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Camerlink, I., Turner, S. P., Farish, M., & Arnott, G. (2017). The influence of experience on contest assessment strategies. *Scientific Reports*, 7, [14492]. DOI: 10.1038/s41598-017-15144-8

Published in:
Scientific Reports

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

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1 Accepted to Scientific Reports 18th October 2017

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3 **The influence of experience on contest assessment strategies**

4 Irene Camerlink¹, Simon P. Turner¹, Marianne Farish¹, Gareth Arnott²

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6 ¹Animal Behaviour & Welfare, Animal and Veterinary Sciences Research Group, Scotland's Rural
7 College (SRUC), West Mains Rd., Edinburgh, EH9 3JG, UK

8 ²Institute for Global Food Security, School of Biological Sciences, Queen's University, Belfast, BT9
9 7BL, UK

10

11 *Correspondence: I. Camerlink, Animal Behaviour & Welfare, Animal and Veterinary Sciences
12 Research Group, Scotland's Rural College (SRUC), West Mains Road, Edinburgh, EH9 3JG, UK,
13 Tel. +44 131 6519363, E-mail address: Irene.Camerlink@sruc.ac.uk (I. Camerlink).

14

15 **The influence of experience on contest assessment strategies**

16

17 **Abstract**

18 Animal contest behaviour has been widely studied, yet major knowledge gaps remain concerning the
19 information-gathering and decision-making processes used during encounters. The mutual assessment
20 strategy, where the individual assesses its own fighting ability (Resource Holding Potential, RHP) and
21 compares it to that of its opponent, is least understood. We hypothesise that individuals need
22 experience of agonistic encounters to become proficient at mutual assessment. Pigs (*Sus scrofa*,
23 n=316) were contested twice. In between contests, animals did or did not (control) receive intense
24 fighting experience. A substantial proportion of the contests reached an outcome with a clear winner
25 without fighting. Non-escalation was highest in RHP asymmetric dyads of the second contest,
26 irrespective of experience. In contest 1 (no experience) and in contest 2 for the experienced animals,
27 costs increased with loser RHP and were unaffected by winner RHP, suggesting a self-assessment
28 strategy. In contest 2 control dyads, which only had experience of one prior contest, a negative
29 relation between winner RHP and costs suggested mutual assessment during the pre-escalation phase
30 but not during escalated aggression. This reveals that a brief and relatively mild experience can be
31 beneficial in the development of mutual assessment whereas profound experience may result in
32 adoption of a self-assessment strategy.

33

34 **Keywords.** Game theory; decision making; mutual assessment; contest costs; fighting ability; pigs;
35 assessment strategy; aggression; contest; experience

36

37 Throughout the animal kingdom access to limited resources may lead to contests, mediated by various
38 forms of agonistic behaviour. The unequal distribution of resources arising from agonistic encounters
39 directly impacts fitness, driving natural selection (1) and sexual selection (2). Despite the importance
40 of animal contest behaviour, major knowledge gaps remain concerning the information-gathering and
41 decision-making processes used during encounters (3; 4; 5). Important asymmetries exist between
42 contestants including fighting ability, termed resource holding potential (RHP; 6), resource

43 ownership, and the value of the resource to each contestant (7). Selection is expected to favour
44 contestants that gather information about such asymmetries and use that to inform decision making (3;
45 7). Game theory models have provided a useful framework to further our understanding of animal
46 contest behaviour, and since the original hawk-dove game (8), that involved no information-gathering,
47 a suite of more realistic models have been developed that differ in the assessment strategies used. A
48 related major knowledge gap concerns how animals develop and acquire the social skills to make
49 appropriate assessments during contests. Specifically, we hypothesise that animals may require
50 experience of multiple agonistic encounters to become proficient at mutual assessment (assessment of
51 relative RHP difference between opponents).

52 Contest theory models can be grouped into three main types that differ in the information about RHP
53 that opponents are presumed to gather. The first, termed pure self-assessment, is a feature of the ‘war
54 of attrition without assessment’ (WOA-WA; 9) and energetic war of attrition (E-WOA; 10; 11). Here,
55 each contestant has information about its own RHP but gathers no information about the opponent.

56 Rivals persist in line with their own RHP, with the accumulated costs only relating to their own
57 actions. Inferior opponents will reach their limits first and give up. The second assessment strategy is
58 encompassed by the cumulative assessment model (CAM; 12), and is also a form of self-assessment.
59 However, in contrast to pure self-assessment, in the CAM costs also accumulate from the opponent’s
60 actions. This means that in the CAM the decision to withdraw is influenced by both an individual’s
61 own RHP, with weak rivals capable of bearing fewer costs, and also the opponent’s RHP, with higher
62 quality individuals inflicting costs at a higher rate. The third model is mutual assessment, which
63 involves an assessment of relative RHP difference between opponents. This is generally interpreted as
64 an individual gathering information about the fighting ability of a rival and comparing this against an
65 assessment of their own ability. This form of assessment is central to the ‘sequential assessment
66 model’ (SAM; 13; 14) and the ‘asymmetric war of attrition’ (AWOA; 15; 16), with the selective
67 advantage that the weaker rival can terminate the contest, minimising costs, as soon as it perceives its
68 inferiority. However, the majority of previous studies supporting mutual assessment were shown to
69 have used inappropriate analyses that could not distinguish it from pure self-assessment and CAM

70 (17). Since the publication of a review (3) summarising these issues and providing researchers with
71 the correct approaches to use, there has been a resurgence of interest in this area. To discriminate
72 between the alternative assessment strategies it is necessary to examine relationships between
73 individual contestants RHP and contest cost (3). All models predict a positive relationship between
74 loser RHP and contest cost (typically measured as contest duration). Therefore it is important to
75 examine the relationship between winner RHP and contest costs, with pure self-assessment predicting
76 a weak positive or non-significant relationship, while mutual assessment and CAM predict this
77 relationship to be negative (3). To discriminate between mutual assessment and CAM it is necessary
78 to examine contests in which opponents are matched for RHP, with CAM predicting a positive
79 relationship between the average RHP of matched pairs and contest cost, while no such relationship is
80 predicted for mutual assessment (3). To date, few studies provide clear evidence for mutual
81 assessment (although see 18 for a comprehensive example of mutual assessment in cuttlefish).
82 Despite this, mutual assessment retains intuitive appeal, perhaps because of our human aptitudes for
83 this strategy (19; 20).

