Behavioural Processes 92 (2013) 47–51

Contents lists available at SciVerse ScienceDirect

Behavioural Processes

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

Probing aggressive motivation during territorial contests in a group-living cichlid fish

Adam R. Reddon*, Daniel Balk[1], Sigal Balshine

Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, Ontario L8S 4K1, Canada

ARTICLE INFO

Article history:
Received 30 August 2012
Received in revised form 1 October 2012
Accepted 12 October 2012

Keywords:
Fighting
Assessment
Motivational probe
Neolamprologus pulcher
Napoleon strategy

ABSTRACT

Many animals fight to win resources, repel competitors or establish dominance in a social group. Mutual-assessment of fighting ability, where competitors gather and compare information about their opponent's as well as their own fighting ability has been the dominant theoretical framework for understanding decision-making during fights. However, self-assessment, where each individual has a cost threshold and fights up until that point, may be more common than previously appreciated. In this study, we attempted to discriminate between these two potential assessment mechanisms in a group-living cichlid fish, *Neolamprologus pulcher* by probing aggressive motivation during a territorial contest. We measured aggressive motivation, and used this metric to investigate assessment rules during an ongoing contest. We predicted that if these social fish use self-assessment, we would observe a positive correlation between the fighting ability of the probed animal and its aggressive motivation. Alternatively, if mutual-assessment is used then we predicted we would find a negative effect of the opponent's fighting ability on the aggressive motivation of the probed fish because fish should be less motivated to fight against formidable opponents. Our results did not support either of these predictions. In contrast we found that small individuals were more aggressively motivated regardless of their opponent's size. We discuss this result in the context of theoretical models of aggression in individuals of small body size.

1. Introduction

Aggressive contests are common when animals resolve conflict by direct interaction (Huntingford and Turner, 1987; Archer, 1988; Maynard-Smith and Harper, 2003; Briffa and Sneddon, 2010). Contests can be costly in terms energy (Briffa and Elwood, 2004; Castro et al., 2006), lost time for feeding and mating (Kemp and Wiklund, 2001), diverted attention from potential predators (Jakobsson et al., 1995), and the risk of injury or death (Enquist and Leimar, 1990). Consequently, contests typically include some form of assessment, which may reduce these costs to one or both competitors (Parker, 1974; Enquist and Leimar, 1983; Arnott and Elwood, 2009a).

Fighting ability (commonly referred to as resource holding potential or power, abbreviated 'RHP' in either case) is a key determinant of fight outcome and dynamics (Parker, 1974; Maynard-Smith, 1982). Models of fighting ability assessment can be broken up into two basic categories: 1) Self-assessment, where animals make the decision to persist or relent in a contest based on a threshold for costs incurred and, 2) mutual-assessment, where each contestant gathers some information about the strength of its opponent and compares that information to its own fighting ability (Maynard-Smith and Parker, 1976; Parker and Rubenstein, 1981; Enquist and Leimar, 1983; Enquist et al., 1990; Mesterton-Gibbons et al., 1996; Payne and Pagel, 1996, 1997; Payne, 1998). Mutual-assessment is more complex, but carries with it the distinct advantage of reducing fight costs for the loser in asymmetric contests (Arnott and Elwood, 2009a).

Perhaps because mutual-assessment is intuitively satisfying, and mirrors the decision-making processes in our own species (Sell et al., 2009, 2010), mutual assessment has become the dominant paradigm in the study of aggression (Taylor and Elwood, 2003; Briffa and Elwood, 2009; Arnott and Elwood, 2009a). The most commonly reported evidence for mutual-assessment is a negative relationship between the degree of asymmetry in fighting ability between the two contestants and the duration of the contest (Taylor and Elwood, 2003). The logic being that closely matched contestants will have greater difficulty determining which one has an advantage, and therefore will need to fight longer before determining which is stronger (Enquist and Leimar, 1983). However, the relationship between fighting ability asymmetry and contest duration can be driven entirely by a positive relationship between the fighting ability of the loser and the duration of the contest

* Corresponding author. Tel.: +1 905 525 9140x26037; fax: +1 905 529 6225.
E-mail address: reddonar@mcmaster.ca (A.R. Reddon).
[1] Current address: Psychology Department, University of Waterloo, 200 University Avenue West, Waterloo, Ontario N2L 3G1, Canada.

0376-6357/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.beproc.2012.10.005

(Taylor and Elwood, 2003). Therefore self-assessment can produce the same result as mutual-assessment.

Fortunately, Taylor and Elwood (2003) recommend a clever way to distinguish between these two forms of assessment by examining the effects of winner and loser fighting ability on contest duration separately. Under mutual assessment, opposite effects of winner and loser fighting ability on the duration of the contest is expected with stronger losers lengthening the contest and stronger winners shortening it. Under self-assessment, only the loser's fighting ability should be positively related to the duration of the contest (because the fight ends when the loser gives up) whereas the winner's fighting ability should be unimportant. The independent analysis of winner and loser fighting ability has been successfully applied in a number of empirical studies on a wide range of taxa (e.g., shore crabs, *Carcinus maenas*: Smallegange et al., 2007; jumping spiders, *Phidippus clarus*: Elias et al., 2008; house crickets, *Acheta domesticus*: Briffa, 2008; sierra dome spiders, *Neriene litigiosa*: Keil and Watson, 2010; cichlid fish, *Neolamprologus pulcher*: Reddon et al., 2011; green anole lizards, *Anolis carolinensis*: Garcia et al., 2012; fallow deer, *Dama dama*: Jennings et al., 2012).

