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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 × 41 × 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, 18 females) were used to stage 29 contests (15 female, 14 male). Some of the fish in the first test period were used in two contests, resulting in 12 contests that involved at least one fish that had previously fought. However, fish never fought the same opponent twice, were chosen randomly with respect to their winner or loser status in the previous contest and were given at least 2 weeks to recuperate within their social group between the two contests. So including the 1-week acclimation period in the testing apparatus, fish had a minimum of 3 weeks in between fights. The fish's extensive daily interactions with its social group between contests probably minimized any winner or loser effects from the previous contest (Hsu et al. 2006). In the second testing period, we used 54 fish (32 males, 22 females) to stage 27 contests (16 male, 11 female). Fish in the second testing period were used only once, and no fish from the first testing period was used in the second. All trials in both test periods were conducted between 0900 and 1200 h. We used SL as a proxy for RHP. Body size has been shown to be a good predictor of fight outcome and to accurately reflect RHP in cichlid fishes (Enquist et al. 1987, 1990; Koops & Grant 1993). Body mass of the fish was highly correlated with SL (Pearson correlation: $r_{89} = 0.92$), so we used SL in all analyses reported here. We computed the percentage size asymmetry for each contest using the following formula: size asymmetry $=$ $|100((\text{loser SL}/\text{winner SL}) \times 100)|$.

Apparatus and Experimental Procedure

Contests were staged in 38 litre (50 × 25 × 30 cm) aquaria subdivided along their length into three equal compartments (each 16.5 × 25 × 30 cm) by two opaque plastic partitions. An opaque PVC pipe (6.50 cm long, 7.50 cm in diameter) was placed into each of two outer compartments as a shelter for the fish. A terracotta flowerpot half was placed in the central compartment. Each contest aquarium was supplied with 1.5 cm of coral sand as substrate. The light schedule and the water for the contest aquaria were maintained in the same conditions as in the social housing aquaria described above.

For each contest, two fish of the same sex (determined by examination of the external genitalia) and generally of similar size were selected haphazardly from two different social groups and placed into each of the two outer compartments of the contest aquarium. The fish in a contest were always unfamiliar with one another. Fish were marked for identification by clipping the dorsal fin in one or two of several possible positions. We routinely use this marking technique in our laboratory to identify individual fish. The marks are temporary, do not affect fish behaviour and are easily recognizable on videotape. The fish show no ill effects from the marking procedure and recover immediately.

Test fish were removed from their social group and placed in one of the two end compartments, visually isolated from their opponent for an acclimation period of 7 days. During this period, test fish could establish territorial ownership over his or her compartment and shelter. Following the week-long acclimation period, the shelter from each fish's end compartment was removed and then we simultaneously raised the two opaque plastic barriers, allowing the fish access to the shelter in the centre chamber as well as access to each other. *Neolamprologus pulcher* are highly territorial and will readily fight for access to a shelter (Desjardins et al. 2005; Taves et al. 2009). In most cases, a vigorous contest quickly began. Trials were stopped after 20 min. All trials were videotaped and later scored by an observer blind to the sex and body size measurements of the fish.

Scoring

When one fish fled from the other three consecutive times without retaliation, or consistently held a submissive posture (head held upwards and tail pointing downwards with unpaired fins folded tightly against the body) while avoiding the other fish, we declared that fish to be the loser and the other fish as the winner. If no fish had clearly emerged victorious within 20 min, we categorized the fight as a tie. For each contest, we scored onset time (the time it took for the fish to begin fighting after the barriers had been raised) and the duration of the display-only phase (the time from the first display to the first instance of physical contact). We also recorded the total duration of the contest, measured from the time the barriers were raised to the point at which the loser relented. The intensity of the contest was measured as the per-minute rate of aggressive behaviour for both fish combined.

Aggressive behaviour in *N. pulcher* is similar to what has been observed in other cichlids (Baerends & Baerends-van Roon 1950; Turner & Huntingford 1986; Barlow et al. 1986; Enquist et al. 1987, 1990; Koops & Grant 1993; Hurd 1997; Neat et al. 1998; Reddon & Hurd 2009). Following previous research in *N. pulcher* (Taborsky 1984; Hamilton et al. 2005; Bergmüller & Taborsky 2007; Mitchell et al. 2009; Riebli et al. 2011), we combined lateral displays (where the fish presents its lateral aspect to its opponent while extending its unpaired fins), frontal puffed throat displays (where the fish faces its opponent head-on and flares its opercula out to the side) and aggressive head-down postures (where the focal fish faces its opponent and lowers its head below the height of its tail, usually while extending its unpaired fins) into one general category of 'aggressive displays'. Likewise, we combined both rams (where the focal fish impacts its opponent with its head without biting) and bites into a single category of 'physical contact behaviour' (for detailed descriptions of the behavioural repertoire of *N. pulcher,* see Sopinka et al. 2009).

