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Complex contests and the influence of aggressiveness in pigs

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Animal contests vary greatly in behavioural tactics used and intensity reached, with some encounters resolved without physical contact while others escalate to damaging fighting. However, the reasons for such variation remains to be fully explained. Aggressiveness, in terms of a personality trait, offers a potentially important source of variation that has typically been overlooked. Therefore, we studied how aggressiveness as a personality trait influenced escalation between contestants matched for resource holding potential (RHP), using detailed observations of the contest behaviour, contest dynamics, and escalation levels. We predicted that winner and loser behaviour would differ depending on personality. This was tested by examining 52 dyadic contests between pigs (*Sus scrofa*). Aggressiveness was assayed in resident-intruder tests prior to the contest. Contests were then staged between pigs matched for RHP in terms of body weight but differing in their aggressiveness. In 27% of the contests a winner emerged without escalated physical fighting, demonstrating that a fight is not a prerequisite between RHP-matched contestants. However, the duration of contests with or without fighting was the same. In contests without a fight, opponents spent more time on mutual investigation and non-contact displays such as parallel walking, which suggests that ritualized display may facilitate assessment and decision making. Winners low in aggressiveness invested more time in opponent investigation and display and showed substantially less aggression towards the loser after its retreat compared to aggressive winners. Aggressiveness influenced contest dynamics but did not predict the level of escalation. Prominent behavioural differences were found for the interaction between personality and outcome and we therefore recommend including this interaction in models where personality is considered. Analyses based on contest duration only would miss many of the subtleties which are shown here and we therefore encourage more detailed analyses of animal contests, irrespective of the level of contest escalation.

Keywords. Aggression, behaviour, contest, personality, pig

Animal contests are typically assessed through simple measures of contest duration and outcome (reviewed by Arnott & Elwood, 2009). However, a great deal of information may be lost using this approach alone, including differences in physiological state and motivation (e.g. Elwood, Wood,

Gallagher, & Dick, 1998). For example, on some occasions, contestants spend time in low cost display behaviour after which the opponent with the lowest resource-holding potential (RHP, or fighting ability) withdraws. On other occasions contestants spend the same amount of time interacting but fight fiercely for that length of time, after which the opponent with the lowest RHP withdraws. In the traditional approach these contests would be rated the same whereas for the contestants there is a large difference in, amongst other things, physiological costs (Briffa & Sneddon, 2007). More detailed analysis of contests, for example inclusion of physiological measures or analysis by phases of escalation (e.g. Hsu, Lee, Chen, Yang & Cheng, 2008; Vieira & Peixoto, 2013; McGinley, Prenter, & Taylor, 2015), can deepen our understanding of contest behaviour (e.g. Jennings, 2014; Schnell, Smith, Hanlon, & Harcourt, 2015).

One situation in which a great deal of information may be lost is when confrontations are resolved without escalated aggression. Many species avoid escalation where possible and contests may naturally end without the occurrence of a fight or even before the opponents make contact (e.g. Bentley, Hull, Hardy, & Goubault, 2009). Here, dominance is settled through threat displays (e.g. Maynard-Smith & Price, 1973; primates: Judge & de Waal, 1993; pigs: Jensen, 1982). Theory predicts (e.g. the sequential assessment model, SAM) that contests ending at the display phase prior to escalated fighting will be of shorter duration (Parker & Rubenstein, 1981; Enquist & Leimar, 1983), while those between RHP-matched individuals will be escalated and of longer duration. However, this overlooks the potential importance of individual differences in behavioural tendencies that may influence escalation patterns (Briffa, Sneddon & Wilson, 2015; Camerlink, Turner, Farish, & Arnott, 2015). Moreover, non-escalated contests are often excluded from analyses because they may count as missing values, for example when outcome criteria are based on the presence of a certain level of escalation. Yet, these contests may provide useful information on contest resolution (as for example in Rudin & Briffa, 2011), and their exclusion has been criticised (Elwood & Arnott, 2013). Neglecting contests that do not perfectly fit into theoretical or statistical models may underestimate the importance of certain strategies such as conflict avoidance.

