate.

208

209 *Testing for aggressiveness*

210 Aggressiveness as a personality trait was the main factor under investigation in this study,
211 and the contests were based on differences in aggressiveness. Aggressiveness was estimated
212 by the resident-intruder (RI) test at 9 weeks of age. The RI test is an established test in
213 behavioural research that is undertaken to obtain a quantifiable measure of individual
214 aggressiveness (Koolhaas et al., 2013). In pigs the RI test has been shown to be consistent
215 over time (D'Eath, 2004) and to be predictive of aggressiveness when animals are mixed with
216 multiple unfamiliar animals (Erhard et al., 1997). In the test a 'resident' was kept individually

217 in a separate part of its home pen. Immediately after, an inferior ‘intruder’ was put into the
218 home pen of the resident, in this case a pig weighing ca. 65% of the body weight of the
219 resident. This created a situation in which the resident was likely to attack the inferior
220 intruder. The latency until one of the animals attacked with a rapid sequence of bites was
221 recorded. If the resident did not attack within 5 min after initial contact the test was ended
222 and the latency was set at 300 s. The test was repeated the following day with a different
223 intruder. The Pearson correlation between the attack latency of both test days was 0.58 ($df =$
224 102, $P < 0.0001$). The attack latencies of both days were summed to obtain a single variable
225 for aggressiveness. This resulted in attack latencies that could take a value between 0 and
226 600, with 0 being highly aggressive and 600 being unaggressive.

227

228 *Contests*

229 Contests were staged between pairs of pigs at 10 weeks of age. Dyads were matched for body
230 weight (on average $3.6 \pm 0.3\%$ difference), a traditional and validated measure of RHP in
231 pigs (Andersen, Andenæs, Bøe, Jensen, & Bakken, 2000; Jensen & Yngvesson, 1998;
232 Rushen, 1987), and differed in aggressiveness as reflected in the attack latency of the RI test.
233 Dyads were formed between animals from opposite sides of the distribution of attack latency
234 (high against low, $N = 16$), or from pigs at one tail of the distribution matched against
235 animals with an average attack latency (high against intermediate, $N = 19$, and low against
236 intermediate, $N = 17$). Both sexes were matched randomly as existing literature is ambiguous
237 and does not give a consistent indication of sex differences for young pigs regarding agonistic
238 behaviour (Clark & D’Eath, 2013; Jensen & Yngvesson, 1998; Rushen, 1987). Excluding sex
239 also facilitated the creation of dyad combinations based on the factors of interest to the

240 research question, namely body weight and aggressiveness. Sex differences were accounted
241 for in the statistical models.

242 The contest arena measured 2.9×3.8 m and had a light bedding of wood shavings covering
243 the solid floor. The two animals entered the contest arena simultaneously from opposite sides.
244 The time was started from the moment both had entered the arena. A single observer recorded
245 the time until the first nose-to-nose contact, the first bite and the first fight, as well as the
246 duration of display behaviour, pushing and fighting, and the frequency of unilateral bites (see
247 ethogram, Table 1). Timing was stopped when a clear winner was apparent, which was when
248 one pig retreated after being attacked and failed to retaliate within 2 min after retreat. The
249 outcome was recorded as undecided if no winner was apparent within 30 min, after which the
250 test was ended, or if a test had to be ended because of repeated escape attempts by one or
251 both of the animals. ‘Contest’ duration refers to the total time that the opponents were in the
252 contest arena, from entering the arena until a winner was apparent. The ‘fight’ duration refers
253 to escalated reciprocal aggression (see ethogram, Table 1). Only contests with an outcome
254 (winner/loser) were retained in the data, which excluded five contests (four were ended due
255 to a fear response or mounting; one contest reached the maximum time without fighting).
256 This resulted in 52 contests (104 pigs, 55 males and 49 females).