Statistical Analysis

All data were tested for normality and transformed when necessary ($\log + 1$). Data were analysed using nonparametric equivalents when they failed to meet parametric assumptions. All 2 × 2 chi-square tests were Yates corrected (Yates 1934). We compared winner and loser size and behaviour using paired *t* tests and the content of male and female contests using Welch's *t* tests (as recommended by Ruxton 2006). We performed ANCOVA analyses to look at the relation between contest duration and intensity, with winner and loser size separately, and to look for correlations between winner and loser behaviour. We included sex in each of these models. Interactions were examined and dropped from the models if they were not significant. All values are presented as mean ± SE.

Ethical Note

Trials were carefully monitored by an observer situated 1.5 m away from the contest tank. Any contest in which fish sustained visible injury or appeared to be excessively distressed was stopped immediately. This criterion resulted in the premature stoppage of one male contest, reducing the total number of contests from 56 to 55. To minimize stress and the risk of injury to the fish (following the recommendation of Huntingford 1984) we limited the contests to a short duration and terminated all contests after 20 min. Following each contest, we inspected each fish for injury, and no animal sustained any visible damage. The methods described for animal housing, capture and marking were assessed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol No. 10-11-71) and adhered to the guidelines of the Canadian Council for Animal Care.

RESULTS

Contest Outcome

Forty-five of the 55 contests had a clear winner and loser. The remaining 10 trials (five of each sex) were undecided within the 20 min contest framework and were scored as ties. All further analysis focused only on the decided contests ($N = 45$).

Winners were larger than losers (paired t test: $t_{44} = -4.33$, $P < 0.001$). Larger fish won 32 of the 45 decided fights ($\chi_1^2 = 8.02$, $P = 0.006$). The tendency for the larger fish to win did not differ between males and females (Yates chi − square test : $\chi_1^2 = 0.08$, $P = 0.78$). In those contests where the contestants differed in body size by 5% or more, the smaller fish emerged victorious in only two of 24 instances; however, when the size difference was less than 5%, small fish won about half of the time (11/21 contests; Yates chi-square test: $\chi_1^2 = 8.54$, $P = 0.003$; Fig. 1).

Contest Structure

Contestants took an average of 51.56 ± 7.02 s to commence displaying (range 3–175 s), and there was no difference between the sexes in display onset time (Welch's t test: $t_{35.5} = 1.04$, $P = 0.31$). Contests frequently began with a near simultaneous display from both competitors, so it was often difficult to discern which fish initiated the contest.

Rates of aggression between winners and losers were significantly positively related (ANCOVA: $R^2 = 0.39$, $F_{1,42} = 25.43$, $P < 0.001$), and there was no effect of sex on this relation ($F_{1,42} = 2.45$, $P = 0.13$). When we considered each category of aggressive behaviour separately, both display ($R^2 = 0.33$, $F_{1,42} = 24.91$, $P < 0.001$) and contact aggression (Spearman correlation: $r_S = 0.43$, $N = 45$, $P = 0.003$) were significantly positively correlated between winners and losers. Winners performed more aggressive acts (displays + contact aggression; paired t test: $t_{44} = 7.40$, $P < 0.001$), displays (paired t test: $t_{44} = 4.86$, $P < 0.001$) and contact aggression (Wilcoxon signed-ranks test: $Z = -5.18$, $N = 45$, $P < 0.001$) than did losers.