Firstly, contrary to current theory, we predict that within a population of RHP-matched individuals, some confrontations will be resolved without a fight and that these non-escalated contests will be of

shorter duration. This will be tested using domestic pigs. In wild populations, pigs frequently show agonistic display towards each other but damaging aggression, including fights, between adults is rare (Mendl, 1995; Marchant-Forde & Marchant-Forde, 2005; D'Eath & Turner, 2009) and is predominantly limited to males during the mating season (Barette, 1986). In contrast, the routine mixing of groups of unfamiliar pigs in commercial husbandry results in long and injurious reciprocal fights irrespective of sex, which is a considerable welfare issue (Marchant-Forde & Marchant-Forde, 2005). However, there are substantial individual differences in the amount of aggression (Turner et al., 2006), and this variation has been related to personality (e.g. Ruis et al., 2000).

Secondly, we hypothesize that variation in contest behaviour (such as ritualized display, non-damaging aggression, and damaging aggression) and contest intensity will be influenced by the personality of the contestants. A personality trait is "a specific aspect of a behavioural repertoire that can be quantified and that shows between-individual variation and within-individual consistency" (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013, p. 467). Personality is related to many behavioural and physiological characteristics (e.g. Stamps & Groothuis, 2010), including the response that an individual shows when faced with an opponent and its subsequent likelihood of winning (e.g. Colléter & Brown, 2011; Melotti, Oostindjer, Bolhuis, Held, & Mendl, 2011). As such, personality has recently been suggested as a component of RHP (reviewed by Briffa et al., 2015). Aggression is one personality trait which can have an important role in contest behaviour. In pigs, aggressiveness is commonly assessed in the resident-intruder test; a test which has demonstrated considerable variation between individuals and a moderate repeatability within individuals (Erhard & Mendl, 1997; D'Eath, 2004). We previously showed that aggressiveness as a personality trait, measured with the resident-intruder test, influenced the initiation of agonistic behaviour during a subsequent contest, although evidence that it formed a component of RHP was lacking, as aggressiveness did not have a significant effect on the outcome or contest duration when an escalated fight occurred (Camerlink et al., 2015). Existing contest theory (e.g. SAM, Enquist & Leimar, 1983) predicts encounters between RHP-matched contestants will be maximally escalated. However, this overlooks the potentially important role of variation in aggressive personality and therefore we predict

that variation in this personality trait will result in variation in escalation level, even between RHP-matched contestants.

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

METHODS

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

Animals and housing

A total of 114 young male and female pigs ((Large White×Landrace) × American Hampshire) from 17 litter groups were studied at 9 wk of age at the research farm (Easter Howgate, UK). Animals were studied over three consecutive batches from April to October 2014. Piglets were kept with their sow in conventional farrowing crates up to 4 wk of age. Thereafter the sow was removed and the piglets remained in the crate for two more weeks. Males were not castrated and the tail and teeth were kept intact. At 6 wk of age pigs were moved to the experimental facilities were they were kept with their siblings in a pen measuring 1.9×5.8 m (~1.0-1.1 m^2 / animal). Pens had a solid floor with straw bedding (~5 kg) and were cleaned daily and provided with fresh straw. Water and pelleted feed was

136 available *ad libitum*. From two weeks prior to testing all pigs were gradually (over six occasions)
137 habituated to the various test situations to reduce the possibility of fear responses during the tests.
138
139 *Resident-intruder test*
140 The resident-intruder (RI) test is an established test in behaviour research that is undertaken to obtain
141 a quantifiable measure of individual aggressiveness which is consistent over time (pigs: D'Eath &
142 Pickup, 2002). The RI test was carried out twice for each pig at 9 wk of age. An individual "resident"
143 pig was kept in a separate part of its home pen for the duration of the test (max 10 min). Then, an
144 approximately 20% smaller and unfamiliar "intruder" pig was introduced into the same compartment
145 (i.e. the resident's home pen). Under these conditions, the resident typically attacks the inferior
146 intruder within a short period of time. The latency until the first attack was recorded. If the resident
147 did not attack within 5 min after initial contact then the test was ended and the latency time was set at
148 300 s. For all pigs the test was repeated the following day with a different intruder. Residents were
149 thus tested twice for their aggressiveness. Pigs were used as either a resident or intruder but never
150 both. Intruders were used a maximum of 3 times. Test results of the second day were moderately
151 correlated with the results of the first day (r_s = 0.58; P<0.001). Similar correlations between test days
152 have been reported previously for this test (r_s = 0.55 – 0.73, Erhard & Mendl, 1997). The attack
153 latencies of both test days were summed to obtain a single value of aggressiveness. Values could
154 range between 0 – 600 sec, with lower values reflecting a more aggressive response.
155
156 *Contest*
157 Contests were staged in a neutral arena between pairs of unfamiliar pigs at 10 wk of age. Opponents
158 were of similar body weight (<5% difference, i.e. matching RHP, with weight a validated measure of
159 RHP in pigs; Andersen et al., 2000; Jensen & Yngvesson, 1998; Rushen, 1987) and differing in their
160 aggressiveness as reflected in the attack latency of the RI test. Body weight ranged from 24 – 48 kg
161 (mean 34 ± 0.5 kg) and the summed attack latency ranged from 27 – 600 s (mean 257 ± 17 s). To
162 ensure a balanced difference in aggressiveness, animals were for the purpose of opponent matching
163 categorized into 'low aggressive' (summed attack latency of ≥360 s), 'intermediate' (121 – 359 s),

