Strategic and tactical fighting decisions in cichlid fishes with divergent social systems

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Abstract

The costs and benefits of engaging in a contest will differ depending on the social situation of the individuals involved. Therefore, understanding contest behaviour can help to elucidate the trade-offs of living in differing social systems and shed light on the evolution of social behaviour. In the current study, we compared contest behaviour in two closely related species of Lamprologine cichlid fish. *Neolamprologus pulcher* and *Telmatochromis temporalis* are both pair-breeding cichlids, but *N. pulcher* are highly social, group-living fish, while *T. temporalis* display no grouping behaviour. To examine how competition varies by species, sex and familiarity, we staged same-sex conspecific contests over a shelter, a resource that is highly valued by both species, where contestants were either familiar or unfamiliar to one another. When we examined tactical and strategic components of these contests, we found that the highly social species had shorter contests and engaged in fewer costly aggressive acts than did the non-social species. Individuals of the highly social species were also more likely to resolve conflicts through the use of submissive displays, while individuals of the non-social species were more likely to flee from conflict. Familiarity increased the use of submissive displays in the highly social species but not in the less social species. Our findings suggest that conflict resolution behaviour and dominance hierarchy formation are fundamentally linked to the evolution of complex social systems.

1. Introduction

Resource contests are common and occur whenever two or more animals resolve a conflict through direct aggressive interaction (Huntingford & Turner, 1987; Archer, 1988). Contests are inherently costly, often involving a considerable expenditure of energy (Briffa & Elwood, 2004; Castro et al., 2006; Mowles et al., 2010; Copeland et al., 2011), and time, which could otherwise be spent on other activities such as foraging (Kemp & Wiklund, 2001) or anti-predator vigilance (Jacobbson et al., 1995; Brick, 1998). In some taxa, contests may also carry a substantial risk of injury or death (Enquist & Leimar, 1990; Neat et al., 1998a; Umbers et al., 2012). As a result, contest tactics (i.e., the behaviours employed within a contest) and strategies (i.e., decisions related to persisting, escalating or withdrawing from a contest) are often fine-tuned to minimize the costs and maximize the benefits of engaging in contests (Parker, 1974; Parker & Rubenstein, 1981; Enquist & Leimar, 1983; Hurd, 1997; Maynard-Smith & Harper, 2003; Arnott & Elwood, 2008, 2009; Briffa & Sneddon, 2010; Elwood & Arnott, 2012). For example, many contests involve ritualized displays and the assessment of opponent strength rather than the dangerous physical interactions that characterize an all-out fight (Parker, 1974; Arnott & Elwood, 2009; Elwood & Arnott, 2012).

The complexity of an animal's social environment, its group size, and the degree of close social bonds among individuals in the group may influence the strategic and tactical components of contest behaviour (Briffa & Sneddon, 2010; Earley & Dugatkin, 2010). Animals that live in permanent groups and rely on each other for communal defence or foraging may have a particularly strong mutual interest in minimizing the costs of conflicts (Dugatkin, 2001; Krause & Ruxton, 2002; Earley & Dugatkin, 2010). If a group member is injured as a consequence of fighting, the entire group may be less productive, or represent a weaker deterrent to predators (Krause & Ruxton, 2002; Cant et al., 2006; Wong et al., 2008; Earley & Dugatkin, 2010). Hence, conflict can be particularly costly for individuals of a social species and has the potential to impede cooperation (Aureli et al., 2002), or lead to group dissolution (Rubenstein & Kealy, 2010), and the evolution of complex social systems may coincide with selection for reduced contest costs (Hurd, 1997; Maynard-Smith & Harper, 2003). Minimizing or avoiding aggression altogether through the use of communicative displays and signals is likely to have been strongly favoured in group-living species (Bergmüller & Taborsky, 2005). One way that group-living animals reduce the cost and frequency

of aggression is by forming dominance hierarchies (Drews, 1993; Sapolsky, 2005). Communicative displays or short, low-cost contests establish and maintain these dominance hierarchies (Clutton-Brock et al., 2009; Ang & Manica, 2010; Dey et al., 2013). Furthermore, individuals within a group often have pre-existing information about the strength of their group mates through prior direct interactions (e.g., winner and loser effects; Dugatkin, 1997; Hsu et al., 2006; Earley & Dugatkin, 2010) or observed interactions between the opponent and a third party (Dugatkin, 2001; Peake & McGregor, 2004; Grosenick et al., 2007; Desjardins et al., 2012) which can inform decision-making within a contest and influence contest strategies and tactics.

Resource contests also provide a useful window into discrimination abilities as they provide a clear social situation in which familiar and unfamiliar individuals should be treated differentially. Some social species live in fluid aggregations with free access for new joiners, while other species live in a relatively permanent social group where existing group members exert control over group membership. In such highly social species, the ability to accurately discriminate between familiar within-group members and unfamiliar individuals from outside the group is essential (Jordan et al., 2010a), and group members are treated differently than non-group members (Johnstone, 1997; D'Ettorre & Heinze, 2005). This claim does not imply that solitary species lack the ability to respond appropriately towards known versus unknown individuals. In fact, individuals of many social and non-social species will respond more aggressively to unfamiliar rivals than they do to familiar rivals, a process known as the 'dear enemy' effect (Wilson, 1975; Qualls & Jaeger, 1991). This 'dear enemy' effect occurs because strangers are less likely to have an established territory of their own, and therefore represent a greater challenge for a territory owner (Qualls & Jaeger, 1991; Temeles, 1994). However, individuals of highly social species with insider control of group membership are predicted to have enhanced capacity for discrimination of familiar and unfamiliar conspecifics relative to individuals of less social species.