257

258 *Physiological parameters*

259 Immediately pre- and postcontest a few drops of blood were obtained from the ear vein by
260 pricking it using a capillary blood lancet with a flat blade. The blood drops were directly
261 applied to the test strips of a blood glucose meter (Accu-Chek, Aviva Blood Glucose System)
262 and blood lactate meter (The EDGE Lactate Analyser) developed for humans. Pig blood is
263 comparable to human blood (Marascalco, Ritchie, Snyder, & Kameneva, 2006; Weng,

264 Cloutier, Pibarot, & Durand, 1996), and therefore the meters developed for humans were
265 regarded as more suitable than ones available for companion animals. The lactate meter had a
266 test range of 0.7–22.2 mmol/litre. In seven cases the upper threshold was reached after
267 fighting and these values were set to 22.2. Sampling order was randomized for the level of
268 aggressiveness and contest outcome. A proportional increase was calculated as the post-test
269 value divided by the pretest value. Owing to practical and technical errors two pretest
270 samples for lactate and glucose, four post-test lactate samples and six post-test glucose
271 samples could not be obtained. This resulted in four missing values for the proportional
272 increase in blood lactate and six missing values for the increase in blood glucose.

273

274 *Statistical analysis*

275 Data were analysed with SAS 9.3 (SAS Inc., Chicago, IL, U.S.A.). Contest data were
276 analysed as described in Briffa et al. (2013), while also including batch and litter as random
277 effects which are important to account for. To test for evidence of assessment of
278 aggressiveness (either self- or mutual assessment), the models detailed below use an
279 appropriate statistical framework (as advocated by Taylor & Elwood, 2003, and reviewed in
280 detail by Arnott & Elwood, 2009a), including winner and loser attack latencies (as our
281 candidate RHP measure of aggressiveness), as well as the difference in attack latency
282 between contestants. Self-assessment of aggressiveness would be indicated by a negative
283 relationship between loser attack latency and contest duration (indicating that more
284 aggressive losers fought for longer), with no significant relationship between winner attack
285 latency and contest duration, nor any relationship between difference in attack latency
286 between contestants and contest duration. With mutual assessment of aggressiveness there
287 would also be a negative relationship between loser attack latency and contest duration but a
288 significant positive relationship between winner attack latency and contest duration

289 (indicating that if losers assess their opponent to be highly aggressive, they give up quickly),
290 and a negative relationship between difference in attack latency and contest duration.

291 Continuous data (attack latency, durations and frequency of biting) were checked for
292 normality of the residuals and were transformed if required to obtain a normal distribution.

293 First, a mixed model was applied to test whether sex, weight and litter had an effect on the
294 attack latency in the RI test, whereby batch was the only random effect in the model
295 statement. Thereafter, normally distributed data were analysed using a mixed model (PROC
296 MIXED) and binary data (e.g. contest outcome) were analysed with a generalized linear
297 mixed model (PROC GLIMMIX) with a binary distribution and logit link function. All
298 models included outcome status as a repeated statement, with the contest as the experimental
299 unit, to account for nonindependence between opponents (Briffa & Elwood, 2010). Batch and
300 litter were included as random effects. The models initially included all relevant explanatory
301 variables and interactions and these were then stepwise removed from the model if the
302 significance level was above 0.10. The explanatory variables were body weight,
303 aggressiveness (in attack latency), sex and the proportional increase in blood lactate and
304 glucose (which were both unaffected by body weight). To assess these variables for both
305 winners and losers the interaction outcome*treatment was assessed (Briffa & Elwood, 2010),
306 with treatment referring to the explanatory variables body weight, attack latency, sex, lactate
307 and glucose. Although dyads were matched for equal body weight we did include the
308 (absolute and relative) difference in weight between the opponents to investigate whether this
309 affected the outcome of the contest. Data are presented as means with SEs, and covariance
310 parameter estimates are obtained by REML (default in SAS).

311

312 **RESULTS**

313 *Aggressiveness as a personality trait*

314 The attack latency in the RI test provided a very accurate reflection of individual
315 aggressiveness during the contest. Pigs with a short attack latency, which were regarded as
316 more aggressive, had a higher probability of initiating the first nose-to-nose contact ($F_{1,82} =$
317 $6.5, P = 0.01$), the first bite ($F_{1,85} = 14.1, P < 0.001$) and the first fight ($F_{1,86} = 9.3, P = 0.004$)
318 than pigs with a long attack latency in the RI test (Fig. 1). Females had a shorter attack
319 latency than males, meaning they were slightly more aggressive in the RI test (males: $293 \pm$
320 24 s; females: 210 ± 25 s; $F_{1,83} = 5.6, P = 0.02$). The attack latency tended to be unrelated to
321 body weight ($F_{1,83} = 2.7, P = 0.10$) and differed significantly between litter groups ($F_{16,83} =$
322 $2.1, P = 0.02$).