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

Data analysis

Data were analysed with SAS version 9.3 (SAS Institute Inc., Cary, NC, USA) using mixed models (MIXED Procedure). Response variables were the proportion of contest time spent on a behaviour (see Table 1 for behaviours analysed), the number of bites, contest duration, and aggressiveness in attack latency (all continuous data). Residuals of the response variables were assessed for the

normality of their distribution (UNIVARIATE Procedure, Shapiro-Wilk statistics) and outliers (Studentized residuals). Model assumptions were tested using the REG (regression) Procedure; variables were tested for multicollinearity (VIF option), homoscedasticity (White test; SPEC option), and independence (Durbin-Watson coefficient; DW option). To obtain normality of the residuals, contest duration (in seconds) was log transformed; the behaviours investigation, nose wrestling, parallel walking, pushing, fighting and bullying (analysed in proportion of contest time) were arcsine square root transformed; and the number of bites (frequency) was square root transformed.

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

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

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

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

Analysis of contest dynamics

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

RESULTS

Contest dynamics and phases of escalation

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

The level of escalation was first assessed by four levels of intensity indicating the maximum intensity that a contestant had shown during the contest, which was either display, pushing, biting, or fighting. The level of escalation did not influence the contest duration (Table 2; $F_{3,84} = 1.39$; $P = 0.25$). Contestants who engaged in mutual fighting (escalation level 4) were on average heavier than pigs who only pushed or bit the opponent (Table 2; $F_{3,82} = 2.82$; $P = 0.04$). Contestants that bit the opponent (level 3) were on average more aggressive than opponents whose maximum level of aggression was pushing (level 2), but animals from escalation level 3 did not differ from level 1 or 4 (Table 2; $F_{3,84} = 2.41$; $P = 0.07$). Escalation level 1 and 2 included only few individuals ($N = 3$ and 9, respectively) and therefore contests were also analysed by the occurrence of a fight as a binary trait (i.e. the absence or presence of a mutual fight).

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

Aggressiveness as a personality trait affecting contest behaviour

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

The most profound effects were observed for the interaction between aggressiveness and contest outcome. Winners which showed little aggression in the resident-intruder test spent more time during the contest on non-damaging opponent investigation (Figure 4a; interaction aggressiveness × outcome $F_{1,83} = 5.91$; $P = 0.02$), more parallel walking (Figure 4b; $F_{1,84} = 6.10$; $P = 0.02$) and tended to spend a greater amount of time on non-agonistic behaviours such as walking, standing and exploring the environment (b = -0.04 ± 0.02 % / s increase of attack latency in losers, with winners set to 0; $F_{1,80} = 3.73$; $P = 0.06$). The most prominent difference was seen after the contest outcome was established.

After the retreat of the loser, winners with an aggressive personality (short attack latency) spent up to 75% of the contest time on bullying behaviour (unilateral biting and chasing by the winner towards the loser), whereas less aggressive winners showed almost no bullying behaviour towards the losers (Figure 4c; aggressiveness × outcome $F_{1,83} = 12.60$; $P < 0.01$). Moreover, losers which were assessed pre-contest as being less aggressive (long attack latency RI test) received more bullying than aggressive losers.