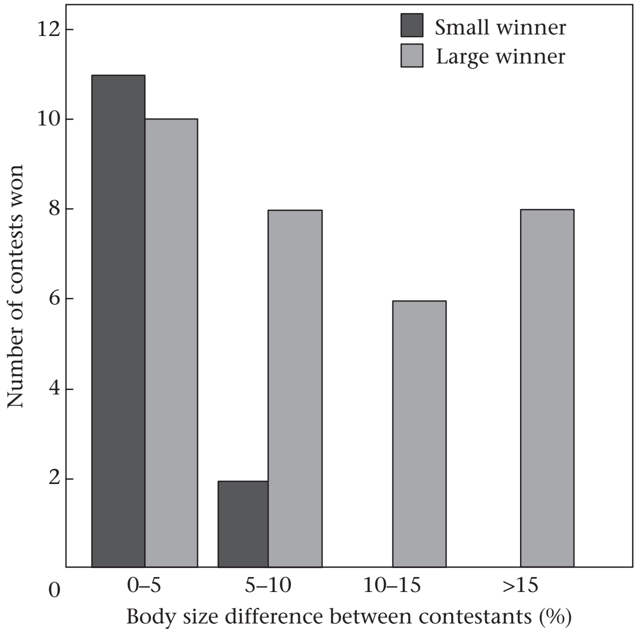

Figure 1. Number of contests won by the larger or the smaller contestant at different levels of body size asymmetry in Tanganyikan cichlids, *Neolamprologus pulcher*.

Display Phase

A period of noncontact display always preceded acts of contact aggression. The display-only phase, measured from the first display of the contest to the first physical contact, lasted an average of 87.89 ± 17.15 s (range 1–510 s). Noncontact displays continued to be used throughout the course of the interaction even after physical contact behaviours were introduced. Therefore, despite the period of display prior to physical contact, the fights did not seem to have a discretely phasic structure. The duration of the display-only phase did not predict the total duration of the contest (ANCOVA: $R^2 = 0.02$, $F_{1,42} = 0.40$, $P = 0.53$). The duration of the display phase was positively correlated with winner SL ($R^2 = 0.12$, $F_{1,42} = 4.46$, $P = 0.04$) but not with loser SL ($R^2 = 0.03$, $F_{1,42} = 0.28$, $P = 0.32$).

Contest Duration

Contests lasted about 10 min on average (mean: 578.4 ± 44.7 s, range 85–1194 s). Male and female contests did not differ in duration (Welch's t test: $t_{40.59} = 0.51$, $P = 0.62$). There was a negative relation between winner size and contest duration (ANCOVA: $R^2 = 0.15$, $F_{1,42} = 7.18$, $P = 0.01$; Fig. 2a), but loser size was not related to contest duration ($R^2 = 0.05$, $F_{1,42} = 2.05$, $P = 0.16$; Fig. 2b) and the sexes did not differ in the above relations ($P > 0.05$).

Contest Intensity

The average contest intensity was 5.6 ± 0.4 aggressive acts/min (range 1.4–13.3 acts/min). This total intensity can be broken up into an average of 4.4 ± 0.3 displays/min (range 0.9–11.0 acts/min) and 1.6 ± 0.2 acts of contact aggression/min (range 0–8.8 acts/min). Male and female contests did not differ in the frequency of aggression (total aggression rate: Welch's t test: $t_{42.6} = 0.17$, $P = 0.86$; display rate: $t_{39.8} = -0.48$, $P = 0.64$; contact aggression rate: $t_{36.4} = 1.08$, $P = 0.29$). Contest duration was negatively correlated with total contest intensity (ANCOVA: $R^2 = 0.25$, $F_{1,42} = 13.81$, $P = 0.001$) and display intensity ($R^2 = 0.20$, $F_{1,42} = 10.12$, $P = 0.003$), but not with contact aggression intensity ($R^2 = 0.08$, $F_{1,42} = 3.80$, $P = 0.06$). There were no sex differences in any of these relationships (all Ps > 0.05).

Total contest intensity was not correlated with winner body size ($R^2 = 0.09$, $F_{1,42} = 0.37$, $P = 0.55$) or loser body size ($R^2 = 0.41$, $F_{1,42} = 1.78$, $P = 0.19$). When the analysis was restricted to contact aggression only, loser size did not correlate with contact aggression intensity ($R^2 = 0.06$, $F_{1,42} = 3.10$, $P = 0.24$); however, winner size and contact aggression intensity were negatively related ($R^2 = 0.13$, $F_{1,42} = 4.92$, $P = 0.03$), so that fights with smaller winners had more intense contact components (more contact aggression per minute). There was no sex difference in this relationship ($F_{1,42} = 1.14$, $P = 0.29$).

DISCUSSION

Contests and conflict are common among members of social groups with dominance hierarchies, as rank is typically determined by aggressive interaction (Drews 1993). Our observations of behaviour within dyadic resource contests in *N. pulcher* may shed light on conflict resolution within social groups.