84 We hypothesize that individuals may require experience of agonistic encounters to be able to assess
85 an opponent's fighting ability, as in mutual assessment. To date, while studies have investigated the
86 role of experience on fight outcome, identifying so-called winner and loser effects (21), to our
87 knowledge no studies have investigated how experience influences contest assessment.

88 This hypothesis was addressed in pigs (*Sus scrofa domesticus*). Domestic pigs allow for a controlled
89 experimental set-up in which genetics and life history are known, whereas, when released to nature,
90 their behaviour soon reverts to the natural behaviour as shown by their ancestors the wild boar (22).
91 Pigs have a broad spectrum of agonistic behaviour, ranging from very subtle ritualized display to long
92 escalated fights, and have been assumed to be capable of mutual assessment (23; 24). Because of the
93 welfare implications of pig aggression under commercial husbandry conditions, their aggression has
94 been well studied, including through the use of contest theory models (25; 26).

95 Contests between pigs include various phases of escalation (26). Animals may switch assessment
96 strategy between different contest phases. For example, killifish (*Kryptolebias marmoratus*; 27) use

97 mutual assessment during initial phases, switching to self-assessment during an escalated phase (27).
98 The extent to which this occurs in other species remains to be investigated. Ignoring potential
99 differences between phases may result in false conclusions about the assessment strategy in use and
100 may overlook, or falsely assume, the occurrence of mutual assessment. This study will therefore also
101 examine whether contestants switch assessment strategies between phases and whether this interacts
102 with experience, with the hypothesis that more experienced individuals will sooner switch to mutual
103 assessment.

104 In addition, various contest costs are measured. In species that by nature aim to avoid damaging
105 behaviour, and instead use ritualized display, the total contest duration may not reflect the actual costs
106 when compared to contests that do escalate into damaging aggression but are shorter in duration (26).
107 This study aims to determine what RHP assessment strategy is used during contests between pigs that
108 have never previously met an unfamiliar conspecific, and how experience of fighting affects these
109 strategies in later contests. This will investigate the prediction that pigs possess the capacity for
110 mutual assessment but that experience of fighting is necessary to become proficient at this.

111

112 **Methods**

113 *Ethical note and justification of sample size*

114 This study was approved by SRUC's animal experiments committee and was carried out under UK
115 Home Office license (project licence PPL60/4330), and in constant collaboration with SRUC's named
116 veterinary surgeon. The study was carried out in accordance with the recommendation in the
117 European Guidelines for accommodation and care of animals, UK Government DEFRA animal
118 welfare codes, and adhered to the ASAB/ABS guidelines. Strict end-points were in place for the
119 termination of contests, ensuring that the welfare of the animals was not compromised. This prevented
120 any injury other than skin lesions due to receiving bites.

121 The sample size was determined based on the treatment design (described in '*Experimental design*')
122 equating to a 2×2×2 design. The minimum amount of dyads per treatment group was set to 15 (n = 30
123 pigs) which needed to be balanced for sex and aggressiveness as a personality trait and needed to

124 guarantee that none of the animals encountered a same conspecific twice on the three staged
125 encounters (other than their siblings). Based on previous work (25) we accounted for a 40% chance of
126 non-escalation and 10% chance of contests without a clear outcome that could limit the use of the data
127 of those contests. This resulted in an aimed sample size of 360 pigs, which resulted in a slightly lower
128 sample size of 316 due to a lower number of piglets born from the allocated sows.

129

130 *Animals and housing*

131 A total of 316 male and female pigs (a commercial type cross of a Large White×Landrace sow
132 serviced by an American Hampshire boar) were studied until 13 weeks of age at the SRUC pig
133 research farm (Easter Howgate, UK). The animal phase was conducted over four consecutive batches
134 from Nov 2014 – Nov 2015. Piglets had been raised in conventional farrowing crates. Males were not
135 castrated and the tail and teeth were kept intact. Piglets remained in their own litter. Piglets were
136 weaned from the sow when they were four weeks of age. After weaning they were kept in the same
137 litter group but moved to a pen measuring 1.9×5.8 m, allowing ~1.0-1.1 m² per pig. Pens had a solid
138 floor which was covered with approximately 5 kg of long straw. Pens were cleaned daily and
139 provided with ~3.5 kg of fresh straw. Pigs had *ad libitum* access to water and pelleted commercial
140 feed. From 6 to 8 weeks of age pigs were habituated to the various test situations (described below) to
141 reduce the likelihood of a fear response during the tests and procedures. Habituation involved
142 gradually exposing pigs to being alone in a known and unknown area for several minutes and to being
143 handled in a weigh crate. At 9 weeks of age each pig was tested twice in a resident-intruder (RI) test
144 to gain an individual estimate of aggressiveness as a personality trait (28). This test (described in
145 detail in 25) measures the latency to attack an inferior intruder. The correlation between the attack
146 latencies of both test days was weak but significant ($r = 0.26$; $P < 0.001$), in contrast to previous work
147 (29: $r = 0.55 - 0.73$), including on the same population of pigs (26: $r = 0.58$; $P < 0.001$). The two test
148 values were summed to obtain a single measure of aggressiveness (as in 28).

