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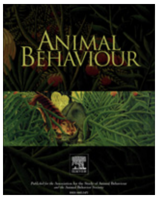

Rules of engagement for resource contests in a social fish

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A rich theoretical framework exists for understanding animal conflict. When two opponents fight over a resource, the duration, intensity and outcome of the fight ought to be determined in large part by the relative difference in resource-holding power between contestants. While our understanding of one-time conflict resolution is excellent, our knowledge is still limited of how these rules scale up when contests occur in a social context where individuals have long-term interactions. Here, we use a convenient model system, *Neolamprologus pulcher*, a small cooperatively breeding cichlid fish, to explore decisions in pairwise contests over resources in a species where two individual contestants are likely to remain in the same social group, and regularly and repeatedly interact. Contests began after approximately 1 min, with a short display phase, and continued in an aphasic manner for an average of 10 min before a clear winner emerged. Information about opponents' body size was important when deciding on the giving-up point, but contestants' own body size was not, suggesting that assessment of opponent size is paramount in contest decision making. No sex differences were detected in contest structure, duration or intensity, and contests between males or between females were indistinguishable. These results offer an important window on conflict in a cooperative breeder and shed insight on rules of engagement within hierarchical social groups.

Contests occur whenever competition between two or more individuals is settled by direct interaction (Briffa & Sneddon 2010). Individuals fight to secure mating opportunities or any other limited resource and such resource contests are widespread throughout the animal kingdom (Parker 1974; Enquist & Leimar 1987; Huntingford & Turner 1987; Archer 1988; Arnott & Elwood 2008; Briffa & Sneddon 2010). Although group-living animals with pronounced dominance hierarchies are thought to have overall lowered aggression, contests may still be extremely important in these species because aggressive interactions establish an animal's position in the hierarchy and high dominance rank often leads to high fitness (Clutton-Brock et al. 1979; Jennings et al. 2004, 2005; Cant et al. 2006; Briffa & Sneddon 2010). Cooperative breeders are species that have a social system in which individuals help rear the offspring of other more dominant individuals and hence forgo or diminish their own reproductive efforts. Contest behaviour may be critical within cooperative breeders, where dominance rank is often closely linked to breeding opportunities (Earley & Dugatkin 2010). It is neither practical nor ethical to study contest behaviour in most cooperatively breeding vertebrates because of their typically large body size and/or prohibitive space required to house entire social groups. As a consequence, contest behaviour is rarely studied in these species (Elwood & Parmigiani 1992; Briffa & Sneddon 2010). In the current study, we aim to explore decision making during resource contests in a cooperatively breeding vertebrate using the convenient Tanganyikan cichlid, *Neolamprologus pulcher* (Taborsky & Limberger 1981).

Neolamprologus pulcher live in social groups consisting of a single breeding pair and on average five to seven subordinate helpers at the nest that form a size-based linear dominance hierarchy (Balshine-Earn et al. 1998; Balshine et al. 2001; Heg et al. 2005; Fitzpatrick et al. 2008). Groups live and breed in the rocky littoral zone and use excavated caves underneath rocks both as shelter from predators and as a nest for eggs and larvae (Taborsky 1984, 1985; Balshine-Earn et al. 1998). Predation pressure in *N. pulcher*'s natural environment is severe (Balshine et al. 2001; Heg et al. 2004), and access to a well-protected shelter is essential for reproduction and survival (Balshine et al. 2001; Heg et al. 2004). There is considerable competition for suitable shelters (Taborsky 1984; Bergmüller et al. 2005), and limitations on shelter availability may be a causal factor in the evolution of group living and cooperative breeding (Emlen 1982; Hatchwell & Komdeur 2000; Kokko & Ekman

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2002; Wong 2010). *Neolamprologus pulcher* frequently aggress against conspecifics in their social groups (Taborsky 1984; Desjardins et al. 2005; Taves et al. 2009; Balshine-Earn et al. 1998; Wong & Balshine 2010a); furthermore, predation or dispersal events regularly result in vacancies in the dominance hierarchy, allowing subordinates to advance in rank or assume a higher rank in another group, and during these events, escalated contests can erupt (Balshine-Earn et al. 1998; Stiver et al. 2006; Fitzpatrick et al. 2008). Because *N. pulcher* are small (<8 cm in adult body length) and adapt well to laboratory conditions, readily performing their full suite of natural behaviours in aquaria (Wong & Balshine 2010b), they offer a unique opportunity to stage controlled dyadic contests in a cooperatively breeding vertebrate (Riebli et al. 2011). Pairwise contests may offer an important window into social conflict resolution within social groups, and understanding the rules of engagement may shed light upon what information is important when making decisions within a social group (Cant et al. 2006; Cant & Johnstone 2009; Field & Cant 2009; Cant 2011; Wong & Balshine 2010a, b).

The simplest way to decide whether to persist in a contest and how hard to fight is to base these decisions on one's own capabilities (fighting ability: termed resource-holding power or potential, hereafter RHP; Parker 1974; Maynard Smith 1982). Such contests have been modelled and are known as 'pure self-assessment' models, where each individual has an RHP-dependent threshold cost that it can bear and will persist in the contest until its own cost threshold is reached (Mesterton-Gibbons et al. 1996; Payne & Pagel 1996, 1997). Individuals with higher RHP have higher cost thresholds and can persist longer and win resources (Briffa & Sneddon 2010). A modified form of self-assessment that allows for higher RHP individuals to also inflict higher costs upon their opponents is known as the cumulative assessment model (Payne 1998). Contests in a wide variety of taxa appear to be consistent with the logic of self-assessment (Bridge et al. 2000; Morrell et al. 2005; Prenter et al. 2006; Stuart-Fox 2006; Brandt & Swallow 2009).