How sociality relates to the tactical and strategic elements of fighting has not yet received much attention (Briffa & Sneddon, 2010; Earley & Dugatkin, 2010). Here, we compared contest behaviour (both the strategic and the tactical components) in two closely related species with similar ecologies, but differing social organization. We staged resource contests for both species involving both familiar and unfamiliar contestants of both

sexes. Our study species were *Neolamprologus pulcher* and *Telmatochromis temporalis*, two very closely related (Day et al., 2007) Lamprologine cichlids endemic to the rocky littoral zone in Lake Tanganyika, East Africa. These cichlid fish species live in the same areas of the lake, and have the same diets, habitat requirements, and predation regimes (Kuwamura, 1986; Brichard, 1989; Konings, 1998). Furthermore, both cichlids are territorial, pair-breeding, substrate spawners with biparental care (Kuwamura, 1986). However, *N. pulcher* are highly social and cooperative, living in large colonies that are comprised of groups of 3–20 individuals with a single breeding pair and one or more non-breeding adult subordinates that assist in raising the offspring of the breeders (Taborsky & Limberger, 1981; Taborsky, 1984; Balshine-Earn et al., 1998; Balshine et al., 2001; Wong & Balshine, 2011a). Conversely, *T. temporalis* do not form groups or cooperate (Mboko & Khoda, 1999; Heg & Bachar, 2006). Both species are small bodied (<80 mm standard length) and readily adapt to the laboratory environment. We staged contests over a shelter, a highly valued commodity readily fought over by both species, as it is essential both for reproduction and as refuge from predators (Balshine-Earn et al., 1998; Desjardins et al., 2005; Taves et al., 2009; Reddon et al., 2011). We predicted that the highly social species, *N. pulcher*, would have less costly contests overall, and display more conflict resolution than would the non-social *T. temporalis*. We further predicted that the social *N. pulcher* would show clear discrimination between familiar and unfamiliar conspecifics, while the non-social *T. temporalis* would be more inclined to treat familiar and unfamiliar opponents similarly. Finally, *N. pulcher* exhibit male-biased dispersal, and female *N. pulcher* tend to remain in their natal group and inherit a breeding position, while males tend to disperse to join or take over new social groups (Dierkes et al., 2005; Stiver et al., 2006; Wong & Balshine, 2011a). Therefore, we predicted that female *N. pulcher* would be more motivated to maintain group cohesion and therefore show greater social discrimination compared to male *N. pulcher* or to *T. temporalis*.

2. Methods

2.1. Study animals

The *Neolamprologus pulcher* and *Telmatochromis temporalis* used in this study were laboratory-reared descendants of wild-caught fish from Lake Tanganyika, Africa. All fish of both species were sexually mature, but had not

yet reproduced. The *N. pulcher* had an average standard length (SL, measured from the tip of the mouth to the caudal peduncle) of 52.3 ± 1.1 mm (mean ± SEM) for females and 50.8 ± 0.9 mm and for males, and a body mass of 4.0 ± 0.24 g for females and 3.7 ± 0.24 g for males. The *T. temporalis* had an average SL of 43.9 ± 0.5 mm for females and 47.6 ± 0.7 mm for males, and body mass of 2.1 ± 0.1 g for females and 2.7 ± 0.1 g for males. In total, 74 pairs were used, with 19 male contestant pairs (10 were familiar and 9 were unfamiliar) and 18 female pairs (9 familiar and 9 unfamiliar) of each species. We set up contests with a standardized size difference between the contesting individuals, such that the larger fish was always 5–20% heavier than the smaller fish (mean size difference was 12.2 ± 0.6% for *N. pulcher*; 13.1 ± 0.5% for *T. temporalis* pairs). We selected this size difference because it elicits robust aggressive behaviour but allows the winner to be reliably predicted a priori (Reddon et al., 2011).

Focal fish of both species were housed in groups for a minimum of two weeks prior to testing. These groups consisted of 8 to 12 individuals with approximately equal numbers of males and females. The groups were housed in 189-l aquaria containing 3 cm of coral sand substrate, two sponge filters, a heater, a thermometer and two terracotta flowerpot halves that served as shelters. We selected the contestants to be either two familiar fish that came from the same aquarium or two fish from different aquaria that had not previously interacted. Although we did not strictly control for relatedness in this experiment, all groups for both species were originally formed from large mixed stock tanks containing hundreds of individuals, and relatedness was presumed to be similar between familiar and unfamiliar pairs of fish. Water temperatures of all aquaria were held at 26 ± 2°C. All fish were fed flake cichlid food *ad libitum* six times per week, and kept on a 13:11 light/dark cycle.

2.2. *Apparatus and experimental procedure*

All fish used were measured, weighed, sexed by examination of the external genital papillae and given a unique dorsal fin clip for identification on the day prior to the contest. For each contest, we placed either two familiar or two unfamiliar same-sex competitors in a 38-l experimental contest aquarium (Figure 1). The contest aquarium was divided into three equal compartments (each 16.5 × 25 × 30 cm) by removable opaque barriers. Each of the three compartments contained an opaque black polyvinylchloride (PVC)
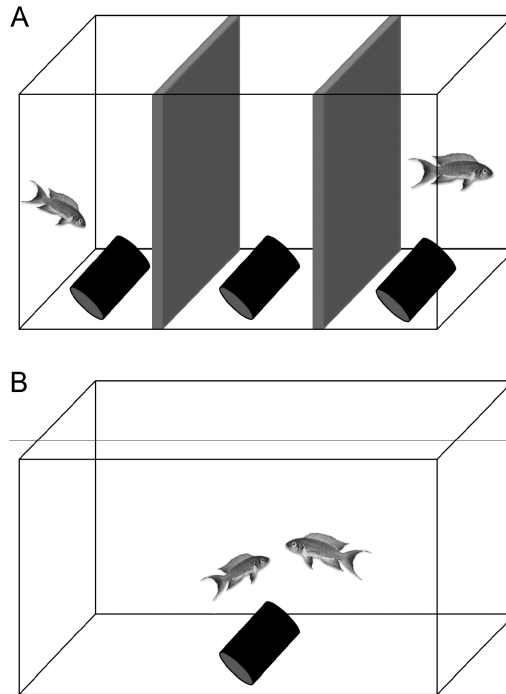
Figure 1. Experimental setup for staged resource contests between pairs of male and female, familiar and unfamiliar, *Neolamprologus pulcher* (a highly social cichlid) and *Telmatochromis temporalis* (a non-social cichlid). (A) During a 1-h acclimation period, the two contestants were each given a shelter in side compartments, but were separated from each other by opaque dividers; (B) following acclimation, the side shelters and barriers are removed, and fish are allowed to contest over the remaining central shelter for 30 min.