149

150 *Experimental design*

151 Details of each of the procedures are given below. Briefly, pigs, naïve to encountering unfamiliar
152 conspecifics (besides the very brief RI test of <5 min in which they encountered but did not fight an
153 inferior pig), were first tested at 10 wk age in a dyadic contest to determine their assessment strategy
154 without experience. Two weeks later, at 12 wk age, 55% of the study population was subjected to
155 group mixing which involved repeated fights. This simultaneous encounter with several unfamiliar
156 conspecifics rapidly increases pigs' experience in fighting. At 13 wk of age, each pig was tested a
157 second time in a dyadic contest to formally test assessment strategy. A timeline of the experimental
158 design is given in Figure 1. Contest costs were measured by contest duration, fight duration, and
159 changes in the number of skin lesions, blood lactate and blood glucose (details described below). Note
160 that 'contest' and contest duration refer to the full time from opponents entering the arena until exiting
161 the arena, whereas 'fight' and fight duration refer only to the time when opponents are mutually
162 attacking each other with bites within the contest.

163

164 *Contest 1*

165 Contests were staged between pairs of pigs at 10 wk of age. Pigs were randomly matched with an
166 opponent of either similar body weight (RHP matched; <5% weight difference) or varying body
167 weight (RHP asymmetry; >20% weight difference) in order to maximise variation in relative weight.
168 Before pairs were randomly matched, the distribution of males and females and variation in attack
169 latency as measured in the RI test was balanced between treatments. Contests were staged in a novel
170 and neutral test arena measuring 2.9×3.8 m. The arena had a solid floor with a light bedding of wood
171 shavings. There were no resources present in the arena. The opponents entered the contest arena
172 simultaneously from opposite sides. The time was started from the moment both had entered the arena
173 fully. Contests were ended when a) a clear winner was apparent; b) after 30 minutes without a clear
174 winner; or c) in the event that a fight or mounting behaviour became too severe or that the animal
175 showed repeated fear behaviour. The determination of a winner was based on the retreat of one pig
176 (the loser) without retaliation for 1 min. In total 157 contests were carried out. Ten contests (6%)
177 reached an end-point due to a fear response or mounting, and in five contests (3%) the maximum time
178 was reached without an established winner.

179

180 *Experience of aggression*

181 At 12 weeks of age (two weeks after contest 1), 55% of the tested pigs were mixed into a new group
182 with unfamiliar pigs to gain experience of aggressive interactions (the percentage being based on
183 equal sized groups in the group mixing). The remaining 45% served as a control group and were by
184 pen (only siblings together) relocated into smaller pens to maintain a similar space allowance per
185 animal while the group size was reduced (due to the removal of pigs for the experience treatment).
186 Control pigs did not encounter any unfamiliar pigs. The mixed groups consisted of three pairs of pigs
187 of mixed weights, originating from different litters so that each pig was familiar to one pig but
188 unfamiliar to four. The inclusion of a familiar pig in the new group was designed to prevent pigs from
189 becoming too distressed, whereas the four unfamiliar pigs were expected to induce an aggressive
190 reaction. Pigs were left undisturbed for the first 24 h after mixing, after which aggression commonly
191 subsides. Pigs remained within this group composition for the rest of the trial to avoid further
192 disruption of dominance relationships. Skin lesions were counted as a reflection of the intensity of
193 engagement in aggression (following 30). Counting took place in the morning before mixing and 24 h
194 after mixing, both on the regrouped animals and on the control animals.

195

196 *Contest 2*

197 At 13 weeks of age all pigs were matched for a second contest to determine how fighting experience
198 influenced assessment ability. Contest 2 was executed as described for contest 1, but with a 2×2
199 treatment design including body weight (matched / asymmetric) and experience of group mixing
200 (control / experienced). Pigs were paired with an opponent they were unfamiliar to, which meant that
201 opponents were not from the same litter and had not encountered each other previously in either
202 contest 1 or during group mixing. Contests were only staged between pigs with similar experience
203 level (control / experienced). Similar to the first contest, blood metabolites and skin lesions were
204 recorded. For contest 2 not all pigs could be matched with an unfamiliar opponent of the same
205 treatment group, and therefore the number of contests reduced to 154. Of these, 30 (10%) reached an

206 end-point due to fear or mounting, and nine (6%) reached the maximum time with no winner (30
207 min).

208

209 *Blood glucose, blood lactate and skin lesions*

210 Blood glucose and blood lactate values were obtained within 3 min pre- and post-contest. A drop of
211 blood was collected from the ear vein by a pin prick which was taken when the pig was located in a
212 weigh crate. The drop of blood was then immediately applied to a test strip on a handheld glucose
213 meter (IME-DC iDia) and lactate meter (The EDGE Lactate Analyser) developed for humans. This
214 method was previously applied with success (25). Sampling order was randomized for treatment
215 group and contest outcome. The proportional increase in blood value (post-test value / pre-test value)
216 was used for analyses. Skin lesions, which are scratches on the body as a result of receiving bites,
217 were counted in the morning before testing and directly after the contest by a single observer.

218

219 *Behavioural observations*

220 The latency until the first contact, first bite, first fight and final retreat was recorded live during the
221 contests by one observer who was blind to the treatments. The latency until the first fight, or the
222 latency until final retreat in the case of no fight, was used to distinguish a pre-escalation phase.
223 Contests were recorded on video and were analysed for the exact fight duration using The Observer
224 XT 10 (Noldus, The Netherlands). Fighting was defined as an aggressive act, e.g. biting and pushing,
225 which the recipient retaliated to with an aggressive act within 5 s, and continued until one opponent
226 retreated or until other behaviour was performed for at least 3 s. The duration of the pre-escalation
227 phase and the fight duration (escalation phase) were used to investigate whether pigs switched
228 between assessment strategies during the contest, by analysing the assessment strategy over the
229 duration of the pre-escalation phase and escalation phase separately.