The price of fighting according to a self-assessment rule is that losers will always pay their maximum threshold cost, even when fighting with a distinctly superior opponent. If a fight is clearly unwinnable, then it is best abandoned early to avoid the costs of fighting (Maynard Smith & Harper 2003), and natural selection is likely to favour individuals that gather information about their opponents and then apply this information during the contest (Enquist & Leimar 1983; Enquist et al. 1990). Hence, in mutual-assessment models, it is assumed that contestants compare the RHP of their opponent with their own RHP and act on this information (Enquist & Leimar 1983; Enquist et al. 1990; for some recent and excellent reviews of these models, see: Arnott & Elwood 2009a; Briffa & Sneddon 2010). Mutual assessment is both intuitively satisfying and the dominant paradigm used to explain animal contests (Taylor & Elwood 2003). A negative relation between RHP asymmetry and contest duration (although similar arguments apply to contest intensity or other measures of cost) has been used as the gold standard to support the notion that contests are settled by mutual assessment. When contestants are closely matched, the asymmetry in RHP is more difficult to detect, and a longer fight is required to determine the winner. Recently, Taylor & Elwood (2003) have shown that this relationship can be generated by the fact that loser RHP is necessarily low whenever asymmetry is substantial. They recommend examining the independent effects of winner and loser RHP on fight cost. Mutual assessment predicts that increasing winner and loser RHP will have equal and opposite effects on contest cost, with increasing loser RHP increasing the cost of a contest and increasing winner RHP decreasing it. Pure self-assessment predicts only the positive effect of loser RHP and no effect of winner RHP. In general, animals living in long-lasting social groups have ample opportunities to gather information about other group members, and mutual assessment mechanisms may be especially common in these systems (Briffa & Sneddon 2010).

Contest behaviour may differ between the sexes, as the rewards for (and costs of) conflict may vary between males and females (Trivers 1972). To date, the vast majority of research on aggressive interactions has focused on understanding male–male contests (Archer 1988). This sex bias is unsurprising, given that theory and empirical research show that males more commonly engage in conspicuous dangerous contests (Trivers 1972; Archer 1988). However, in many species, females too engage in contests (Ayer & Whitsett 1980; Archer 1988; Gowaty & Wagner 1988; Berglund et al. 1993), and when fight tactics have been investigated in both sexes, interesting differences are often revealed (Holder et al. 1991; Draud et al. 2004; Arnott & Elwood 2009b; but see Barlow et al. 1986; Koops & Grant 1993). Both male and female *N. pulcher* engage in resource contests (Desjardins et al. 2005; Taves et al. 2009), and there are reasons to predict they will behave similarly in contests. Male and female *N. pulcher* are rather monomorphic, and females are often described as being equally aggressive as males and generally masculinized (Aubin-Horth et al. 2007; Desjardins et al. 2008a, b; Wong & Balshine 2010b). However, males typically disperse prior to reaching dominant status, whereas females are more philopatric, often inheriting breeding status in their natal groups (Stiver et al. 2004, 2006, 2008). These different life history trajectories mean that the value of winning a shelter or dominance status may vary between males and females and that the selection pressure for aggressive behaviour in males and females may differ.

In the current study, we describe the structure of dyadic *N. pulcher* resource contests for both males and females, focusing on the information that each individual uses to make decisions. Collectively, we sought to understand the underlying logic of resource contests in a cooperative breeder, and in particular, to determine whether decision making based on self-assessment or mutual assessment provides the best fit with *N. pulcher* contest behaviour. Our ultimate goal was to improve our understanding of conflict resolution within small-scale animal societies, by elucidating the decision-making mechanisms used by a highly social animal in a conflict situation.

METHODS

Study Animals and Housing Conditions

We used 90 sexually mature *N. pulcher* (50 males and 40 females) in this study. The average standard length (SL; measured from the tip of the snout to the caudal peduncle) of the animals was 5.44 ± 0.09 cm (range 4.27–7.15 cm). All study animals were laboratory-reared descendents of wild-caught breeding stock collected from Lake Tanganyika. All fish included in this study were subordinate helpers taken from permanent social groups maintained in the laboratory. Each social group in the laboratory consisted of a single dominant breeding pair and 2–10 subordinate helpers of varying size (1–8 cm) and was housed in a 189 litre ($92 \times 41 \times 50$ cm) aquarium with 3 cm of coral sand for substrate, two terracotta flowerpot halves as breeding shelters and two large sponge filters. Water was held at a constant temperature of 25 ± 2 °C and kept within chemical parameters that mimic the natural environment of the species. The fish were exposed to a 14:10 h light:dark cycle prior to and during the study. Fish were fed daily ad libitum with prepared cichlid flakes prior to and during the course of the study.

In total, we staged 56 same-sex contests (26 female, 30 male). The study was conducted in two testing periods, the first of which ran from October 2008 to February 2009 and the second from April to August 2010. During the first testing period, 36 fish (18 males,