tube (6.5 × 10 cm) that both species readily use as shelter (Figure 1a). The sides and back of the contest aquaria were covered with translucent plastic wrap to minimize disturbance and reduce light reflection. We placed the two rivals in opposite-end side compartments, with a coin toss used to determine which compartment contained the smaller vs. the larger individual. The two fish were given one h to habituate to their environment and to establish territorial ownership over their own shelter (Figure 1a). After the 60-min habituation period, we removed the shelters from the end compartments, and the opaque barriers, providing the two fish with an opportunity to contest with one another over ownership of the PVC tube in the middle of the aquarium (Figure 1b). This procedure has been used previously to stage contests in *N. pulcher* and reliably elicits a fight (Desjardins et al., 2005; Taves et al.,

2009; Reddon et al., 2011). After 30 min both fish were removed from the experimental aquarium and returned to their original group tank.

2.3. Behavioural scoring

All aggressive and submissive behaviours performed by both the eventual loser (typically the smaller fish) and the eventual winner (typically the larger fish) during the 30 min trial were scored. The behaviours recorded are described in the ethogram found in Table 1, which was modified from Sopinka et al. (2009). All trials were scored live for behaviour, and videotaped for later confirmation of contest duration measures. A trained observer who was blind to the sex and level of familiarity of the contestants scored all trials. Briefly, the behaviours observed during the trials included aggressive displays (aggressive head-down postures as well as frontal displays); overt physical attacks (chases, rams, bites, and mouth wrestles); and submission (submissive head-up posture, submissive displays and fleeing). All behaviours were scored and analysed separately for the eventual winner and the eventual loser where possible, to avoid the pitfalls of composite measures (Taylor & Elwood, 2003; Briffa & Elwood, 2010; Reddon et al., 2011, 2013).

We declared a fish the loser of the contest when it displayed submission (a posture, display, or flee) to the other fish three times in succession (Reddon & Hurd, 2009; Reddon et al., 2011). Total fight duration was calculated as the time elapsed between the initial aggressive behaviour (either a display or overt physical attack) performed by either fish, to the third submissive act (display or flee) from the losing fish (Reddon & Hurd, 2009; Reddon et al., 2011). Within each fight, the total number of aggressive bouts was also calculated. The absence of aggressive behaviour from either fish for longer than 7 s was considered a break from aggression, and delineated a bout within the contest. For one trial (between unfamiliar *N. pulcher* males), the number of bouts could not be scored due to a malfunction of the video recording equipment.

We scored all aggressive behaviours produced by either the winner or the loser and calculated the per-minute rate at which these behaviours occurred. Rates of submissive displays and fleeing were calculated by scoring these behaviours per aggressive behaviour received (Reddon et al., 2012; O'Connor et al., 2013). We also scored the rate at which both fish engaged in mutual aggression (mutual aggressive displays or mutual overt physical attacks). Mutual overt physical attacks included mouth wrestling and simultaneous biting. These represent a highly escalated phase of a cichlid fight,

Table 1.

Ethogram used to score behaviours during staged contests between pairs of *Neolamprologus pulcher* (a highly social cichlid) and *Telmatochromis temporalis* (a non-social cichlid) over a shelter.

Type of behaviour	Description
Aggression (displays)	
Aggressive posture	Focal fish lowers its head and raises its tail in front of its opponent.
Frontal display	Also called a puffed throat or an opercular flare. Focal fish extends out its opercula and lower jaw. Often associated with an aggressive posture.
Head shake	Focal fish thrashes its head from left to right repeatedly.
Tail beat*	Focal fish thrashes its tail directing a jet of water in the direction of its opponent.
Pseudo-mouth wrestle	Both fish rapidly move back and forth while facing each other, as if about to mouth wrestle (see below), but no physical contact is established.
Aggression (overt physical attacks)	
Chase	Focal fish quickly darts towards another fish.
Ram	Focal fish makes contact with another fish using the head or mouth region, but no obvious bite is taken and jaws remain closed.
Bite	Focal fish bites another fish.
Mouth wrestle	Also known as a mouth fight. Focal fish and its opponent lock jaws and push against one another in a reverse tug-of-war.
Submission (displays)	
Submissive posture	The head of the focal fish is directed upwards, sometimes entirely vertically, and the tail is downwards.
Submissive display	Focal fish is positioned with a submissive posture accompanied by a quivering tail. Sometimes the entire body quivers.
Hook/J Display**	Focal fish swims towards another fish, and then turns sharply away at the last moment and quivers submissively.
Submission (flees)	
Flee	Focal fish quickly swims away from another fish.

This ethogram is based on a recent ethogram for *N. pulcher* (Sopinka et al., 2009) and on behavioural observations of *T. temporalis* in the laboratory and field. For the most part, the two species studied showed the same behaviours. There were two species-specific behaviours observed, one observed in *T. temporalis* (*), and the other in *N. pulcher* (**).

involving considerable expenditure of energy, reduced attention to predators, and heightened injury risk (Enquist & Jakobsson, 1986; Enquist et al., 1990; Koops & Grant, 1993; Brick, 1998; Neat et al., 1998a, b). Therefore,

the degree to which mutual overt physical attacks are used in a contest is an important indicator of contest cost (Brick, 1998).