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

DISCUSSION

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

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

To fight or not to fight

303 The main difference between contests was the occurrence of a fight or the absence thereof whereas in
304 both situations a clear winner and loser were present. This confirms that RHP-matched pigs can settle
305 dominance relationships without needing to fight. This finding contrasts contest theory (e.g. SAM,
306 Enquist & Leimar, 1983), as does the finding that contest duration did not differ between escalated
307 and non-escalated contests.
308 The absence of a fight in some contests, together with an increase in parallel walking, a form of
309 ritualized display, suggests that some form of assessment was made at a pre-fight phase (Mendl &
310 Erhard, 1997; Arnott & Elwood, 2009). Display behaviour such as parallel walking has been studied
311 in deer (Jennings & Gammell, 2013), were it has been suggested to aid opponent assessment (Clutton-
312 Brock, Albon, Gibson, & Guinness, 1979; Jennings & Gammell, 2013). Contestants that invest more
313 time in investigation and display may obtain more accurate information and consequently be better
314 able to assess their opponent, resulting in a decision to avoid fighting. Conversely, animals with a low
315 motivation to fight will be unwilling to escalate the contest and may therefore be expected to engage
316 in longer periods of display prior to disengagement. It is possible that both of these mechanisms have
317 a role in explaining the greater investment in display in contests that ended without a fight.
318 Contests in which the opponents avoid fighting or physical contact may occur frequently (e.g. Bentley
319 et al., 2009; Rudin & Briffa, 2011). In analyses these contests are often ignored because the read-out
320 parameters such as winning or losing may be absent or too subtle to fulfil the criteria. Elwood and
321 Arnott (2013) previously discussed the issue of differing conclusions depending on whether
322 researchers considered all contests or restricted analyses to escalated fights only. They advocated that
323 in terms of furthering our understanding of animal contest behaviour, valuable information is lost if
324 analyses are restricted to fights only. The decision to avoid fighting can be a strategy in itself
325 (Maynard-Smith & Price, 1973; Parker & Rubenstein, 1981) and this should be taken into account
326 when analysing animal contests, in particular when conclusions about assessment strategies are made.
327 The present findings reiterate the importance of studying contest behaviour in addition to the
328 traditional measures of contest duration and outcome before conclusions are drawn about the
329 assessment ability of animals.
330

Effect of aggressiveness as a personality trait on contest behaviour

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

Interactions between outcome and aggressiveness in our statistical models revealed that winners which had a long attack latency in the resident-intruder test, indicating low aggressiveness, invested more time in non-damaging opponent investigation, parallel walking and non-agonistic behaviours such as walking and exploration of the environment. These behaviours are less likely to escalate into damaging aggression, as was reflected in the analysis of contest dynamics, which suggests that more aggressive winners were taking more risks with their behaviour. Previously, we showed that pigs with a more aggressive personality were more likely to initiate aggression, especially bites, during the contest (Camerlink et al., 2015). Here we show that initiation of such behaviour has a high probability of transitioning into a fight. Moreover, after victory high aggressive winners continued to exert aggressive behaviour on the loser whereas low aggressive winners did not. This is in line with previous work showing that high aggressive pigs are more persistent in their aggressive behaviour (D'Eath, 2002). Together these results provide a consistent image that more aggressive personalities are more willing to engage in fighting, shown through a willingness to attack and through persistent aggressiveness. This is in line with other studies on personality, whereby animals with a proactive coping style are more bold and rigid in their aggressive behaviour (Koolhaas et al., 1999; Briffa et al., 2015; pigs: Bolhuis, Schouten, Schrama, & Wiegant, 2005; Melotti et al., 2011). Rudin and Briffa (2012) also reported interactions between personality (boldness) and contest outcome in sea anemones, whereby losers were less bold than winners. The profound behavioural differences related to the interaction between personality and outcome in the current study would suggest that, where

possible, researchers should try to incorporate these factors into their setup and analyses. Mendl and Erhard (1997) suggested that pigs differing in their aggressiveness as a personality trait may apply different contest assessment strategies, and this is the focus of another study that we have conducted.

Securing the outcome with bullying behaviour

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

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

CONCLUSION

Contrary to predictions from contest theory, a substantial percentage of RHP-matched contests were settled without a fight. However, the duration of contests with and without fighting did not differ. These results highlight that RHP-matched contestants can solve conflicts by avoiding escalated damaging behaviour, and these contests should be studied rather than disregarded when investigating

387 questions of assessment ability and aggressive strategies. Bullying behaviour just after the retreat of
388 the loser, which was strongly related to aggressiveness, suggests that contestants employ different
389 tactics to determine contest outcome. Given the important influence of personality on contest
390 dynamics, we recommend that, where possible, this be considered in future studies of animal contests.
391
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396
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492

493 **TABLES**

494 **Table 1.** Ethogram of the major behaviours recorded during the contest*.