230

231 *Statistical analyses*

232 First, descriptive statistics for all of the contests were investigated. Then, contests without a clear
233 winner (time-out or end-point) were excluded. Contests where an endpoint occurred within the minute

234 after an outcome was reached were included (e.g. when repeated mounting occurred within one
235 minute after final retreat). Data were analysed with SAS version 9.3 (SAS Institute Inc., Cary, USA).
236 Results are presented as LSmeans with standard error unless stated otherwise.

237

238 Model assumptions

239 Residuals of the continuous response variables were assessed for the normality of the distribution
240 (UNIVARIATE Procedure, Shapiro Wilk statistics) and outliers (using Studentized residuals).
241 Contest duration, the pre-escalation duration and the fight duration were skewed and were log
242 transformed to reach a normal distribution. The number of skin lesions were square root transformed
243 (sqrt) to reach normality of the residuals. All models were tested for multicollinearity (REG
244 Procedure; VIF option), independence (REG Procedure; Durbin Watson option), and
245 homoscedasticity (AUTOREG Procedure; Arch option). The variance components covariance
246 structure (VC; default in SAS) best fitted the models as assessed through the Akaike Information
247 Criterion (AIC) and the Bayesian Information Criterion (BIC). All models were specified based on the
248 best model fit as assessed through the AIC and BIC.

249

250 Analyses on the individual level

251 Basic statistics were calculated on the individual level as most of the measurements were obtained per
252 individual. To select the most suitable measures of contest cost for further analyses, Pearson
253 correlations were estimated between contest duration, fight duration, the number of skin lesions,
254 blood lactate and blood glucose. Based on those correlations (section '*Results – Measures of contest
255 costs*') the variables contest duration (as traditional measure), fight duration, and skin lesions were
256 retained. Analyses of fight duration excluded those contests in which no fight occurred. Differences in
257 the occurrence of escalation between contests and treatment groups were analysed through
258 contingency tables with Chi Square analysis. Paired t-tests were applied to test the differences
259 between winners and losers in terms of the number of skin lesions and the body weight (contest 1 and
260 2 analysed jointly).

261

262 Analyses on the dyad level

263 Only three variables that were measured on the individual level were retained in the further analyses
264 (these were body weight, skin lesions and attack latency). Further analyses were therefore carried out
265 at the dyad level, with the three pig-level variables separated by winner and loser within a dyad (e.g.
266 winner lesions, loser lesions). Assessment strategy is traditionally analysed by the direction of the
267 relationship between fighting ability (RHP) and the contest costs (e.g. contest duration) for winners
268 and losers separately (3). RHP matched and RHP asymmetric dyads were analysed jointly (as a linear
269 scale of RHP difference). RHP difference was initially included in all models as a fixed effect but was
270 omitted as it did not significantly affect the contest costs. RHP difference did affect escalation level
271 and therefore these statistics are presented by RHP matched versus asymmetric dyads. General Linear
272 Mixed Models (MIXED Procedure) were run for the response variables contest duration, the duration
273 of the pre-escalation phase, fight duration (escalation phase), winner skin lesions, and loser skin
274 lesions. The strength and direction of the slope of contest costs against winner and loser RHP were
275 assessed through the three-way interaction between contest number (1 / 2), experience (contest 1 /
276 contest 2 control / contest 2 experienced) and RHP, for both winner and loser separately in the same
277 model. This three-way interaction at the same time allowed to assess the differences between the
278 slopes of the treatment groups. The combination of sexes in the dyad (MM / FF / MF) was included as
279 fixed effect. Winner and loser aggressiveness was initially included as a covariate in all models as it
280 has previously been shown to affect contest behaviour (25; 26), but was excluded as it was non-
281 significant and reduced the model fit. Batch (group tested in the same week) was included as the
282 random effect. Beta values are back-transformed LSmeans.

283

284 *Data availability*

285 The datasets generated during and/or analysed during the current study are available on request from
286 the corresponding author.

287

288 **Results**

289 *Measures of contest costs*

290 The correlations between the various measures of contest costs reveal that fight duration and skin
291 lesions, both in contest 1 and in contest 2, best captured the total contest costs in terms of duration,
292 fatigue and injury (Table 1). In contest 1 fight duration correlated at greater than $r = 0.50$ with all
293 other measures of contest cost, and in contest 2 between $r = 0.38$ and $r = 0.80$. The number of skin
294 lesions, which reflects each bite that an animal had received, was an equally good measure. However,
295 skin lesions can be measured in each contest on a continuous scale whereas fight duration can only be
296 applied in contests in which an escalated fight occurred. Skin lesions also provide a distinction in
297 costs between the winner and the loser, with losers having on average double the number of skin
298 lesions as compared to winners (winners: 32 ± 3 lesions; losers: 61 ± 4 lesions; $t_{279} = -9.89$, $P < 0.001$).
299 Based on the correlations in Table 1 we continued the analysis with only the duration of the pre-
300 escalation phase, the fight duration and the number of skin lesions for winners and losers.