2.4. Statistical analyses

Of the 74 trials run, there were 4 trials in which the fish were inactive. These 4 trials were excluded from subsequent analyses, leaving 70 trials ($N = 8$ for familiar female *N. pulcher* pairs and unfamiliar female *T. temporalis* pairs; $N = 9$ for all other groups). We examined the frequency of aggressive acts (broken down into displays and physical attacks) for both the winners and losers, along with the number of submissive acts (broken down into submissive displays and flees) by the loser per aggressive act received from the winner (Reddon et al., 2012). We also examined latency to first aggressive act by either fish, the number of aggressive bouts within contests, the total time spent engaged in aggressive bouts (the sum of all aggressive bouts), and total contest duration (from the first aggressive act to the third submissive act from the losing fish). We examined all behaviours using analysis of variance (ANOVA) models with species, sex, and familiarity as independent variables. Because we had specific predictions regarding interactions (e.g., we predicted less aggression in familiar female *N. pulcher* pairs), we also included all interaction effects in the models. All residuals were checked for normality and equality of variances, and all variables except for the total number of bouts were log-transformed to meet assumptions. Tukey's HSD post-hoc tests were employed following significant ANOVAs to determine where among the groups the differences lay. All values are presented as untransformed mean ± SEM, with $\alpha = 0.05$. Statistical analyses were conducted in JMP 10 (SAS Institute, 2012) or R version 2.15 (R Development Core Team, 2012).

2.5. Ethical note

Fish were marked for individual identification by removing a small amount of fin tissue from the dorsal fin of each fish. Fin clipping does not adversely affect behaviour (Stiver et al., 2004), and these fin clips grow back within a fortnight. Fish recovered immediately from the fin-clipping procedure. Two observers, situated 1.5 m away, watched all trials simultaneously. If fish had sustained a visible injury or appeared to be unduly distressed, the contest would have been stopped. This never occurred, and so no trials needed to be stopped prematurely. Following each contest, the fish were returned to

their home aquaria and monitored for signs of distress during the following
week. No adverse after-effects of the contest were detected in any of the
fish. 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 both
Canadian laws and the guidelines of the Canadian Council for Animal Care
and the Animal Behaviour Society/Association for the Study of Animal Be-
haviour.

3. Results

3.1. Differences in contest tactics

The non-social species, *T. temporalis*, were more aggressive overall. *T. tem-
poralis* winners performed more aggressive displays than winners of the
highly social species, *N. pulcher* (Tables 2 and 3; Figure 2a). Although
marginally non-significant, *T. temporalis* winners also tended to use more
overt physical attacks than did *N. pulcher* winners (Table 2). *T. temporalis*
contestants performed more mutually aggressive displays (i.e., using mutual
aggressive displays without overt contact) than did pairs of the highly social
N. pulcher (Tables 2 and 3; Figure 2b).

As well as species difference in rates of aggression, we found that both
familiarity and sex influenced aggressive behaviour. Surprisingly, familiar
pairs of *T. temporalis* performed more aggressive displays than did unfa-
miliar *T. temporalis* pairs (Tables 2 and 3; Figure 2a). *T. temporalis* males
engaged in more highly costly mutually aggressive attacks (i.e., mutual bites,
mouthfights) than *T. temporalis* females, or *N. pulcher* pairs (Tables 2 and 3;
Figure 2c).

Losing fish performed aggressive displays and physically attacked op-
ponents at similar rates regardless of species, sex and level of familiarity
(Table 2).

3.2. Differences in contest strategy

Species, sex and level of familiarity did not influence the total contest dura-
tion (i.e., the time from the first aggressive behaviour to the final submissive
display or flee from the losing fish; Table 2). However, *T. temporalis* were
faster to initiate aggression than were *N. pulcher* (Tables 2 and 3; Figure 3a).

Table 2.

Results of analysis of variance (ANOVA) models investigating the influence of species (*Neolamprologus pulcher* or *Telmatochromis temporalis*), sex (male or female), familiarity (familiar or unfamiliar) and interaction effects on behaviours observed during staged contests between pairs of male and female, familiar and unfamiliar, highly social (*N. pulcher*) and non-social (*T. temporalis*) cichlids.

Type of behaviour		Model DF	Error DF	*F*	*p*
Aggression (displays)	**Winner aggressive displays**	**7**	**62**	**25.58**	**<0.001**
	Loser aggressive displays	7	62	0.55	0.79
	Mutual aggressive displays	**7**	**62**	**6.99**	**<0.001**
Aggression (overt physical attacks)	Winner physical attacks	7	62	1.86	0.09
	Loser physical attacks	7	62	1.52	0.18
	Mutual physical attacks	**7**	**62**	**2.34**	**0.03**
Submission (displays)	**Loser submission per aggression received**	**7**	**62**	**5.01**	**<0.001**
Submission (flees)	**Loser flees per aggression received**	**7**	**62**	**6.73**	**<0.001**
Contest timing	**Latency to first aggressive display**	**7**	**62**	**2.33**	**0.03**
	Number of bouts	**7**	**61**	**27.66**	**<0.001**
	Time spent engaged in aggressive bouts	**7**	**61**	**11.23**	**<0.001**
	Overall contest duration	7	62	1.42	0.21

Bold text indicates cases where the overall model is significant ($\alpha = 0.05$). For significant factors within significant overall models, see Table 3.

Within contests, *T. temporalis* fights had more aggressive bouts than *N. pulcher* fights, with familiar *N. pulcher* pairs displaying the fewest number of aggressive bouts (Tables 2 and 3; Figure 3b). Furthermore, the total time spent engaged in aggressive bouts (i.e., the sum of all aggressive bouts) differed between species and was based on familiarity; within the overall contest, familiar *N. pulcher* spent the least time engaged in aggressive bouts (Tables 2 and 3; Figure 3c).