323

324 *Contest duration*

325 The total duration of the contest, from the moment that the contestants entered the arena until
326 a winner was apparent, was on average 5½ min (339 ± 19 s). Of this time, pigs spent on
327 average 87 ± 6 s on display behaviour, 35 ± 6 s on nondamaging but energetically demanding
328 mutual pushing and 54 ± 6 s on fighting. The individual aggressiveness of the winner and
329 loser (in attack latency) did not influence the contest duration, the duration of display or
330 pushing, or the duration of fighting (all $P > 0.10$). However, asymmetry in attack latency did
331 affect durations. The greater the difference in aggressiveness, i.e. attack latency, between the
332 opponents the longer the contest was (Fig. 2; $b = 0.37 \pm 0.1$ s/s difference in attack latency;
333 $F_{1,79} = 4.5, P = 0.04$). Thus, contests between a highly aggressive opponent and one showing
334 little aggression took longest to reach an outcome. This was also apparent for the duration of
335 the display phase ($b = 0.13 \pm 0.0$ s/s difference; $F_{1,84} = 9.6, P = 0.003$) and the duration of
336 mutual pushing ($b = 0.11 \pm 0.0$ s/s difference; $F_{1,79} = 5.8, P = 0.02$), but not for the fight

337 phase ($F_{1,58} = 1.4$, $P = 0.24$). Analysis of biting behaviour revealed that the more aggressive
338 contestant within a dyad bit the opponent more frequently (bites/min; excluding bites during
339 mutual fights) when asymmetry was greater whereas the less aggressive animal did not alter
340 its biting behaviour when the opponent was relatively more aggressive (Fig. 3; $F_{2,85} = 6.8$, P
341 $= 0.002$). The duration of the total contest, the display phase and the pushing phase was
342 longest when the two opponents were males and shortest when they were females (Table 2).
343 The duration of the contest, as well as the duration of the separate phases, was unaffected by
344 winner and loser body weight (all $P > 0.10$), but heavier dyads escalated more often to the
345 fighting phase than lighter dyads (fight did not occur: 33 ± 2 kg; fight occurred: 35 ± 2 kg;
346 $F_{1,83} = 5.9$, $P = 0.02$).

347

348 *Contest outcome*

349 Aggressiveness during the RI test, reflected in attack latency, was unrelated to the contest
350 outcome, with the attack latency of the losers being 264 ± 25 s and the attack latency of the
351 winners being 249 ± 24 s ($F_{1,86} = 0$, $P = 0.99$). The outcome of the contests between weight-
352 matched pigs was most related to which animal initiated the first bite ($F_{1,83} = 10.6$, $P <$
353 0.002). In 65% of all contests the pig that initiated the first bite won the contest. However, as
354 shown above, the first bite was almost always initiated by the more aggressive opponent. As
355 illustrated in Fig. 4, the relationship between aggressiveness and winning is obscured by the
356 occurrence of a fight. If the recipient of the first bite retaliated and the contest proceeded into
357 a fighting phase, then aggressiveness and bite initiation did not determine the outcome
358 between size-matched pigs. If, however, the recipient of the first bite did not retaliate or if
359 retaliation did not result in escalated fighting, then bite initiation was directly related to a high
360 likelihood of winning (in the 14 contests without a fight 13 were won by the opponent that

361 initiated the first bite). The next best predictor of contest outcome was the absolute weight
362 difference between the opponents. Dyads were matched for equal weight but an average size
363 difference of $3.6 \pm 0.3\%$ remained, with a maximum of 9.4%. Despite the minimal weight
364 differences the winners were on average 0.5 ± 0.3 kg heavier than the losers ($F_{1,83} = 9.7$, $P =$
365 0.002). All other variables were unrelated to the contest outcome ($P > 0.10$).