301

302 *Contest escalation*

303 Depending on the treatment group, between 37 to 74% of the contests with a clear winner did not
304 escalate into fighting (Table 2). Instead, in these contests dominance relationships were established
305 through milder forms of agonistic behaviour, such as a single bite followed by immediate retreat.
306 The highest number of contests without escalation, 74%, occurred in RHP asymmetric dyads of
307 contest 2, irrespective of whether they had undergone the regrouping experience or not (Table 2;
308 asymmetric dyads: contest 1 vs. contest 2 control: $\chi^2(1) = 10.3$, $P = 0.002$). Overall, the percentage of
309 non-escalation was higher in contest 2 as compared to contest 1 ($\chi^2(1) = 14.58$, $P < 0.001$). Within
310 contest 2, the inexperienced (control) group did not differ from the experienced group ($\chi^2(1) = 0.61$,
311 $P = 0.49$). RHP asymmetric dyads tended to escalate less than dyads in which the opponents were
312 matched ($\chi^2(1) = 3.18$, $P = 0.09$). Matched dyads tended to escalate more in C2 than in C1 (Table 2;
313 C1 vs. C2 control: $\chi^2(1) = 4.03$, $P = 0.06$). Due to the absence of a fight in some of the contests, the
314 fight duration (i.e. escalation phase) was analysed only for 89 dyads in contest 1 and for 54 dyads in
315 contest 2 (control $n = 23$; experienced $n = 31$).

316

317 *Assessment abilities in contest 1*

318 Body weight was used as a proxy measure of fighting ability (RHP). Indeed, across contests the
319 heavier opponent was more likely to win (winner: 46 ± 0.7 kg; loser: 44 ± 0.7 kg; $t_{277} = 4.71$, P
320 <0.001). In contest 1, when none of the pigs had encountered an unfamiliar pig before, the contest
321 duration increased with loser RHP ($b = 10$ s / kg; $t_{267} = 1.97$; $P = 0.05$). Likewise, the number of skin
322 lesions on the winner's body increased with the increase of loser RHP (Figure 2; $b = 21.6$ lesions / kg;
323 $t_{268} = 2.85$; $P = 0.005$). Pre-escalation duration, fight duration and the number of lesions on the loser
324 were unaffected by loser RHP and none of the measures were significantly affected by winner RHP.
325 Thus, stronger losers inflicted more injuries on the winner than weak losers, irrespective of the size of
326 the winner.

327

328 *Experience of regrouping aggression*

329 Skin lesions on the body, which are a reflection of the number of bites received, provide information
330 on the amount of engagement in fights. Pigs undergoing the regrouping experience had on average
331 124 ± 89 skin lesions on their body. In contrast, control pigs (i.e. those that had not been regrouped
332 but were relocated and had a change in group composition due to the removal of group mates) had
333 only 7 ± 10 skin lesions. Although this indicates that control pigs did bite their siblings, the intensity
334 as reflected by the mean number of skin lesions was negligible in comparison with the regrouped pens
335 (lesions control vs. experienced: $t_{135} = 23.31$; $P < 0.001$).

336

337 *Assessment ability after experience*

338 In control dyads, which had experience of contest 1 but no profound fighting experience, the duration
339 of the pre-escalation phase was influenced by winner and loser RHP indicative of mutual assessment.
340 The pre-escalation phase increased with loser RHP ($b = 10$ s / kg; $t_{265} = 2.38$; $P = 0.02$) and decreased
341 with increasing winner RHP ($b = -10$ s / kg; $t_{265} = -2.21$; $P = 0.03$). All other measures of contest costs
342 were not significantly affected by winner and loser RHP.

343 Animals that had received profound fighting experience had a longer contest duration than control
344 dyads, which was due to a longer pre-escalation phase (Table 3). As this was due to more non-
345 damaging behaviour, as the number of injuries did not differ between the control and experienced

346 dyads (Table 3). In experienced dyads, the number of skin lesions on the winner's body increased
347 when loser RHP increased ($b = 14.2$ lesions / kg; $t_{268} = 2.19$; $P = 0.03$) but was unaffected by winner
348 RHP. The number of skin lesions on the loser's body, in line with winner lesions, also increased with
349 loser RHP ($b = 21.8$ lesions / kg; $t_{268} = 2.07$; $P = 0.04$) but was unaffected by winner RHP. In other
350 words, the stronger the loser was the more injuries it delivered to the winner, irrespective of the
351 winner's size, but in addition this also resulted in the loser receiving more injuries in return. Winner
352 and loser RHP did not affect the contest duration, pre-escalation duration, or fight duration.

353

354 *Switching strategies between and within contests*

355 Comparing between the three treatments (contest 1; contest 2 control; contest 2 experienced), there
356 was a significant difference between the slopes of the relationship of winner RHP and the duration of
357 the pre-escalation phase. In contest 1, and contest 2 for the experienced dyads, there is no relationship
358 between winner RHP and the duration of the pre-escalation phase, whereas for the contest 2 control
359 group there was a significant negative relationship (Table 4). Table 4 also reveals that for contest 2
360 control dyads the assessment strategy differs between the pre-escalation phase and the escalation
361 phase, indicative of switching between strategies within a contest. The relationship between loser
362 RHP and injuries on the winner's body also significantly differed between contests, with a positive
363 relationship in contest 1 and contest 2 dyads with experience, contrasted to the absence of such a
364 relationship in contest 2 control dyads (Table 4), supporting pure self-assessment in the former two
365 types of contest.

366

367 *Influence of sex and aggressiveness on contest costs*

368 Aggressiveness as a personality trait, as determined pre-contest in a resident-intruder test through
369 attack latency, was included in the models as a covariate. Losers that were scored pre-contest as being
370 more aggressive showed a shorter pre-escalation phase in contest 1, meaning a shorter time until the
371 first attack was made ($b = -1$ s pre-escalation / s attack latency (0 – 600 s), $F_{1,138} = 16.88$, $P < 0.001$).
372 The sex of the opponents had profound effects on the contest costs in terms of the durations of
373 behaviours and the number of skin lesions, irrespective of weight matching. Contests between two

374 male opponents were most costly, regardless of the age, body weight or experience of the pigs. For
375 example, the average number of skin lesions in male-male contests in contest 2 was 3.7 times greater
376 than in male-female contests and 2.2 times greater than in female-female contests. The details of the
377 sex differences will be published separately to do justice to the many aspects of sex differences in pig
378 contest behaviour.

