Animal Behaviour 107 (2015) 31–40

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Giant Australian cuttlefish use mutual assessment to resolve male-male contests

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ARTICLE INFO

Article history:
Received 12 January 2015
Initial acceptance 11 February 2015
Final acceptance 15 May 2015
Published online
MS. number: 15-00033R

Keywords:
contest competition
fighting ability
game theory
resource-holding potential
sequential assessment model
visual signalling

Game theory models provide a useful framework for investigating strategies of conflict resolution in animal contests. Model predictions are based on estimates of resource-holding potential (RHP) and vary in their assumptions about how opponents gather information about RHP. Models can be divided into self-assessment strategies (energetic war-of-attrition, E-WOA; cumulative assessment model, CAM) and mutual assessment strategies (sequential assessment model, SAM). We used laboratory-staged contests between male giant Australian cuttlefish, *Sepia apama*, to evaluate RHP traits and to test game theory models. Mantle length was a key indicator of RHP because it predicted contest outcome, whereby larger individuals were more likely to win a contest. Winners and losers did not match behaviours, ruling out the E-WOA. There was no relationship between contest outcome, duration and escalation rates, arguing against the CAM. Persistence to continue a contest was based on RHP asymmetry, rather than loser and/or winner RHP, providing support for the SAM. Motivation to fight was determined from a male's latency to resume a contest following the introduction of a female during a contest. The latency to resume a contest was negatively related to the size of the focal male and positively related to the size of their opponent. These results show that competing males are able to gather information concerning RHP asymmetries, providing support for mutual assessment. Furthermore, males showed significant behavioural differences in their responses to relatively larger than to relatively smaller opponents. Using an integrative approach, our study provides a well-substantiated example of mutual assessment.

Animals competing over limited resources are likely to incur costs, including increased energy expenditure and risk of predation, injuries or fatal attacks (Maynard Smith, 1974; Maynard Smith & Price, 1973). During contests, animals may gather information from multiple sources to assess the potential costs and benefits of continued conflict, in turn facilitating economic and tactical decision making (Maynard Smith & Parker, 1976; Parker, 1974). The decision to withdraw from a contest is usually influenced by the fighting ability of a contestant, termed resource-holding potential (RHP; Maynard Smith, 1974; Parker, 1974; Parker & Stuart, 1976). The information that facilitates these decisions will be dictated by the assessment capabilities of the species (Taylor & Elwood, 2003).

Game theoretical approaches serve as an analytical tool for understanding the patterns of behaviour observed in contests across many taxa. Currently, three major game theory models may be applied to animal contests to determine the assessment strategy used for decision making (Table 1). The models can be divided into self-assessment and mutual assessment strategies. The self-assessment models include the energetic war of attrition (E-WOA; Payne & Pagel, 1996; 1997) and the cumulative assessment model (CAM; Payne, 1998). These models assume that contestants evaluate their own RHP, but fail to assess their opponent's RHP. Contestants differ in rates of escalation within phases (i.e. periods defined by behaviours of similar aggressive intensity). The decision point to withdraw is determined by the weaker individual's threshold for costs. For the E-WOA model, the threshold is based on self-imposed energetic costs. For the CAM, the threshold is determined by combined costs that accumulate as a function of time and energy expenditure, as well as the damage inflicted by the opponent. Mutual assessment is modelled through the sequential assessment model (SAM), which assumes that contestants evaluate their own RHP relative to their opponent's RHP (Enquist & Leimar, 1983). In this model, contests progress through a series of successive phases, which are thought to provide increasingly accurate information about the RHP asymmetry between contestants.

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http://dx.doi.org/10.1016/j.anbehav.2015.05.026
0003-3472/

Table 1
Summary of contest dynamics predicted by game theory models (E-WOA, CAM, SAM) of contest resolution

Predictions	Energetic war of attrition (E-WOA)	Cumulative assessment (CAM)	Sequential assessment (SAM)
Behavioural matching	Matched in type, frequency & intensity	Unmatched in type, frequency & intensity	Unmatched in type, frequency & intensity
Rates of escalation	Escalation within phases	Escalation within phases	No escalation within phases
Contest duration correlation	(+) loser RHP and (/) winner RHP	(+) loser RHP and (−) winner RHP	RHP asymmetry
Latency to resume a contest correlation	(−) focal male RHP and (/) opponent RHP	(−) focal male RHP and (/) opponent RHP	(−) focal male RHP and (+) opponent RHP
Decision making based on	Own RHP	Own RHP	Relative RHP

Five-step process to discriminate between game theory models: (1) test for behavioural matching; (2) test for escalation within phases; (3) test relationship between contest duration and RHP measurements; (4) test relationship between latency to resume a contest and RHP measurements; (5) test decision-making abilities in the context of aggression. (+) = positive correlation; (-) = negative correlation; (/) = no correlation.

Predictions for these three models are based on estimates of RHP and vary in their assumptions about how opponents gather information about RHP (Table 1).