3.3. Differences in contest resolution

Familiar female *N. pulcher* displayed the highest rates of submission (Tables 2 and 3; Figure 4a), and were the least likely to end antagonistic interactions by fleeing (Tables 2 and 3; Figure 4b).

Table 3.
Results of analysis of variance (ANOVA) models investigating the influence of species (*Neolamprologus pulcher* or *Telmatochromis temporalis*), sex (male or female), level of familiarity (familiar or unfamiliar) and interaction effects on behaviours observed during staged contests between pairs of male and female, familiar and unfamiliar, highly social (*N. pulcher*) and non-social (*T. temporalis*) cichlids.

Type of behaviour		Model effect	F	p
Aggression (displays)	**Winner aggressive displays**	**Species (*N. pulcher* or *T. temporalis*)**	**144.59**	**<0.001**
		Sex (male or female)	1.17	0.28
		Familiarity (familiar or unfamiliar)	**7.96**	**0.006**
		Species × Sex	0.61	0.44
		Species × Familiarity	**19.46**	**<0.001**
		Sex × Familiarity	1.49	0.23
		Species × Sex × Familiarity	1.01	0.32
	Mutual aggressive displays	**Species (*N. pulcher* or *T. temporalis*)**	**44.89**	**<0.001**
		Sex (male or female)	0.75	0.39
		Familiarity (familiar or unfamiliar)	0.91	0.34
		Species × Sex	1.12	0.29
		Species × Familiarity	0.84	0.36
		Sex × Familiarity	0.07	0.80
		Species × Sex × Familiarity	0.03	0.87

Table 3.
(Continued.)

Type of behaviour	Model effect	F	p
Aggression (overt physical attacks)	**Mutual physical attacks**		
	Species (*N. pulcher* or *T. temporalis*)	**6.83**	**0.01**
	Sex (male or female)	**4.93**	**0.03**
	Familiarity (familiar or unfamiliar)	1.09	0.30
	Species × Sex	2.78	0.10
	Species × Familiarity	0.24	0.63
	Sex × Familiarity	0.15	0.70
	Species × Sex × Familiarity	0.01	0.94
Submission (displays)	**Loser submission per aggression received**		
	Species (*N. pulcher* or *T. temporalis*)	**13.09**	**<0.001**
	Sex (male or female)	3.54	0.06
	Familiarity (familiar or unfamiliar)	**6.01**	**0.02**
	Species × Sex	**5.09**	**0.03**
	Species × Type	**4.01**	**0.04**
	Sex × Familiarity	2.67	0.11
	Species × Sex × Familiarity	3.30	0.07
Submission (flees)	**Loser flees per aggression received**		
	Species (*N. pulcher* or *T. temporalis*)	**20.41**	**<0.001**
	Sex (male or female)	3.35	0.07
	Familiarity (familiar or unfamiliar)	**6.83**	**0.01**
	Species × Sex	**9.02**	**0.003**
	Species × Familiarity	1.85	0.18
	Sex × Familiarity	2.88	0.09
	Species × Sex × Familiarity	**6.10**	**0.02**

Table 3.
(Continued.)

Type of behaviour	Model effect	F	p
Contest timing	**Latency to first aggressive behavior**		
	Species (*N. pulcher* or *T. temporalis*)	**12.53**	**<0.001**
	Sex (male or female)	0.05	0.83
	Familiarity (familiar or unfamiliar)	0.05	0.83
	Species × Sex	0.09	0.77
	Species × Familiarity	0.01	0.94
	Sex × Familiarity	0.70	0.41
	Species × Sex × Familiarity	2.68	0.11
	Number of aggressive bouts		
	Species (*N. pulcher* or *T. temporalis*)	**160.38**	**<0.001**
	Sex (male or female)	2.17	0.15
	Familiarity (familiar or unfamiliar)	0.02	0.88
	Species × Sex	0.13	0.71
	Species × Familiarity	**25.51**	**<0.001**
	Sex × Familiarity	0.11	0.74
	Species × Sex × Familiarity	3.92	0.05
	Time spent engaged in aggressive bouts		
	Species (*N. pulcher* or *T. temporalis*)	**60.85**	**<0.001**
	Sex (male or female)	**5.55**	**0.02**
	Familiarity (familiar or unfamiliar)	0.02	0.87
	Species × Sex	2.14	0.15
	Species × Familiarity	**8.42**	**0.005**
	Sex × Familiarity	0.50	0.48
	Species × Sex × Familiarity	0.04	0.85

Bold text indicates significant factors within significant overall models ($\alpha = 0.05$).

4. Discussion

Contests among highly social cichlid *N. pulcher* were more subdued than the contests observed in the non-social cichlid *T. temporalis*. Moreover, females of the cooperatively breeding *N. pulcher* were most likely to use submissive displays and least likely to flee from an aggressive encounter when familiar with one another. Collectively, our results illustrate that both the tactical (i.e., the behaviours employed within a contest) and strategic (i.e., decisions related to persisting, escalating or withdrawing from a contest) components of contest behaviour differed between two closely related and ecologically similar cichlids with disparate social systems, suggesting an interrelationship between social system and the dynamics of resource contests.

4.1. Differences in contest behaviour

The highly social *N. pulcher* used fewer and less costly aggressive acts than the non-social *T. temporalis*. Social *N. pulcher* were also less aggressive in terms of the latency to use aggression, the number of aggressive bouts during a contest, and the total time spent engaged in an aggressive bout, as well as the frequency of mutual overt physical attacks (i.e., mouthfights), which is a measure of highly escalated and costly conflicts (Brick, 1998; Neat et al., 1998a). Taken together, our results support the notion that individuals of a group-living species show behavioural adaptations geared towards greater minimization of the costs of conflicts.

