

ASSESSMENT GAMES AND COMPETITIVE BEHAVIOUR OF THE  
MANGROVE TREE-DWELLING CRAB, *SELATIMUM BROCKII* (DE MAN,  
1887) (DECAPODA, GRAPSIDAE)

BY

B. GODSALL<sup>1</sup>) and I. M. SMALLEGANGE

Division of Biology, Imperial College London, Silwood Park, Ascot, SL5 7PY, U.K.

ABSTRACT

Game theoretical models have been developed to understand the decisions of individuals to continue or stop fighting. These can be split into self assessment models (cumulative assessment model (CAM), war of attrition without assessment (WOA-WA), energetic WOA), where contestants only have information on their own fighting persistence, and mutual assessment models (sequential assessment game: SAM), where contestants exchange information on each other's competitive ability. Here, we assess if self or mutual assessment occurs in fights between male mangrove tree-dwelling crabs, *Selatium brockii* (De Man, 1887). Contests were staged in the presence of a female between focal crabs belonging to either of two different absolute size classes against a smaller, size-matched, and larger opponent. In line with mutual assessment models and CAM, contest duration increased when contestants were more matched in competitive ability (i.e., size) but was not significantly different between focal crab sizes. However, this pattern differed between focal crab size classes when competitors were smaller, with contests lasting longer for the larger size class. Different behaviours with different levels of aggression were employed during contests, suggesting that mutual assessment occurs. However, unlike current model predictions, the different behaviours were not used in increasing order of aggressiveness. Instead, the sequence of behaviours used during a contest both increased and decreased in aggressiveness. These observations suggest that contests are a form of unbalanced partial assessment, corroborating other recent empirical findings, and challenging theoreticians to formalize such contest dynamics.

RÉSUMÉ

Des modèles théoriques de jeu ont été développés pour comprendre les décisions des individus pour continuer ou arrêter de se battre. Ils peuvent être partagés en modèles d'auto-évaluation (modèle d'évaluation cumulative, CAM), guerre d'usure sans évaluation (WOA-WA), WOA énergétique, où les adversaires ont seulement des informations sur leur propre persistance à se battre et modèles d'évaluation cumulatifs (jeux d'évaluation séquentielle: SAM), où les adversaires échangent des informations sur la capacité de compétition de chacun. Nous étudions ici l'évaluation auto et mutuelle qui intervient dans les combats entre crabes mâles arboricoles de la mangrove, *Selatium*

---

<sup>1</sup>) e-mail: bengodsall@googlemail.com

*brockii* (De Man, 1887). Des combats ont été organisés en présence de femelles entre mâles appartenant soit à deux classes de taille différentes (plus petits ou plus grands) soit entre mâles de même taille.

En accord avec les modèles d'évaluation mutuelle et CAM, la durée du combat augmente quand les combattants présentent une même capacité de compétition (i.e., taille), mais sans différence significative entre les tailles de crabe examinés. Cependant ce modèle diffère entre crabes expérimentés quand les concurrents sont plus petits, avec des combats plus longs pour la classe de plus grande taille. Différents comportements avec différents niveaux d'agression ont été employés au cours des luttes, suggérant que l'évaluation mutuelle existe. Cependant, contrairement aux prédictions du modèle actuel, les différents comportements n'ont pas été utilisés dans un ordre croissant d'agressivité. Au contraire, la séquence de comportements utilisés au cours d'un combat à la fois augmente et décroît en agressivité. Ces observations suggèrent que ces combats sont une forme d'évaluation en partie déséquilibrée, corroborant d'autres découvertes empiriques récentes, et posant un défi aux théoriciens qui formalisent ces combats dynamiques.

## INTRODUCTION

Individuals competing for limited resources incur costs relating to time, energy, injury or susceptibility to predation (e.g., Parker, 1974; Maynard Smith & Parker, 1976). Selection should therefore favour decision-making whether to continue or retreat from a contest that optimally balances the costs associated with competing over resources against the benefits of gaining access to the contested resource. Several game theory models have been developed to describe how information is used to make such optimal decisions. These models can be grouped into 'self assessment' and 'mutual assessment' models. Both use a measure of overall fighting ability, or resource-holding potential (RHP: Parker, 1974) of an individual to determine its probability of winning a fight. RHP is quantified using a measurable, species-specific trait that is correlated to an individual's relative fighting ability, for example animal body size or size of an animal's weaponry (Huntingford & Turner, 1987; Riechert, 1988).

'Self assessment' models state that competitors use only information they have on their own RHP to decide when to retreat from a contest. Examples of self assessment models include the 'war of attrition without assessment' (WOA-WA: Mesterton-Gibbons et al., 1996), the 'energetic war of attrition' (E-WOA: Payne & Pagel, 1996b, 1997) and the 'cumulative assessment model' (CAM; Payne, 1998; table I). These models assume that during a contest, costs (e.g., time or energy use) accrue as a result of an individual's own actions (Mesterton-Gibbons et al., 1996; Payne & Pagel, 1996b; Taylor & Elwood, 2003; Arnott & Elwood, 2009). Decisions to continue fighting are based on a cost threshold, which, when crossed, results in the individual retreating (Maynard Smith & Parker, 1976; Mesterton-Gibbons et al., 1996; Payne & Pagel, 1996; Taylor & Elwood, 2003; Arnott & Elwood, 2009; Briffa & Elwood, 2009). In situations where an individual's