379

380 **Discussion**

381 The aim of this study was to investigate whether pigs, being a highly intelligent mammal, use mutual
382 assessment during a dyadic contest and whether significant experience of fighting alters the
383 assessment strategy. In addition, we investigated whether pigs adopt different assessment strategies in
384 the pre-escalation phase compared to the escalated phase of a contest. From different proxy measures
385 of contests costs, fight duration and skin lesions as a reflection of the number of bites received best
386 reflected the costs accumulated during a contest.

387 Experience profoundly affected the response to the contest situation, albeit not as expected. Most
388 profoundly, the number of contests that escalated into a fight was reduced by a third in the second
389 contest, irrespective of the level of experience. RHP asymmetric dyads in contest 2 escalated least,
390 which would be in line with mutual assessment, as the inferior individual may decide to retreat
391 without getting into an injurious fight. Applying the appropriate game theory models suggests that
392 mutual assessment was, however, only present in the pre-escalation phase in the control dyads of
393 contest 2. In these contests opponents apparently switched from mutual assessment in the pre-
394 escalation stage to no clear assessment strategy in the escalated phase. Overall, profound experience
395 did not differ from mild experience (control group which had experience of contest 1) in terms of
396 fight escalation but mild experience was more beneficial for the subsequent use of mutual assessment
397 than profound experience.

398

399 *The effect of experience*

400 Experience reduced the likelihood of an escalated fight. Both in the experienced and control
401 treatments more encounters were resolved without escalating to fighting in the second contest.

402 Although it seems likely that this was an effect of the experience gained from the first contest, it is not
403 possible to disentangle this from a potential temporal confound because the two contests were staged
404 at different ages, albeit only three weeks apart. The question arises as to how much and what type of
405 experience is necessary to optimise assessment ability.

406 Experience of fighting, evidenced through skin lesions compared to an unmixed control group, clearly
407 altered aggressive behaviour in the subsequent dyadic contest. Compared to controls, the experienced
408 group showed longer contest durations. However, this was driven by a longer, low cost non-damaging
409 pre-escalation phase, rather than an increase in actual costs as seen from the number of skin lesions.
410 The increased time in investigation and display in the experienced group, together with fewer costs
411 relative to contest duration, is consistent with an enhanced assessment ability. However, testing the
412 formal predictions through the relationship between RHP and contest costs revealed mutual
413 assessment only in the control dyads of contest 2, which had experience of a single contest (contest 1).
414 Consistent with the predictions for mutual assessment, the duration of the pre-escalation stage
415 significantly increased with loser RHP whereas it significantly decreased with winner RHP. The
416 slopes of naïve (contest 1), control and experienced dyads indeed significantly differed from each
417 other. This relationship was, however, only for the pre-escalation phase and only for the control dyads
418 in the second contest. By contrast, for contest 1 and the experienced dyads in contest 2, the results
419 were consistent with predictions for pure self-assessment, with positive relationships between loser
420 RHP and contest costs. Speculating on the differences between the two types of second contests, the
421 results suggest that the intense mixing experience with multiple unfamiliar individuals may have
422 favoured the use of a self-assessment strategy, perhaps due to the costs associated with trying to gain
423 information from a range of aggressively competing conspecifics (3). This is in contrast to the control
424 dyads that remained housed with familiar conspecifics, a situation that may have favoured the
425 development of enhanced information-gathering skills during low escalation phases and was thus
426 revealed by evidence supporting mutual assessment in the pre-escalation phase.

427

428 *Switching strategies*

429 As detailed above, control dyads in contest 2 showed mutual assessment during the pre-escalation
430 phase but not during the phase of escalated mutual fighting where they showed no evidence of any
431 form of assessment. This indicates a switch between strategies in line with previous findings. Hsu et
432 al (27) showed that killifish (*Kryptolebias marmoratus*) apply mutual assessment during the display
433 phase whereas they switch to self-assessment during escalation. This is in line with the behavioural
434 observations in pigs, where during the pre-escalation phase opponents show mutual investigation (26)
435 and behaviour such as parallel walking which is said to inform the individual about the opponent's
436 size (31), whereas during the escalated phase the aim is to deliver attacks at maximum intensity. The
437 dyads of contest 1 and of contest 2 with fighting experience did spend more time in the pre-escalation
438 phase (as shown in Table 3) but did not show this switching between strategies. The pre-escalation
439 phase can consist of social interactions that, as described above, can assist in mutual assessment, but
440 can also consist of behaviour unrelated to the opponent (e.g. exploring the environment). That mutual
441 assessment was apparent for contest 2 control dyads but not for others may have been due to a
442 different behavioural repertoire in the pre-escalation phase.

443

444 *Contest costs*

445 The cost of a contest is an essential measure in the application of game theory models for animal
446 contests. Traditionally the total contest duration is used as a measure of costs. In previous work it was
447 shown that total contest duration can be a poor measure of costs when opponents engage in non-
448 agonistic behaviours during the course of the contest (26). Indeed, in the current work total contest
449 duration poorly related to the costs that more directly reflect energetic effort and risk of injury.
450 Moreover, the longer contest duration due to a longer non-damaging display phase (pre-escalation
451 phase) does not equate to more actual costs, as shown in contest 2. Fight duration has been suggested
452 as a better measure of costs but this can only be recorded in contests in which a fight occurs. Across
453 species and studies, varying levels of non-escalation have been reported, with the current work having
454 up to 74% of the dyads not escalating into a fight depending upon the treatment group. Non-escalated
455 contests reveal important information on the decision making process of the contestants and therefore
456 suitable measures are required to assess the costs in these contests as well. Moreover, contest duration

457 and fight duration apply to both contestants, implying that the costs would be the same for both
458 winner and loser. In reality the costs for the loser and winner are likely to differ, and measures on the
459 individual are therefore more accurate.