Contests between pairs of familiar *T. temporalis*, the non-social cichlid, were the most intense fights observed, suggesting that this less social species has the capacity to discriminate familiar and unfamiliar conspecifics. However, the direction of the relationship was contrary to our predictions. We presumed that both cichlid species would show 'dear enemy' effects, and respond less aggressively to known versus unknown competitors (Wilson, 1975; Qualls & Jaeger, 1991). However, intense aggression with a familiar individual might reflect the flexible or context specific nature of repeated interactions between the same individuals, which often do not adhere to game theoretic predictions based on one-off interactions between strangers (Dugatkin et al., 1997, 2001; Leiser, 2003; Hsu et al., 2006; Riechert, 2013; Tierney et al., 2013). In the current study, all individuals were sexually mature, but had never reproduced. It is possible that non-breeding *N. pulcher* are less willing than non-breeding *T. temporalis* to pay high contest costs to win a shelter (which are used both for breeding and as refuge from predators
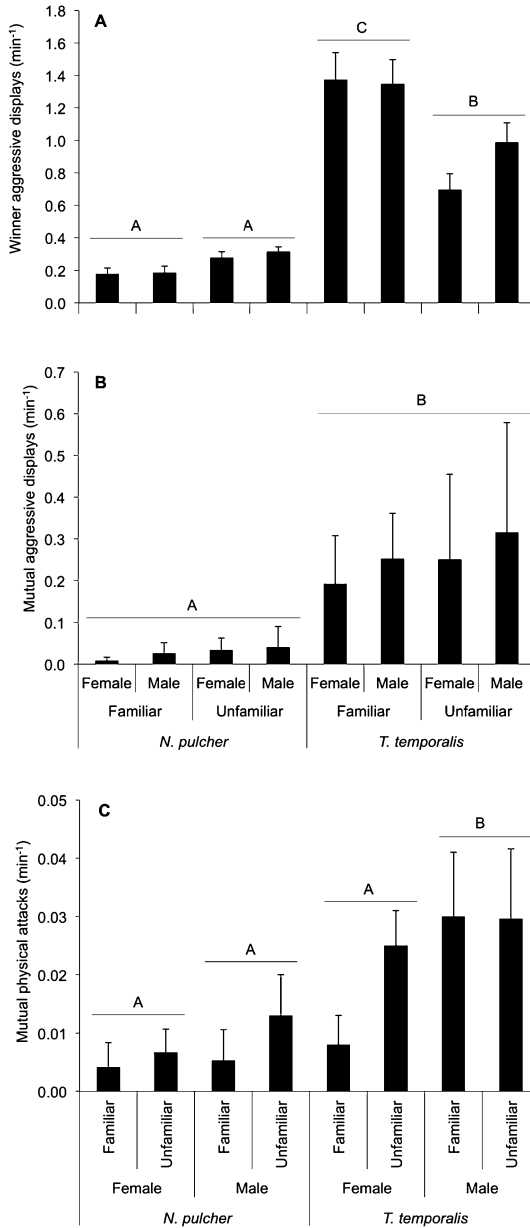
in both species), while motivation to secure a shelter would be equivalent between breeders in both species. It is also possible that contests are intensified in *T. temporalis* when these fish are presented with their first opportunity

to hold a territory. Indeed, male *T. temporalis* fights were the most costly in terms of rates of highly escalated mutual physical attacks. A valuable future endeavour would be to examine contests between pairs of established breeders, as these could reveal whether aggressive motivation, strategy or tactics differ across life history stages in each species.

4.2. Differences in conflict resolution

Within social groups, it is common to observe frequent low-intensity conflict between group members, which sets and maintains the dominance hierarchy (Dugatkin, 1997, 2001; Clutton-Brock et al., 2009; Ang & Manica, 2010; Wong & Balshine, 2011b; Dey et al., 2013). For the highly social, cooperatively breeding cichlid *N. pulcher*, minimized contest costs and enhanced use of contest resolution mechanisms likely promote the formation, maintenance and stability of a hierarchical social structure. A previous study (Hert, 1984) showed that *N. pulcher* breeders were able to distinguish their own familiar helpers from unknown individuals of the same size, and act more aggressively towards the unknown strangers. Furthermore, subordinate individuals show a preference for joining familiar over unfamiliar groups (Jordan et al., 2010b). Finally, studies (Balshine-Earn & Lotem, 1998; Frostman & Sherman, 2004) have found that *N. pulcher* males direct more aggressive behaviour toward unfamiliar neighbours than towards familiar neighbours, showing discrimination both within the social group and with known neighbours. In the current study, we found that female *N. pulcher* discriminated between familiar and unfamiliar contestants and were more likely to use submissive displays to end contests rather than flee. We predicted that female *N. pulcher* would display greater social discrimination than would male *N. pulcher*, or *T. temporalis* of either sex because of male-biased dispersal in *N. pulcher* (Stiver et al., 2006; Wong & Balshine, 2011a). No sex differences were observed in *N. pulcher* contests between unfamiliar rivals, consistent with the results of previous studies (Reddon et al., 2011, 2012,