366

367 *Physiological costs*

368 Prior to the contest the average blood lactate value measured 2.4 ± 0.1 mmol/litre (range 0.7–
369 6.7) and blood glucose measured 6.1 ± 0.1 mmol/litre (4.3–8.5). After the contest lactate
370 increased to 10.4 ± 0.7 mmol/litre (0.7–>22.2) and glucose to 7.4 ± 0.1 mmol/litre (5.0–11.1).
371 From these values the proportional change was calculated and used for further analyses.
372 Blood lactate, but not blood glucose, increased with the overall contest duration, whereby
373 each minute blood lactate increased on average 45% compared to the precontest value ($F_{1,79}$
374 = 10.6, $P = 0.002$). During escalated fighting, blood lactate increased on average 402% per
375 minute spent in this behaviour compared to the pretest value ($F_{1,52} = 9.1$, $P = 0.004$), and
376 blood glucose increased 21% per minute of fighting compared to the pretest value ($F_{1,52} =$
377 14.9, $P < 0.001$). The traditional measure of contest costs, namely contest duration, is
378 typically plotted against RHP to study assessment strategies. Substituting contest duration
379 with blood lactate revealed no relationship that could indicate an assessment strategy (there
380 were no significant relationships between lactate and aggressiveness, difference in
381 aggressiveness or body weight). The blood values prior to the contest as well as the
382 proportional increase during the contest did not influence the contest outcome (all $P > 0.10$).

383

384 **DISCUSSION**

385

386 *Aggressiveness as a component of RHP*

387 Aggressiveness, assayed in terms of attack latency during a resident-intruder test, did not
388 directly relate to the outcome of the contest, suggesting aggressiveness is not a component of
389 RHP. This was contrary to our initial prediction that the more aggressive individual in a
390 contest would be more likely to win. However, aggressiveness showed an indirect
391 relationship with contest outcome via bite initiation in contests without an escalated fight.
392 The more aggressive individuals almost always initiated the first bite, which validated our
393 personality measure from the RI test. If the contest did not then proceed to an escalated fight,
394 this bite initiation was an effective strategy for winning, which is in line with existing
395 literature (e.g. Guderley & Couture, 2005). Rather than viewing aggressiveness as a
396 component of RHP the aggressiveness displayed by an individual can also be viewed as a
397 signal of intent (Laidre & Johnstone, 2013; Searcy & Nowicki, 2005). More aggressive pigs
398 were more likely to initiate biting, which would reflect an honest signal of their intention to
399 attack. However, the fact that aggressiveness was unrelated to outcome suggests it does not
400 provide an honest signal of RHP. This is further supported by examining those contests that
401 escalated to fighting, because in these cases bite initiation, and thus aggressiveness, did not
402 affect the outcome. Thus, more aggressive pigs signal their intent to attack, but this does not
403 disclose accurate information on their likelihood of winning. It has been debated whether
404 honest signals of intent could be evolutionarily stable (e.g. Maynard Smith & Parker, 1976;
405 Maynard Smith, 1979). The inclusion of handicap theory (proposing that high-quality
406 individuals are better able to display costly signals than low-quality individuals; Zahavi,
407 1975) showed that honest signalling was probable (e.g. Enquist, 1985; Grafen, 1990). More

408 recent models show that honest and deceitful signals can coexist in a stable system (Adams &
409 Mesterton-Gibbons, 1995; Számadó, 2000).

410

411 *Assessment of aggressiveness*

412 We found no evidence that aggressiveness is assessed as part of either a self- or mutual
413 assessment strategy. The correct statistical framework was used (Arnott & Elwood, 2009a;
414 Taylor & Elwood, 2003), in which effects of winner and loser measures of RHP
415 (aggressiveness expressed as attack latency) on contest cost were examined. Furthermore, we
416 tested a number of measures of contest cost including duration and duration of separate
417 phases, and we used blood lactate and blood glucose to provide measures of physiological
418 costs. However, the results of this study should be interpreted with some caution as the
419 sample size was limited (although comparable with other studies, e.g. 48 contests in Rudin &
420 Briffa, 2012), and 27% of the dyads did not fight. The fact that some contests did not escalate
421 is something that should be taken into account as it may comprise a substantial part of the
422 sample size. For example, Stuart-Fox (2006) reported that in only 42 of 107 contests did both
423 opponents escalate to biting and McGinley et al. (2015) reported that in only 34 of the 85
424 contests did the opponents come into contact. These high frequencies of nonescalated
425 contests may point out that conflict avoidance is an important strategy which deserves further
426 research attention.