Contest winners were usually larger than losers. Interestingly, winner but not loser size was negatively correlated with contest duration and contact aggression intensity. None of the assessment models explicitly make this prediction. Larger winners won contests more quickly and with less intense contact aggression. Well-matched contestants had longer fights with more intense aggressive behaviour; however, these results were driven by winner absolute body size not the size differences between winners

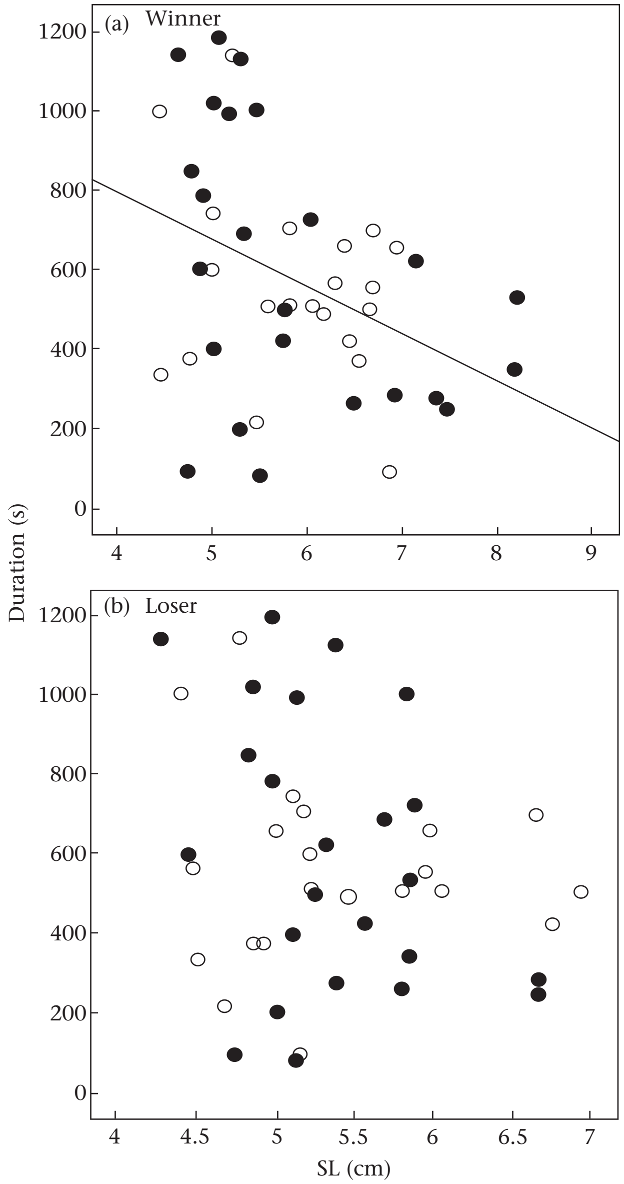

Figure 2. Linear relation between contest duration and (a) winner and (b) loser body size (standard length, SL) in Tanganyikan cichlids, *Neolamprologus pulcher*. Solid circles: males; open circles: females.

and losers. Our results are incompatible with the logic of self-assessment as it appears that *N. pulcher* perceive information about their opponent's RHP and alter behaviour accordingly. Our results are also incompatible with the logic of mutual assessment, where individuals compare opponent and own RHP. It is worth noting that while the cumulative assessment model cannot be conclusively discriminated from mutual assessment model using the current method (both models make similar predictions about winner and loser RHP and contest cost; see Briffa & Elwood 2009), the lack of a relation between loser size and contest duration in our study is inconsistent with the logic of cumulative assessment, where the decision to relent is ultimately based on the loser's own cost threshold (Payne 1998).

In reality, a complex blend of assessment strategies may better describe contest behaviour across taxa (for recent reviews, see: Arnott & Elwood 2009a; Briffa & Sneddon 2010). Contest behaviour that does not conform precisely to any of the existing models has been observed in a variety of taxa (e.g. Jennings et al. 2004; Briffa & Elwood 2002; Kelly 2006; Briffa 2008; Elias et al. 2008; Hsu et al. 2008). Our results are most consistent with opponent assessment without self-assessment. Other studies have found some evidence for opponent-only assessment. For example, Arnott & Elwood (2010) found some indication of opponent-only assessment during contests in another cichlid (*Amatitlania nigrofasciata*), fish with fighting experience showed longer delays to resume fighting following interruption by a simulated predator attack when their opponent was a large fish. Prenter et al. (2008) found that swordtail males (*Xiphophorus helleri*) assess the length of each other's swords and use this information when deciding to persist in a contest, but do not seem to fight with reference to their own sword length. Perhaps most convincingly, Rillich et al. (2007) found that male crickets (*Gryllus bimaculatus*) decide to give up and flee from a contest based primarily on the actions of their opponent. Combined with these previous results, our study suggests that opponent assessment without any form of self-assessment may represent a heretofore under-appreciated mechanism of assessment in animal contests.