Figure 2. Aggressive contest behaviour measured in male and female, familiar and unfamiliar, pairs of *Neolamprologus pulcher* (a highly social cichlid) and *Telmatochromis temporalis* (a non-social cichlid). *N. pulcher* displayed significantly fewer (A) aggressive displays from the winning fish, and performed significantly fewer (B) mutually aggressive displays. Male *T. temporalis* pairs displayed the highest rates of (C) highly escalated mutual overt physical attacks. Different letters indicate statistically significant differences among groups (ANOVAs with Tukey's HSD post-hoc tests, $\alpha = 0.05$).
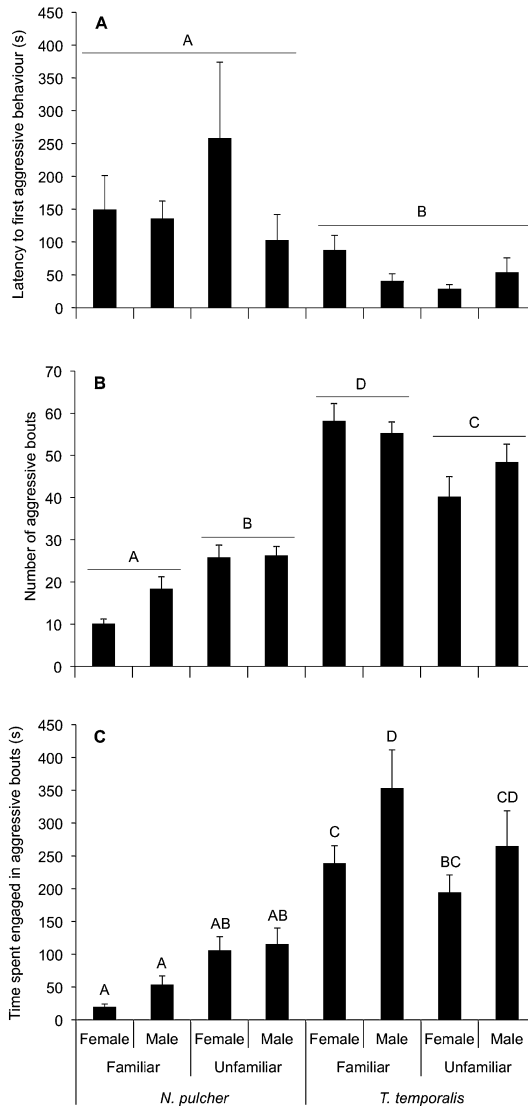
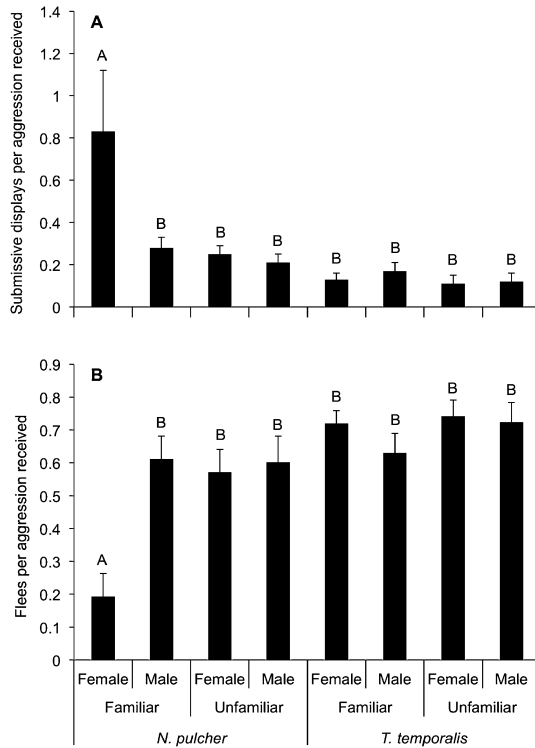**Figure 3.** Metrics of aggressive contest duration measured in male and female, familiar and unfamiliar, pairs of *Neolamprologus pulcher* (a highly social cichlid) and *Telmatochromis temporalis* (a non-social cichlid). *N. pulcher* were (A) slower to initiate contests, had (B) fewer aggressive bouts during contests and (C) spent less time engaged in aggressive bouts, with familiar female *N. pulcher* spending the least amount of time engaged in aggressive bouts. Different letters indicate statistically significant differences among groups (ANOVAs with Tukey's HSD post-hoc tests, $\alpha = 0.05$).

Figure 4. Contest resolution behaviour measured in male and female, familiar and unfamiliar, pairs of *Neolamprologus pulcher* (a highly social cichlid) and *Telmatochromis temporalis* (a non-social cichlid). Familiar female *N. pulcher* were (A) most likely to use submissive displays to end an antagonistic interaction and (B) least likely to flee from conflict. Different letters indicate statistically significant differences among groups (ANOVAs with Tukey's HSD post-hoc tests, $\alpha = 0.05$).

2013). However, pairs of familiar female *N. pulcher* typically ended the contest by repeated submission from the losing fish, while unfamiliar female *N. pulcher* typically fled from the aggressive encounter. For a female *N. pulcher*, remaining in the group territory and maintaining access to the group shelter system is paramount for survival and therefore submitting rather than fleeing may be the preferred way to terminate a conflict. For a highly social, cooperatively breeding species, it is important to not only minimize conflicts with other group members, but also to avoid eviction from the group's joint territory and shelter system (Aureli et al., 2002; Wong et al., 2008; Rubenstein & Kealy, 2010; Wong & Balshine, 2011a). *N. pulcher* appear to have evolved strategies to resolve conflicts that permit losers to remain within the same

spatial area as their competitors. It has been argued that in *N. pulcher*, submissive behaviours serve as appeasement signals that reduce aggression from more dominant group members (Bergmüller & Taborsky, 2005), and promote stability within the group by increasing dominant tolerance of subordinates within the same spatial area. In contrast, the non-social *T. temporalis* and unfamiliar *N. pulcher* typically ended the contest by fleeing, resolving conflicts by leaving the spatial area occupied by a more formidable individual. Submissive displays are likely to be less important for *T. temporalis*, given that these fish typically live on a separate territory away from conspecifics other than their mate. The most common aggressive interactions for *N. pulcher* will be with other group members, while for *T. temporalis*, most aggression is likely to occur with neighbours and other intruders, and these conflicts are best resolved by spatial segregation. The evolution of a sophisticated submission communication system may facilitate social tolerance and form part of the foundation of group living.

4.3. Conclusion

Our results demonstrate that species with contrasting social systems differ in their contest behaviour and tendency to display social discrimination. Individuals of a highly social species showed less aggression relative to a less-social cichlid species. Moreover, females who are permanent group residents showed the greatest discrimination between familiar and unfamiliar individuals, displaying more conflict resolution behaviour with familiar partners. The tactical use of conflict resolution mechanisms and differential treatment of familiar versus unfamiliar individuals appear to represent key behavioural innovations associated with the evolution of complex sociality.