427 McGinley et al. (2015) recently questioned the validity of using total contest duration as a
428 surrogate measure for contest cost. Results from this study add to those concerns. Blood
429 lactate, which is a more direct measure of cost, increased almost 10-fold more per minute of
430 fighting than per minute of total contest duration. In the present study, contest duration
431 comprised the time from entering the contest arena until a clear winner was apparent. In

432 between agonistic interactions, and before an outcome was reached, opponents could spend a
433 considerable amount of time in activities unrelated to conflict and also using low-cost display
434 behaviour. The duration of escalated fighting and phases of physical contact (e.g. pushing)
435 may therefore provide better measures of cost than the overall contest duration, as may
436 measuring the intensity of a contest.

437 That aggressiveness (in terms of attack latency) did not seem to form part of the information-
438 gathering process used by pigs is perhaps unsurprising for a number of reasons. First,
439 assessing aggressiveness might be highly cognitively demanding. It implies an awareness of
440 one's own consistency in behaviour (Held, Mendl, Laughlin, & Byrne, 2002; Mendl & Paul,
441 2004). Self-knowledge of one's own morphological traits, which generally remain the same
442 over a sustained period of time, may naturally occur through movement and executing
443 strength and does not have to be cognitively demanding (Fawcett & Mowles, 2013). Self-
444 knowledge of aggressiveness, however, would require memory of one's past behaviour, and
445 possibly the consistency thereof over time, and subsequently using that information in an
446 encounter. In terms of mutual assessment, assessing the aggressiveness of oneself as well as
447 that of an opponent would seem like a rather difficult task. Erhard et al. (1997) suggested that
448 pigs may be capable of assessing aggressiveness. When we investigated this using the
449 recommended framework, there was no evidence that aggressiveness is assessed. Second,
450 given that there was no effect of aggressiveness on contest outcome, it would not provide a
451 reliable RHP cue for assessment, with alternative morphological traits such as body weight
452 providing much better candidates for assessment. Indeed, there was some support for this.
453 Although pigs were matched for body weight, the small difference that existed was sufficient
454 for heavier individuals to be more likely to win. Body weight is therefore further validated as
455 an RHP trait. Moreover, although not the focus of this study, the finding that heavier dyads
456 were more likely to escalate the contest to fighting than lighter dyads is suggestive of self-

457 assessment. The assessment abilities of pigs in relation to traditional RHP measures (body
458 weight and size) are currently the focus of study by our research group.

459

460 *Asymmetry in aggressiveness between opponents*

461 When RHP is reflected in body size, a greater asymmetry between the opponents is expected
462 to decrease the contest cost and duration (e.g. Taylor & Elwood, 2003). We found that when
463 the asymmetry in aggressiveness increased the contrary occurred, whereby the contest
464 duration and the duration of display and mutual pushing increased, while the fight duration
465 remained unaffected. A greater asymmetry in RHP traits is assumed to facilitate the
466 assessment of fighting ability and would thus sooner result in withdrawal of the inferior
467 individual (Arnott & Elwood, 2009a; pigs: Andersen et al., 2000), and may avoid escalated
468 fighting. Irrespective of assessment of aggressiveness, the behavioural interactions within a
469 contest might explain this discrepancy. The difference in unilateral biting behaviour suggests
470 that pigs showing little aggression attempt to avoid a conflict by refraining from biting the
471 opponent. More aggressive pigs bite, regardless of the contest duration, more often than less
472 aggressive pigs when the asymmetry in aggressiveness is large (Fig. 3). This may be a logical
473 response to the level of challenge. When both opponents retaliate equally to each other's
474 attacks, the intensity of the contest may rapidly increase and contestants may sooner move
475 towards escalated aggression (Maynard Smith & Price, 1973). If one opponent avoids
476 confrontation but does not signal a clear retreat the contest may be prolonged until eventually
477 one gives up, either with or without escalated aggression prior to the withdrawal. As
478 opponents were expected to be physically similar in strength, the fighting phase itself seemed
479 to unfold irrespective of absolute aggressiveness or the asymmetry in aggressiveness between
480 the opponents.