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

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

496

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

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

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

^{a,b} Values lacking a common superscript letter differ by P <0.05.

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

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

FIGURE CAPTIONS

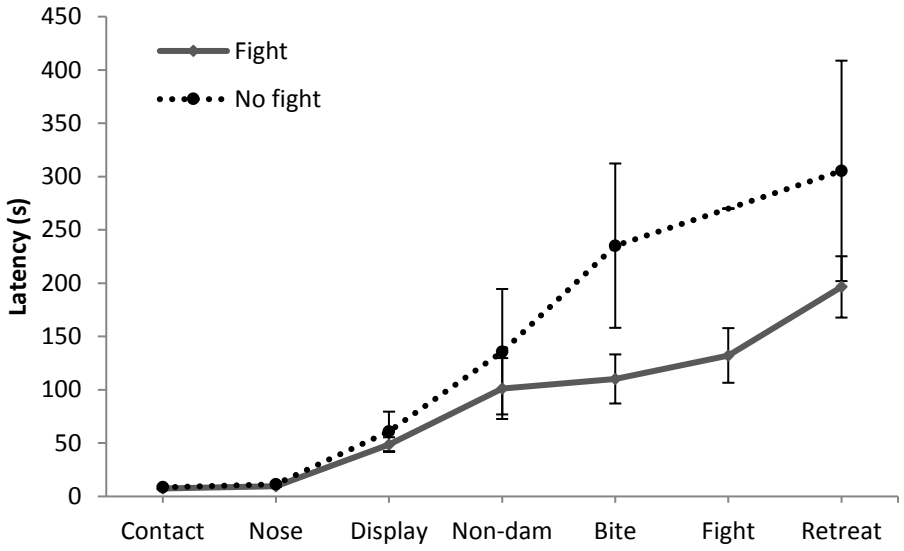
Figure 1. Average latency (with standard error bars) after entering the arena at which the first occurrence of the behaviour listed on the x-axis was observed, displayed for contests with and without a fight.