Neolamprologus pulcher always displayed prior to making physical contact, but the length of this display-only period was quite variable, and sometimes was extremely brief (minimum observed = 1 s). Displays did not cease once physical contact began and they continued at a high rate until the contest was settled. Lower-cost displays are thought to facilitate opponent assessment (Enquist et al. 1990; Keeley & Grant 1993; Hurd 1997; Reddon & Hurd 2009; Arnott & Elwood 2009b, c, 2010) and appear to be an important component of *N. pulcher* contests.

We found no sex differences in any measured aspect of contest behaviour. Male and female *N. pulcher* contests were of similar length and intensity. Winner RHP appeared to have the same effect on contest duration, intensity and outcome in both sexes. Our study convincingly demonstrates that fight tactics do not differ in any substantive way between the sexes in this species and that male and female aggressive behaviour and contest decision making are indistinguishable. This contrasts with what has been found in some other species (Cole et al. 1980; Holder et al. 1991; Johnsson et al. 2001; Briffa & Dallaway 2007; Draud et al. 2004; Arnott & Elwood 2009b) where males and females fight according to different rules.

Interestingly, the size difference threshold that was usually decisive (~5% difference in SL) is strikingly similar to the size difference observed between rank-adjacent members of naturally occurring *N. pulcher* social groups (Taborsky 1984, 1985). It is possible that *N. pulcher* dominance hierarchies maintain a level of size stratification, either by suppression from dominant members (Taborsky 1984; Wong et al. 2008) or via self-restraint by subordinates (to avoid punishment; Wong et al. 2008), such that each member of the dominance hierarchy can physically dominate its immediate subordinate (Wong et al. 2007). There is some evidence of strategic growth in *N. pulcher* males (Heg et al. 2004) but not in females (Hamilton & Heg 2008; Heg 2010), providing some support for this hypothesis, at least in males. Our results suggest that the size stratification of the dominance hierarchy may be influenced by assessment of groupmate RHP.

The rate of aggression in our staged resource contests was approximately 10-fold higher than the rates of aggression reported among subordinate helpers within a stable *N. pulcher* social group (Wong & Balshine 2010b). In the Wong & Balshine (2010b) study, when a helper was removed from the dominance hierarchy, the ascending fish (that moved into the vacated dominance position) approximately doubled its rate of aggression within the group, resulting in a rate of aggression that was still approximately five-fold lower than the aggression rates we observed during our staged resource contests. Apparently, alterations to the dominance hierarchy in *N. pulcher* are resolved through aggression, but rates of aggression between familiar group members are typically lower than aggression observed in resource contests between strangers. *Neolamprologus pulcher* do naturally engage in escalated contests, for example, during territory take-overs or group-joining events (Balshine-Earn et al. 1998; Stiver et al. 2006; Fitzpatrick et al. 2008), and in these situations we would expect to observe aggression rates closer to what we have observed in the staged contests. Within an established social group, however, individuals appear to constantly engage in low-level aggression rather than punctuated bouts of escalated aggression, although these may occasionally occur. The decision rules that dictate this day-to-day low-level aggression are likely to share a mechanistic basis with the rules used in escalated contests; therefore, the decision-making mechanisms we have described here should help elucidate the nature of aggressive conflict within permanent social groups and conflict resolution within animal societies.

In summary, we found evidence for opponent RHP assessment during staged dyadic resource contests in a cooperatively breeding vertebrate. The evidence suggests that assessment of opponent size appears to be germane to strategic and tactical decision making during *N. pulcher* contests, and is more important than assessment of one's own RHP, a prediction not explicitly made by any of the existing models of contest behaviour. We found no evidence for sex differences in contest behaviour: male and female *N. pulcher* fought by the same rules and made decisions based on the same information, suggesting that the costs and benefits of aggression are similar in males and females of this species. To our knowledge this is the first study to stage controlled contests in a cooperatively breeding vertebrate and to investigate the decision-making process during these conflicts.

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