460 Physiological costs indicated by changes in blood lactate and glucose have previously been used to
461 reflect contest costs for the individual contestants and can be measured regardless of the level of
462 escalation (a.o. 32; 33). However, baseline values for lactate and glucose are subject to individual
463 variation and depend upon factors such as time of day and the time of the last meal. In pigs, skin
464 lesions are a direct cost from aggression as they reflect the number of bites received in the contest.
465 Even if no mutual fight occurs, some lesions will appear due to unilateral bites. Skin lesions can
466 therefore be recorded regardless of the occurrence of an escalated fight. We assessed durations of
467 behaviour, glucose and lactate as well as skin lesions as proxy measures of contest costs. From these,
468 fight duration and skin lesions showed the strongest correlations with the other proxy measures and
469 therefore best reflected the contest costs.

470

471 *Implications for further research and animal welfare*

472 Animal contests have long been analysed using the traditional approach of correlating winner and
473 loser RHP against contest costs. The analysis of animal contests does however continue to develop
474 profoundly, with advances in the interpretation of models (17), the required framework to distinguish
475 between models (3), various manners to statistically analyse animal contests (34), and the exploration
476 of new factors contributing to RHP (e.g. personality, 35; 36). We propose that, as also advocated in
477 (37), new measures of contest costs that better reflect the metabolic effort and fitness consequences
478 should be considered where relevant. Where species specific measures exist, such as for example skin
479 lesions in pigs and acrorhagial peels in sea anemones (*Actinia equine*; 38), these may be preferred
480 over traditional proxy measures of contest costs. In addition, the use of total contest duration as a
481 measure of contest costs should be reconsidered, especially for species that spend time in non-
482 agonistic behaviour during a contest.

483 Aggression is an important animal welfare problem in pig husbandry and research contributing to the
484 understanding of pigs' assessment abilities during agonistic encounters can inform future efforts to

485 find effective methods of controlling it. The influence of experience, even when brief, reduced the
486 likelihood of an encounter escalating into a fight. Despite the initial costs of fighting, the gained
487 experience may reduce costs on the long term when animals are older and costs are likely to be more
488 severe. Early mixing of unfamiliar pigs to enhance their social abilities has been suggested as a
489 method to reduce aggression as a welfare problem in practice (39). This has been tested in young
490 piglets from an applied perspective, mainly in terms of farm management strategies, but had never
491 been tested in a game theoretical approach. We are currently investigating the effect of early life
492 experience (at 14 days of age) using the same formal setting which allows animal contest models to be
493 applied. The results are similar to the current study, but with the pigs being nine weeks younger when
494 they receive their experience, the costs to gaining this experience are substantially less (40). This
495 shows that there can be substantial benefits in allowing animals to gain experience early in life to
496 improve animal welfare.

497

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581 Publishers, Netherlands, 2017).

582

583 **Acknowledgements**

584 This research was funded by the Biotechnology and Biological Sciences Research Council (BBSRC).
585 SRUC receives financial support from the Scottish Government.

586

587 **Author contributions**

588 IC: designed and conducted the experiment; analysed data; wrote the manuscript; prepared the
589 figures. SPT: designed the experiment; corrected the manuscript. MF: designed and conducted the
590 experiment. GA: designed the experiment; advised in data analysis; wrote the manuscript.