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

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

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

527 **Figure 1**



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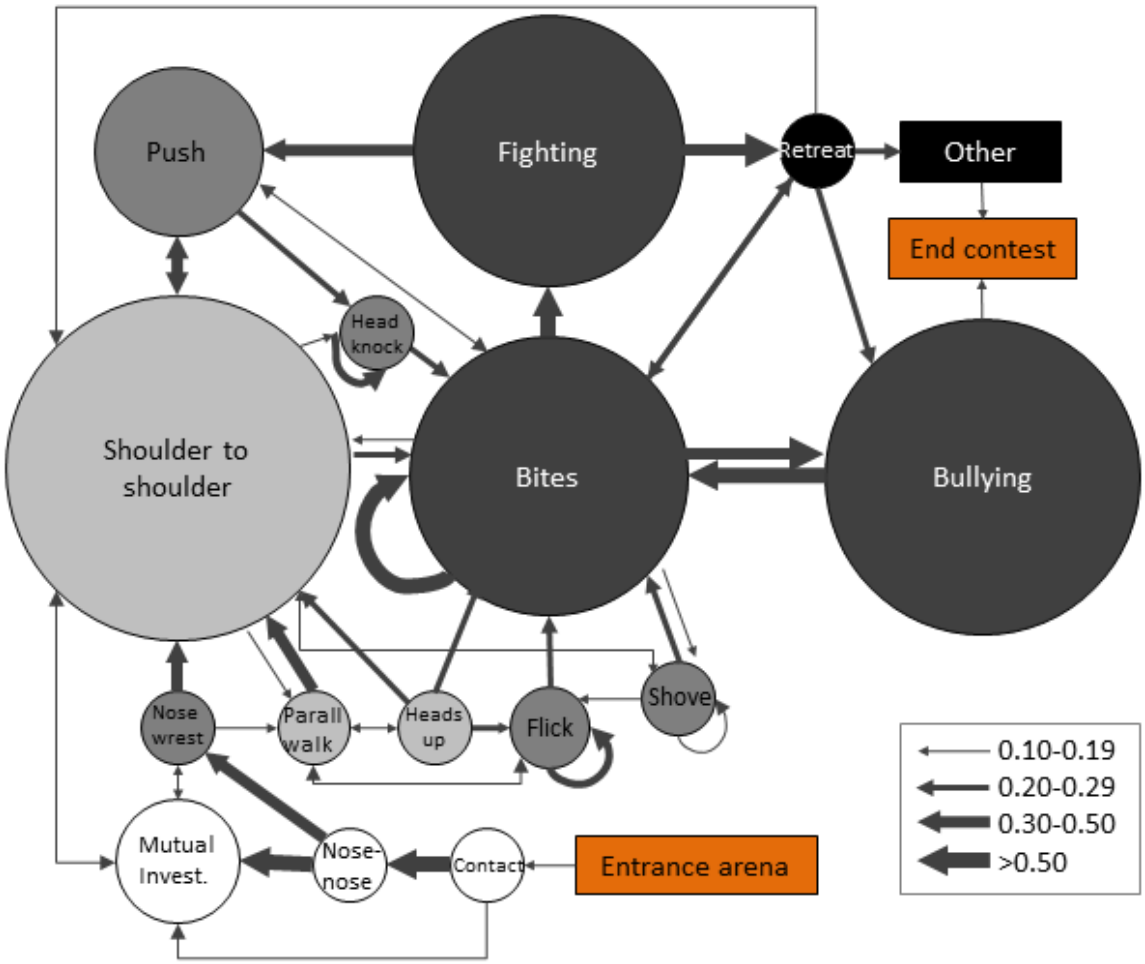
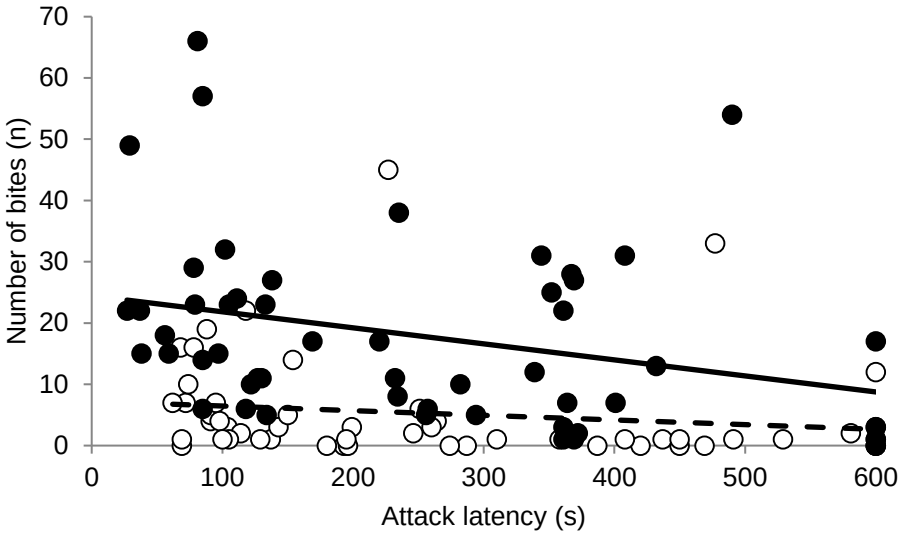
530 **Figure 2**



531

532 **Figure 3**

533



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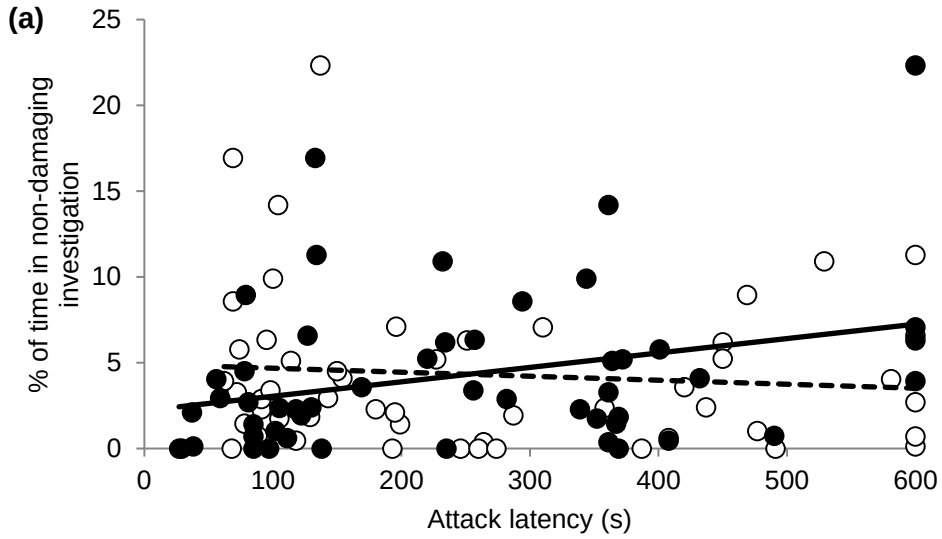
536 **Figure 4 a – c**