Recently, Arnott and Elwood (2009a) suggested that assaying aggressive motivation during an ongoing contest might be another way to discriminate between self- and mutual-assessment. The motivational probe technique involves interrupting one of two fighting animals with a simulated predator attack and measuring the latency for this disturbed animal to resume fighting its rival. The duration until resuming the fight can be taken as an inverse metric of aggressive motivation. This assay was initially developed for use during fights in the hermit crab (*Pagurus bernhardus*; Elwood et al., 1998; Briffa and Elwood, 2001), but has been subsequently adapted for use during contests in a fish, the convict cichlid (*Amatitlania nigrofasciata*; Arnott and Elwood, 2009b, 2010). The motivational probe assay assumes that the interruption by a novel startle stimulus will activate antipredator responses in the startled animal, and that the motivation to continue fighting will be put in conflict with the motivation to avoid predators (Culshaw and Broom, 1980; Elwood et al., 1998). Presumably, animals that are more motivated to fight will show shorter latencies to resume aggression than those that are less motivated, and thus latency to resume aggression can be taken as an inverse measure of aggressive motivation (Elwood et al., 1998; Arnott and Elwood, 2009a,b, 2010). This method offers several potential advantages over the measures of contest cost taken at the end of a fight (e.g. fight duration, injury or energy expenditure). Namely, contest cost measures taken at the end of a contest can only provide insight into the final decision made by the loser (as the loser decides when the fight is over) while measuring aggressive motivation throughout a contest may provide information about the ongoing decision-making process in both winners and losers.

In this study, we applied the motivational probe technique for the first time to staged resource contests in the group-living cichlid fish, *N. pulcher*. *N. pulcher* are small cichlid fish endemic to Lake Tanganyika, Africa that form permanent social groups consisting of a single dominant breeding pair and 1–20 subordinate non-reproductive adults (Taborsky and Limberger, 1981; Taborsky, 1984, 1985; Balshine-Earn et al., 1998; Balshine et al., 2001; Wong and Balshine, 2011a). The subordinate helpers may be either related or unrelated to the breeding pair and to each other (Stiver et al., 2008). *N. pulcher* groups are organized as strict linear dominance hierarchies that are determined by body size and hence fighting ability (Taborsky, 1984, 1985; Balshine et al., 2001; Wong and Balshine, 2011a,b). Rank in the dominance hierarchy is strongly related to fitness outcomes of *N. pulcher*, and only a few fish ever attain a dominant breeding position (Stiver et al., 2004; Wong and Balshine, 2011a). Dominance relationships are formed and tested by direct aggressive interactions (Arnold and Taborsky, 2010; Riebli et al., 2011), and therefore fighting behaviour in general and the assessment of fighting ability in particular is of paramount importance to the social structure of *N. pulcher* groups (Taborsky, 1984, 1985; Hamilton et al., 2005; Wong and Balshine, 2011b; Reddon et al., 2011).

A previous study on fighting behaviour in *N. pulcher* found that body size asymmetry between the competitors predicted contest duration and that a 5% advantage in body size was sufficient to determine which individual would win (Reddon et al., 2011). However, the results from Reddon et al. (2011) did not fit perfectly with any of the extant contest assessment models. Namely, opponent size was the primary determinant of fight dynamics and the fighting ability of the losing fish did not predict the duration or intensity of contests. In the present study, we aimed to further investigate the aggressive assessment abilities in this highly social fish using the motivational probe technique (Elwood et al., 1998). We predicted that if the latency to resume aggression correlates negatively with the probed individual's fighting ability and positively with its opponent's fighting ability then mutual-assessment likely underlies *N. pulcher* contests. In contrast, if the latency to resume aggression was uncorrelated with opponent fighting ability but negatively related to the probed individual's fighting ability then this would suggest that self-assessment is a better fit. We test these two competing predictions here.

2. Materials and methods

2.1. Animals

The fish used in this study were the laboratory-reared descendents of *N. pulcher* collected from Lake Tanganyika, Africa. The fish lived within naturalistic social groups, housed one group per 189 L glass aquarium (92 × 41 × 50 cm). Each group consisted of a dominant breeding pair and 2–10 adult subordinate helpers. Each group was housed in an aquarium that contained a pair of flowerpot halves to serve as brood chambers, two large foam filters (10 × 10 × 30 cm), and 3 cm of crushed coral sand substrate. Aquaria were maintained at 26 ± 2 °C and exposed to a 14L:10D light cycle. Fish were fed commercial cichlid flake food (Hagen Nutrafin basix) once daily, 6 days per week.

We used 50 (26 males and 24 females) subordinate helper fish from these groups to form 25 experimental pairs. The fish ranged in size from 44.0 to 65.8 mm standard length (SL, measured from the tip of the snout to the caudal peduncle). We also weighed each fish and found that SL and mass were strongly correlated ($r = 0.94$, $N = 50$, $p < 0.0001$), so we chose to use SL for all analyses to be consistent with previous research on contest behaviour in this species (Reddon et al., 2011, 2012). Fish were always paired with an unfamiliar, same sex, individual. Pairs were not size matched and the size asymmetry within each pair ranged from 0.7 to 26.9% different in SL. *N. pulcher* naturally fight with individuals from their own group and with potential group joiners over shelters and to establish dominance rank (Wong and Balshine, 2011a,b; Riebli et al., 2011, 2012; Reddon et al., 2011, 2012).

2.2. Procedure

Contests took place in a 38 L aquarium (50 × 26 × 30 cm). A permanent transparent barrier separated the contest aquarium into two equally sized compartments (25 × 26 × 30 cm) and a pair of fish from two randomly chosen social groups were placed into these two compartments. The pair of fish had no visual contact for a 3 h acclimation period because an opaque, removable barrier was inserted adjacent to the transparent barrier. We chose a 3 h acclimation time because prior work in our lab has suggested that a 3 h