591

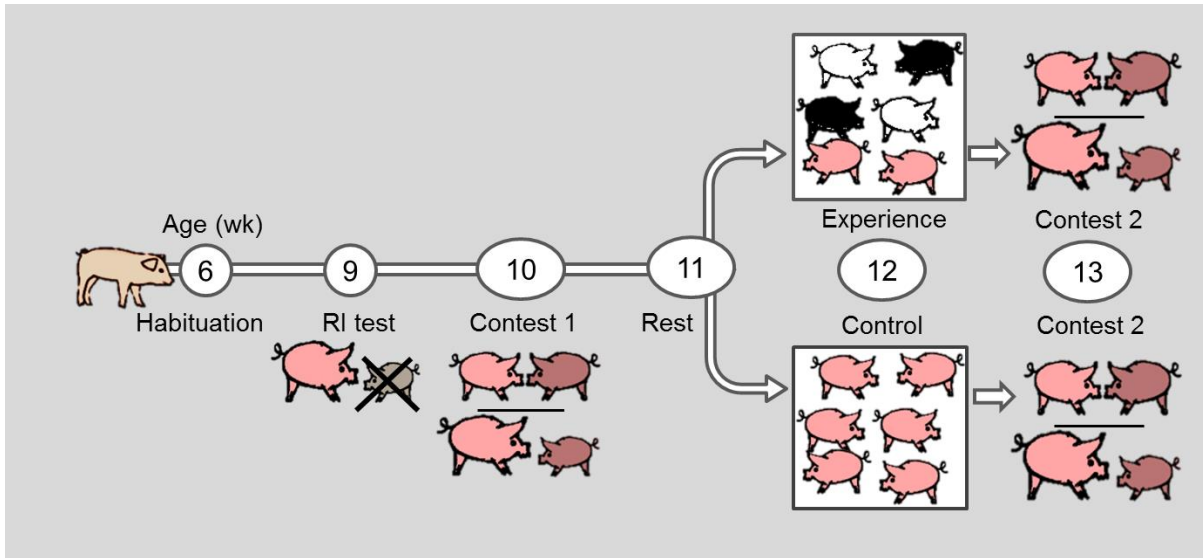
592 **Competing interests**

593 The authors declare no competing financial interests.

594 **Figure legends**

595

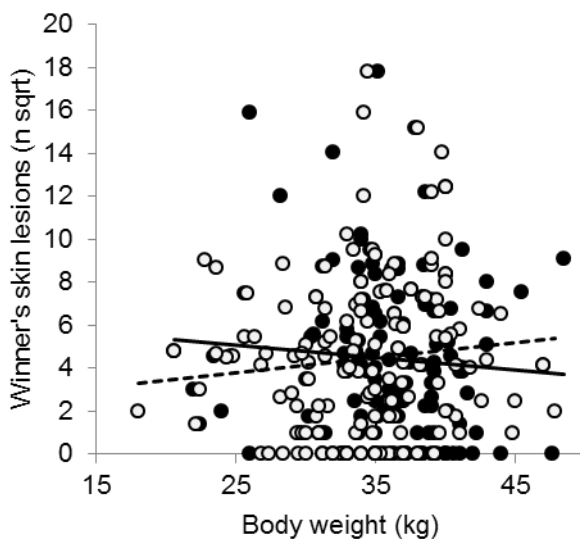
596 **Figure 1. Experimental design.** Graphical presentation of the various tests by week of age.



597

598

599 **Figure 2. Assessment strategy before experience.** The relationship between winner and loser body
 600 weight for skin lesions on the winner's body as measure of contest costs in contest 1. Winners (n =
 601 135): ● / — ; Losers (n = 135): ○ / ---.



602

603 **Tables**

604 **Table 1. Proxy measures of contests costs.** Pearson correlation coefficients between various proxy
 605 measures of contest costs for contest 1 (values above the diagonal) and contest 2 (values below the
 606 diagonal). All correlations are significant at $P < 0.001$.

| | Contest duration | Fight duration | Blood lactate | Blood glucose | Skin lesions |
|------------------|---------------------|-------------------|------------------|------------------|-----------------|
| Contest duration | | 0.51 | 0.20 | 0.25 | 0.36 |
| Fight duration | 0.61 | | 0.62 | 0.50 | 0.70 |
| Lactate | 0.37 | 0.61 | | 0.58 | 0.49 |
| Glucose | 0.19 | 0.38 | 0.51 | | 0.45 |
| Skin lesions | 0.55 | 0.80 | 0.59 | 0.37 | |

607

608

609 **Table 2. Non-escalation.** Values are the percentage of contests that reached an outcome (clear
 610 winner) without fighting. The number of contests out of which the percentage is calculated is
 611 presented in parentheses.

| | Contest 1 | Contest 2 Control | Contest 2 Experienced |
|----------------|-------------------------|-------------------------|-------------------------|
| RHP Matched | 37 ^a (25/68) | 56 ^b (19/34) | 45 ^b (19/42) |
| RHP Asymmetric | 39 ^a (29/75) | 73 ^b (22/30) | 74 ^b (23/31) |

612 ^{a,b} Values lacking a common superscript letter differ by $P < 0.10$.

613

614

615 **Table 3. Contest costs.** Means with SE for the selected proxy measures of contests costs by treatment
 616 group. Values are back-transformed LSmeans with the lower and upper confidence intervals.

| | Contest 1 | Contest 2 Control | Contest 2 Experienced | <i>P</i> -value |
|----------------------|------------------------------|------------------------------|------------------------------|-----------------|
| Contest duration (s) | 263 (184 – 342) ^a | 159 (107 – 211) ^b | 209 (140 – 278) ^a | 0.03 |
| Pre-escalation (s) | 106 (65 – 148) ^a | 52 (30 – 74) ^b | 85 (49 – 121) ^{ac} | 0.004 |
| Fight duration* (s) | 25 (15 – 35) | 51 (16 – 86) | 41 (14 – 67) | 0.35 |
| Winner lesions (n) | 30 (11 – 50) | 11 (0 – 24) | 12 (0 – 25) | 0.29 |
| Loser lesions (n) | 66 (36 – 97) ^a | 31 (9 – 53) ^b | 36 (12 – 59) ^{ab} | 0.23 |

617 *Only for contests including a fight; ^{a,b} Values lacking a common superscript letter differ by *P* < 0.10.

618

619

620 **Table 4.** Winner and loser RHP (body weight) in relation to various contest costs for contest 1,
621 contest 2 control (no fighting experience except contest 1), and contest 2 of dyads that received
622 profound fighting experience. Values are back-transformed beta estimates for the change in costs per
623 kg of increase in body weight. The *P*-value indicates the significance of the change in the slope
624 between the treatment groups.

625

| | | Contest 2 | | Contest 2 | | <i>F</i> _{3,265} | <i>P</i> -value |
|--------------------------------------|--------|---------------|--------------|--------------|------|---------------------------|-----------------|
| | | Contest 1 | Control | Experience | | | |
| Contest duration (s / kg) | Winner | 10.0 | -9.9 | 10.1 | 0.38 | 0.77 | |
| | Loser | 10.2* | 10.2 | 10. | 1.56 | 0.20 | |
| Pre-escalation (s / kg) | Winner | 10.2 | -9.7* | 10.2 | 2.97 | 0.03 | |
| | Loser | 10.0 | 10.4* | -9.9 | 2.05 | 0.11 | |
| Fight duration ^a (s / kg) | Winner | -9.6 | 10.3 | -9.6 | 1.26 | 0.29 | |
| | Loser | 10.3 | -9.7 | 10.4 | 1.04 | 0.38 | |
| Winner lesions (n / kg) | Winner | -8.5 | 7.9 | -6.5 | 0.70 | 0.56 | |
| | Loser | 21.6** | -1.2 | 14.2* | 3.63 | 0.01 | |
| Loser lesions (n / kg) | Winner | -10.2 | 1.5 | -16.6 | 0.94 | 0.42 | |
| | Loser | 19.4 | 1.5 | 21.8* | 2.06 | 0.11 | |

626

627 ^a Fight duration includes the contests with a fight only (n = 144) opposed to all contests (n = 270).

628 *RHP significantly affects the contest costs by *P* < 0.05; ** by *P* < 0.01.