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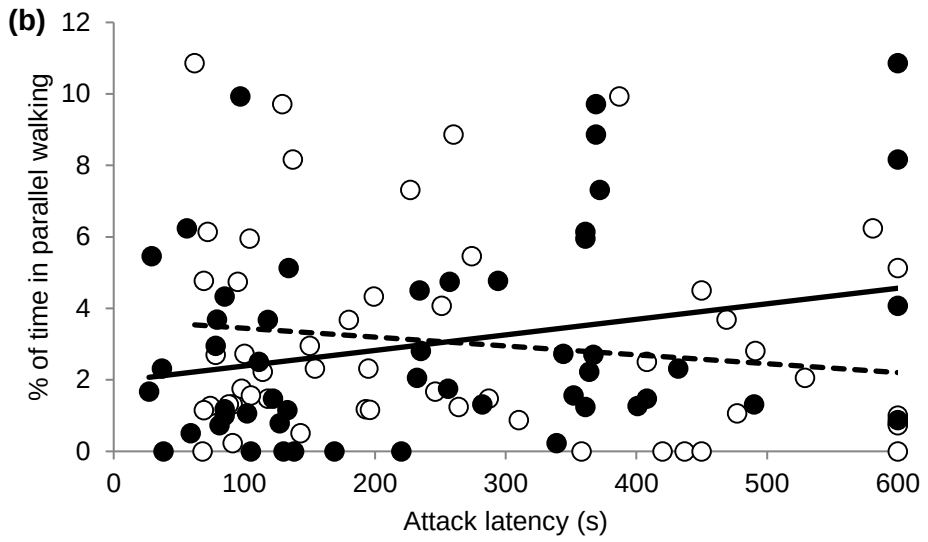
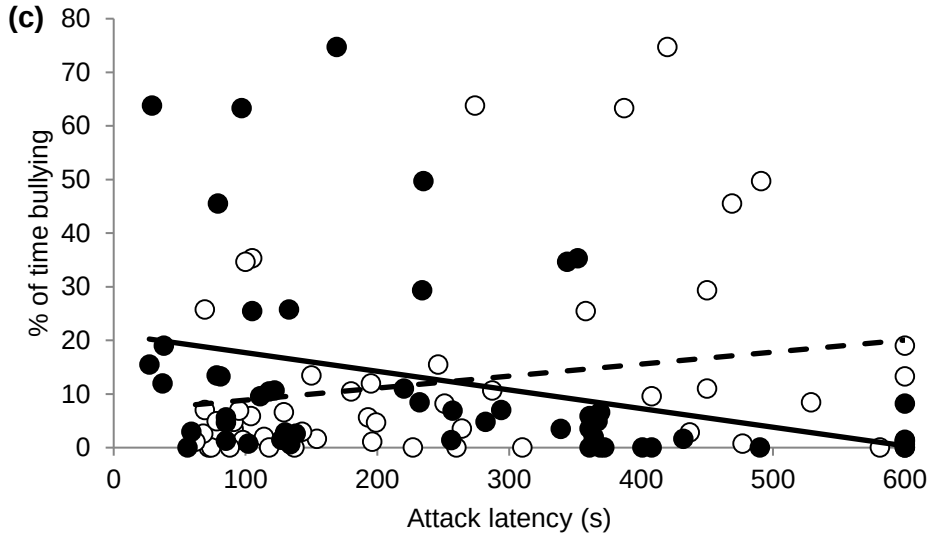

(b)
% of time in parallel walking
Attack latency (s)
0
2
4
6
8
10
12
0
100
200
300
400
500
600

539

540


(c)
% of time bullying
Attack latency (s)
0
10
20
30
40
50
60
70
80
0
100
200
300
400
500
600

541