Mutual assessment is assumed to be a more efficient strategy than self-assessment because animals can minimize costly and futile persistence by gathering information about relative RHP (Enquist & Leimar, 1983). However, studies on a wide range of animal contests that have shown mutual assessment (e.g. Englund & Olsson, 1990; Junior & Peixoto, 2013; Kemp, Alcock, & Allen, 2006; Pratt, McLain, & Lathrop, 2003) have recently been called into question (Briffa & Elwood, 2009; Elwood & Arnott, 2012; Taylor & Elwood, 2003). Taylor and Elwood (2003) contended that such studies may have actually presented artefacts of alternative mechanisms. For example, a negative association between contest duration and RHP asymmetry, which is thought to be indicative of the SAM (i.e. mutual assessment), could also arise if the weaker contestant accrued costs faster than its opponent (i.e. self-assessment, E-WOA). Taylor and Elwood (2003) recommended a statistical framework to distinguish between mutual and self-assessment strategies. This framework has been implemented in many studies, revealing that self-assessment is more prevalent than previously thought (e.g. Brandt & Swallow, 2009; Prenter, Elwood, & Taylor, 2006; Stuart-Fox, 2006). However, distinguishing between assessment strategies remains a challenge, and consequently several recent studies report inconclusive results (e.g. Batista, Zubizarreta, Perrone, & Silva, 2012; Egge, Brandt, & Swallow, 2011; Jennings, Gammell, Carlin, & Hayden, 2004; Kelly, 2006).

Recently, there has been renewed debate about whether mutual assessment is more cognitively complex than self-assessment because of its apparent requirement for comparative decision making (Elwood & Arnott, 2012, 2013; Fawcett & Mowles, 2013). Elwood and Arnott (2012) and Fawcett and Mowles (2013) argued that mutual assessment could entail cognitively simple threshold decision making. They noted that the original SAM model (i.e. mutual assessment) does not require an explicit comparison of RHP; rather, information about RHP is directly transmitted as a relative measure (i.e. as error-prone estimates of relative fighting ability). Moreover, Elwood and Arnott (2012) argued that many studies provide insufficient evidence of individuals comparatively assessing RHP, and that many claims of comparison of body size, claw size or dewlap size still need to be substantiated. One experimental approach to substantiate such claims involves assessing the motivational state of an animal in a contest by using a novel stimulus that causes a contestant to temporarily cease fighting (see Arnott & Elwood, 2009a; Elwood, Wood, Gallagher, & Dick, 1998). The latency to resume the contest provides a measure of the individual's motivation to fight (see Table 1 for predictions). Another approach is to test the ability of a contestant to assess relative values (e.g. body size or claw size) in the context of aggression (see e.g. dogs, *Canis familiaris*, Taylor, Reby, & McComb, 2010). Testing such capabilities during a contest may validate claims of mutual assessment.

This study investigated the assessment strategy used to resolve conflict in male giant Australian cuttlefish, *Sepia apama*. These cuttlefish engage in dynamic signalling during agonistic contests, similar to other species in which game theory models have been tested (e.g. hermit crabs, Briffa & Elwood, 2001; chameleons, Stuart-Fox, 2006; wasps, Tibbetts, Mettler, & Levy, 2010). Contests typically occur in the presence of females during their reproductive season (austral winter months: May–August). However, even in the absence of females, males engage in contests in both field (Hanlon, 1999) and laboratory settings (Schnell, 2014). The fighting tactics of males are influenced by body size, which varies widely at maturity. Small males tend to reduce direct aggression by being surreptitious or through deceptive signalling (i.e. female mimicry; Hanlon, Naud, Shaw, & Havenhand, 2005). Large males regularly engage in agonistic contests, which are typically mediated through visual displays but can escalate to physical pushing and grappling (Hall & Hanlon, 2002). Variation in body size and its effect on agonistic behaviours suggest that this species has evolved the ability to assess the size of its opponents and alter its behaviour accordingly. However, the assessment strategy used during these contests has not been tested. The application of game theory models to cuttlefish contests may be an effective tool for determining patterns of fighting behaviour (i.e. self-assessment or mutual assessment strategy) in this particular system.

The central aim of our study was to determine the fighting strategy used by giant Australian cuttlefish during male–male contests. First, we assessed the male traits that may be associated with RHP. Second, we used specific predictions of the three major game theory models (E-WOA, CAM, and SAM; see Table 1 for predictions) to determine whether the decision to withdraw from a contest was based on the absolute RHP of the loser (self-assessment) or on the RHP of the loser relative to the winner (mutual assessment). Third, the contestant's assessment of RHP was substantiated by measures of motivation and aggression.

METHODS

Study Species, Collection and Husbandry

Thirty-four male and four female adult giant Australian cuttlefish were caught via scuba in coastal areas of Sydney, Australia (34°50′S, 151°22′E) between April and May 2012. They were transported (<50 min) to the aquarium facility at Cronulla Fisheries Research Centre in a custom-made transport tank (9.0 × 8.0 cm and 8.0 cm high, maximum capacity = 3 subjects). Water in the transport tank was oxygenated and maintained at a natural ambient sea temperature (15–17 °C). Sex was determined by coloration and the dimorphic state of the fourth arm. Subjects were housed individually in open-air tanks that received a constant flow (approximately 10 litres/min) of filtered ambient sea water. Cuttlefish were fed a mixed diet of food items including live Australian ghost