481

482 *Integrating personality with contest theory*

483 More aggressive animals were more likely to initiate a bite whereas they were not more likely
484 to win when they did so. This is similar to the findings of Bolhuis, Schouten, Schrama, and
485 Wiegant (2005) that proactive pigs initiated more fights but did not acquire higher social
486 ranks. As outlined above, this could be seen as a dishonest or unreliable signal of fighting
487 ability whereas it is an honest signal of intent (Adams & Mesterton-Gibbons, 1995; Laidre &
488 Johnstone, 2013; Számadó, 2000). It may have been that these animals were more willing to
489 engage in aggression (Hofmann & Schildberger, 2001), which would be in line with the
490 measure of aggressiveness from the RI test. It could also be that they initially overestimated
491 their RHP compared to that of the opponent. If this is true, it is unlikely to result from being a
492 large pig in a litter of smaller siblings as body weight compared to littermates did not affect
493 bite initiation (results not shown). Overall, the behaviour shown by the pigs with a more
494 aggressive personality is in line with previous studies showing that animals with a proactive
495 coping style, which reflects personality, are more aggressive, rigid and impulsive in their
496 behaviour (Koolhaas et al., 1999; pigs: Bolhuis et al., 2005; Melotti, Oostindjer, Bolhuis,
497 Held, & Mendl, 2011). A personality trait has been defined as ‘a specific aspect of a
498 behavioural repertoire that can be quantified and that shows between-individual variation and
499 within-individual consistency’ (Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013, p.
500 467). As such, the attack latency in the RI test showed considerable variation between
501 individuals and a moderate correlation within individuals. This repeatability adds to the
502 existing studies that indicate that the RI test reflects aggressiveness as a personality trait
503 (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; D’Eath, 2004). The evidence for a
504 link between animal personality and contest behaviour has recently been reviewed (Briffa et
505 al., 2015). However, the majority of studies in this area have focused on investigating links

506 along the bold–shy personality spectrum, and proactive–reactive behavioural syndrome, and
507 contest behaviour (Briffa et al., 2015: Table 1, out of 16 cited studies only one investigated
508 links between aggression directly and RHP). The limited research that has been conducted on
509 aggressiveness in relation to contest behaviour has produced conflicting results (McEvoy et
510 al., 2013; Wilson et al., 2013; see above). Our study adds another layer of complexity by the
511 findings of an indirect effect of aggressiveness on contest behaviour (bite initiation). While
512 this may provide an honest signal of intent, it did not form a component of RHP, revealed by
513 a lack of effect on contest outcome. Animal personality is a broad concept and attributed
514 personality types often depend strongly on the tests that are chosen to reflect the personality
515 type and the subsequent interpretation of the test results (Carter et al., 2013). Studying
516 aggressiveness specifically as a component of personality, rather than personality as a whole,
517 enables a closer understanding of how aggressive behaviour specifically may affect contest
518 decisions, and may aid in the understanding of contest behaviour.

519

520 *Sex differences*

521 The literature is ambiguous about sex differences for aggressiveness and contest behaviour in
522 pigs (Clark & D’Eath, 2013; Jensen & Yngvesson, 1998; Rushen, 1987). We therefore
523 randomly staged contests with regard to sex. Male dyads had the longest contest duration and
524 spent most time in display and mutual pushing. Intersexual differences in contests have been
525 acknowledged in various species and might be due to energy reserves and hormonal state
526 (Briffa & Sneddon, 2007), as well as different selection pressures acting on each sex (Arnott
527 & Elwood, 2009b). The duration of escalated fighting did not differ between the sexes, which
528 implies that males and females fight up to their maximum capacity and are at this age similar

529 in strength or persistency. We recommend that sex differences are considered in the study of
530 aggressiveness, including when pigs are prepubertal.

