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Aggressiveness as a component of fighting ability in pigs using a game-theoretical framework

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Understanding animal contests has benefited greatly from employing the concept of fighting ability, termed resource-holding potential (RHP), with body size/weight typically used as a proxy. However, victory does not always go to the larger/heavier contestant and the existing RHP approach thereby fails to accurately predict contest outcome. Aggressiveness, typically studied as a personality trait, might explain part of this discrepancy. We investigated whether aggressiveness forms a component of RHP, examining effects on contest outcome, duration and phases, plus physiological measures of costs (lactate and glucose). Furthermore, using the correct theoretical framework, we provide the first study to investigate whether individuals gather and use information on aggressiveness as part of an assessment strategy. Pigs, *Sus scrofa*, were assessed for aggressiveness in resident–intruder tests whereby attack latency reflects aggressiveness. Contests were then staged between size-matched animals diverging in aggressiveness. Individuals with a short attack latency in the resident–intruder test almost always initiated the first bite and fight in the subsequent contest. However, aggressiveness had no direct effect on contest outcome, whereas bite initiation did lead to winning in contests without an escalated fight. This indirect effect suggests that aggressiveness is not a component of RHP, but rather reflects a signal of intent. Winner and loser aggressiveness did not affect contest duration or its separate phases, suggesting aggressiveness is not part of an assessment strategy. A greater asymmetry in aggressiveness prolonged contest duration and the duration of displaying, which is in a direction contrary to assessment models based on morphological traits. Blood lactate and glucose increased with contest duration and peaked during escalated fights, highlighting the utility of physiological measures as proxies for fight cost. Integrating personality traits into the study of contest behaviour, as illustrated here, will enhance our understanding of the subtleties of agonistic interactions.

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

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

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contest and attacking an opponent (glossary of Briffa et al., 2015). Intuitively, one might predict that a more aggressive individual may be more likely to win against a less aggressive opponent. If so, aggressiveness would constitute an important determinant of RHP. However, the importance of integrating animal personality within existing contest theory has only recently been acknowledged (Briffa et al., 2015), with aggressiveness generally having been overlooked. However, boldness has been studied in contest settings in sea anemones, with boldness being correlated with aggressiveness (Rudin & Briffa, 2012). Aggressiveness might account for part of the discrepancy with existing studies in which, contrary to expectations, the contestant with apparently superior RHP does not win. This gives rise to the need to examine whether aggressiveness, in terms of a consistent behavioural response, is a component of RHP determining the overall chances of victory in a contest. To date, only two studies have examined the effect of aggressiveness on contest outcome, with Wilson, Grimmer, and Rosenthal (2013) finding that agonistic behaviour during a contest predicts dominance during a feeding trial in sheepshead swordtail fish, *Xiphophorus birchmanni*, while McEvoy, While, Sinn, and Wapstra (2013) found no effect of aggressiveness, measured as a combined score of agonistic behaviour towards a species model, on contest outcome in a social lizard species, *Egernia whitii*. In light of these conflicting results there is clearly a need to better understand the role of aggressiveness in animal contests.

In addition to influencing fight outcome, correlates of RHP provide animals with a means to gather information about the fighting ability of the opponent. Fighting is energetically costly and also bears the risk of injury or death (e.g. Briffa & Elwood, 2005; Glass & Huntingford, 1988; Kelly & Godin, 2001). Selection should therefore favour individuals that make appropriate decisions based on assessment of the costs and benefits of fighting (Maynard Smith & Parker, 1976; Parker, 1974; Parker & Rubenstein, 1981), although such assessment does not always occur (Elwood & Arnott, 2012; Mesterton-Gibbons & Heap, 2014). There are two classes of theoretical models of animal contests that differ in their assumptions about the information-gathering abilities of contestants (reviewed by Arnott & Elwood, 2009a; Elwood & Arnott, 2012). The first type, termed self-assessment, assumes that each contestant has knowledge of its own RHP, but gathers no information about the opponent (e.g. 'war of attrition without assessment', Mesterton-Gibbons, Marden, & Dugatkin, 1996; 'energetic war of attrition', Payne & Pagel, 1996, 1997; 'cumulative assessment model' (CAM), Payne, 1998). In these models, two animals compete up to a particular threshold at which point one gives up. Opponents each accrue costs (e.g. energy expenditure and injury) in line with their individual RHP, meaning that the inferior opponent will typically reach its threshold sooner and give up. In CAM costs also accrue due to the actions of the opponent, with superior opponents being better at inflicting costs. The second type, termed mutual assessment (e.g. 'sequential assessment model', Enquist & Leimar, 1983), involves individuals gathering information concerning relative fighting ability, typically interpreted as gathering information about an opponent's RHP and comparing this against their own ability. This need not be a cognitively demanding task (see Elwood & Arnott, 2013; Fawcett & Mowles, 2013 for discussion of this topic), yet it can be difficult to discriminate from other forms of assessment (Briffa & Elwood, 2009). Mutual assessment has the advantage that the weaker contestant can terminate the contest as soon as it perceives it is inferior to an opponent and likely to lose, thus minimizing fight costs for both itself and the winner. However, assessing an opponent may be difficult and costly, and basing decisions on individual thresholds (self-assessment) to determine the degree of escalation and contest winner may be a more economical option under certain circumstances (see Mesterton-Gibbons & Heap, 2014 for relative costs of mutual and self-assessment). This may account for mounting recent empirical evidence of self-assessment (e.g. Brandt & Swallow, 2009; Copeland, Levay, Sivaraman, Beebe-Fugloni, & Earley, 2011; Rudin & Briffa, 2011; Tanner & Jackson, 2011; Martinez-Cotrina, Bohorquez-Alonso, & Molina-Borja, 2014; Tsai, Barrows, & Weiss, 2014).

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

Here we outline a framework to examine whether aggressiveness is a component of RHP and whether or not it forms a part of the assessment strategy (either self- or mutual assessment) used in the decision-making process of contesting animals. To test for assessment we examined the relationship between winner and loser aggressiveness and contest duration, using the framework advocated to discriminate between assessment strategies when using traditional RHP measures (Taylor & Elwood, 2003, reviewed in detail by Arnott & Elwood, 2009a). Furthermore, we also examined the duration of display phases and escalated fighting to indicate whether the assessment strategy may switch from one contest phase to another (e.g. Hsu, Lee, Chen, Yang, & Cheng, 2008). Pigs provide a useful model system to test the outlined predictions. In commercial pig production, aggressive behaviour is a problem and has therefore been researched for a number of decades, generating a vast amount of knowledge including the behavioural pattern occurring during contests (McGlone, 1985; Rushen & Pajor, 1987). The social structure of domestic pigs is based on a dominance hierarchy formed through aggressive interactions (Meese & Ewbank, 1972), making them an ideal study system to investigate the influence of aggressiveness. While there is considerable descriptive work on pig aggression, the information-gathering and decision-making processes used by pigs to resolve aggressive encounters are poorly understood. As such, theoretical models developed to study contests offer a useful framework to better understand aggressive encounters between unfamiliar pigs.

In this study we assayed individual differences in aggressiveness, using the established resident–intruder (RI) test (Erhard & Mendl, 1997), which provides a measure of aggressiveness that is consistent over time (Clark & D'Eath, 2013; D'Eath, 2004). The resultant measure of attack latency provides an unambiguous, quantifiable measure of aggression in a format that can be interpreted within an RHP framework. Contests were then staged