531

532 *Lactate and glucose*

533 The levels of blood lactate increased linearly with the contest duration and fight duration,
534 consistent with existing literature (Briffa & Sneddon, 2007). There were no differences
535 between the winner and loser for either the precontest value of blood lactate and glucose or
536 the proportional increase during the contest. Previous studies showed that losers have higher
537 blood lactate (e.g. Neat, Taylor, & Huntingford, 1998b; Schuett & Grober, 2000) and lower
538 glucose values than winners (Briffa & Elwood, 2005). The absence of a winner–loser effect
539 for metabolic costs suggests that losers retreated for reasons other than energetic constraints.
540 Pig blood is comparable to that of humans (Marascalco et al., 2006; Weng et al., 1996), and
541 in humans blood lactate has been studied in relation to exercise and sport competitions
542 (reviewed by Billat, 1996). Blood lactate measured during the contests was comparable to
543 values reported in human sport physiology (Billat, 1996). Some fights resulted in extreme
544 values, around 20 mmol/litre, which compare to short-lived intense peak performances in
545 human sport competitions (Billat, 1996; Vescovi, Falenchuk, & Wells, 2011). In commercial
546 pig production, the energetic costs of aggression are typically ignored by farmers. The lactate
547 values observed in this study, in which aggressive interactions were limited to a maximum of
548 30 min in contrast to commercial practice in which aggressive interactions continue over a
549 sustained period of time, emphasize that fights are extremely energetically demanding and
550 should not be overlooked.

551

552 *Conclusion*

553 Aggressiveness as a personality trait had no effect on the outcome of the contest, suggesting
554 it does not form an important component of RHP in pigs. However, it did influence contest
555 behaviour, in terms of bite initiation, and the fact that bite initiation was related to contest
556 outcome could be interpreted as an indirect effect of aggressiveness on contest outcome. This
557 personality trait could also act as an honest signal of intent. However, despite providing a
558 source of potentially useful honest information regarding behavioural consistency that would
559 be predictive of future behaviour, there was no evidence that pigs assessed aggressiveness.
560 The appropriate theoretical approach comparing different models of assessment was used to
561 reach this conclusion.

562

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568

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793 **Tables**

794

795 **Table 1.** Ethogram

Behaviour	Description
Nose-to-nose	Nose approaches within 5 cm of the snout of the other
Display	Parallel walking (move simultaneously with the shoulders next to each other); heads up (both have their nose lifted high up in the air alongside each other); shoulder-to-shoulder (standing or moving with the shoulder against the shoulder of the other without real pressure)
Mutual pushing	Head or shoulder is used to move the other aside by applying pressure
Unilateral bite	Opens mouth and delivers a bite that contacts the other
Mutual fight	Rapid sequence of bites which are retaliated with a similar aggressive act from the opponent within 5 s
Withdrawal	Turns its head away from the opponent and retreats from further attacks by not showing any aggressive behaviour within 10 s

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799 **Table 2.** Duration (s) of the total contest and its separate phases ($N = 52$) for the different
 800 combinations of sexes in a dyad

Duration	MM	MF	FF	<i>P</i>
Contest	366 ± 27^b	$363 \pm 35^{a,b}$	266 ± 25^a	0.07
Display	112 ± 11^b	86 ± 8^b	56 ± 6^a	<0.001
Pushing	65 ± 15^b	26 ± 8^b	16 ± 8^a	<0.001
Fighting	50 ± 6^a	57 ± 9^a	57 ± 16^a	0.58

801 Dyads are male–male (MM, $N = 15$), male–female (MF, $N = 25$) and female–female (FF, $N =$
 802 12). Values are back-transformed means with SEs. *P* values indicate the significance of the
 803 overall effect of sex on duration. Fight duration is given only for the contests with a fight (N
 804 = 38: 11 MM, 18 FM, 9 FF). Values lacking a common letter differ by $P < 0.05$.

805

806 **Figure captions**

807

808 **Figure 1.** Probability of initiating behaviour in a contest depending on the aggressiveness of
809 a pig as reflected in the attack latency in the RI test. The lines show the probability of
810 initiating the first nose-to-nose contact, the first bite and the first fight. Note that a low value
811 for attack latency indicates high aggressiveness and a high value indicates low
812 aggressiveness.

813

814 **Figure 2.** The relationship between the contest duration and the absolute difference in attack
815 latency between the opponents as measured in the RI test, which reflects aggressiveness.

816

817 **Figure 3.** The effect of asymmetry in aggressiveness, shown in the difference in attack
818 latency from the RI test, on the rate of unilateral biting per minute (separate from fights) for
819 the most aggressive opponent (circles and solid line) and the least aggressive opponent
820 (crosses and dashed line).

821

822 **Figure 4.** Values depict the average attack latency (AL; s) for contestants that did or did not
823 initiate the first bite in a contest that either did or did not include a fight, with the number of
824 winners and losers per outcome.