References

Ang, T.Z. & Manica, A. (2010). Aggression, segregation and stability in a dominance hierarchy. — Proc. Roy. Soc. Lond. B: Biol. Sci. 277: 1337-1343.

Archer, J. (1988). The behavioural biology of aggression. — Cambridge University Press, Cambridge.

Arnott, G. & Elwood, R.W. (2008). Information gathering and decision making about resource value in animal contests. — Anim. Behav. 76: 529-542.

Arnott, G. & Elwood, R.W. (2009). Assessment of fighting ability in animal contests. — Anim. Behav. 77: 991-1004.

Aureli, F. (1997). Post-conflict anxiety in nonhuman primates: the mediating role of emotion in conflict resolution. — Aggr. Behav. 23: 315-328.

Aureli, F., Cords, M. & Van Schaik, C.P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. — Anim. Behav. 64: 325-343.

Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M. & Werner, N. (2001). Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). — Behav. Ecol. Sociobiol. 50: 134-140.

Balshine-Earn, S. & Lotem, A. (1998). Individual recognition in a cooperatively breeding cichlid: evidence from video playback experiments. — Behaviour 135: 369-386.

Balshine-Earn, S., Neat, F.C., Reid, H. & Taborsky, M. (1998). Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. — Behav. Ecol. 9: 432-438.

Bergmüller, R. & Taborsky, M. (2005). Experimental manipulation of helping in a cooperative breeder: helpers 'pay to stay' by pre-emptive appeasement. — Anim. Behav. 69: 19-28.

Brichard, P. (1989). Cichlids and all the other fishes of Lake Tanganyika. — THF Publications, Neptune City, NJ.

Brick, O. (1998). Fighting behaviour, vigilance and predation risk in the cichlid fish *Nannacara anomala*. — Anim. Behav. 56: 309-317.

Briffa, M. & Elwood, R.W. (2004). Use of energy reserves in fighting hermit crabs. — Proc. Roy. Soc. Lond. B: Biol. Sci. 271: 373-379.

Briffa, M. & Elwood, R.W. (2010). Repeated measures analysis of contests and other dyadic interactions: problems of semantics, not statistical validity. — Anim. Behav. 80: 583-588.

Briffa, M. & Sneddon, L. (2010). Contest behavior. — In: Evolutionary behavioral ecology (Westneat, D.F. & Fox, C.W., eds). Oxford University Press, Oxford, p. 246-265.

Cant, M., Llop, J.B. & Field, J. (2006). Individual variation in social aggression and the probability of inheritance: theory and a field test. — Am. Nat. 167: 837-852.

Castro, N., Ros, A.F.H., Becker, K. & Oliveira, R.F. (2006). Metabolic costs of aggressive behaviour in the Siamese fighting fish, *Betta splendens*. — Aggr. Behav. 32: 474-480.

Clutton-Brock, T., West, S., Ratnieks, F. & Foley, R. (2009). The evolution of society. — Phil. Trans. Roy. Soc. B 364: 3127-3133.

Copeland, D.L., Levay, B., Sivaraman, B., Beebe-Fugloni, C. & Earley, R.L. (2011). Metabolic costs of fighting are driven by contest performance in male convict cichlid fish. — Anim. Behav. 82: 271-280.

Day, J.J., Santini, S. & Garcia-Moreno, J. (2007). Phylogenetic relationships of the Lake Tanganyika cichlid tribe Lamprologini: the story from mitochondrial DNA. — Mol. Phylogenet. Evol. 45: 629-642.

Desjardins, J.K., Hazelden, M.R., Van der Kraak, G. & Balshine, S. (2005). Males and females provide support for the 'Challenge Hypothesis': steroid hormones and territoriality in a cooperatively breeding cichlid fish. — Behav. Ecol. 17: 149-154.

Desjardins, J.K., Hofmann, H.A. & Fernald, R.D. (2012). Social context influences aggressive and courtship behavior in a cichlid fish. — PloS ONE 7: e32781.

D'Ettorre, P. & Heinze, J. (2005). Individual recognition in ant queens. — Curr. Biol. 15: 2170-2174.

Dey, C.J., Reddon, A.R., O'Connor, C.M. & Balshine, S. (2013). Network structure is related to social conflict in a cooperatively breeding fish. — Anim. Behav. 85: 395-402.

Dierkes, P., Heg, D., Taborsky, M., Skubic, E. & Achmann, R. (2005). Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. — Ecol. Lett. 8: 968-975.

Drews, C. (1993). The concept and definition of dominance in animal behaviour. — Behaviour 125: 283-313.

Dugatkin, L.A. (1997). Winner and loser effects and the structure of dominance hierarchies. — Behav. Ecol. 8: 583-587.

Dugatkin, L.A. (2001). Bystander effects and the structure of dominance hierarchies. — Behav. Ecol. 12: 348-352.

Earley, R.L. & Dugatkin, L.A. (2010). Behavior in groups. — In: Evolutionary behavioral ecology (Westneat, D.F. & Fox, C.W., eds). Oxford University Press, Oxford, p. 285-307.

Elwood, R.W. & Arnott, G. (2012). Understanding how animals fight with Lloyd Morgan's canon. — Anim. Behav. 84: 1095-1102.

Enquist, M. & Leimar, O. (1983). Evolution of fighting behaviour: decision rules and assessment of relative strength. — J. Theor. Biol. 102: 387-410.

Enquist, M. & Leimar, O. (1990). The evolution of fatal fighting. — Anim. Behav. 39: 1-9.

Frostman, P. & Sherman, P. (2004). Behavioral response to familiar and unfamiliar neighbors in a territorial cichlid, *Neolamprologus pulcher*. — Ichthyol. Res. 51: 283-285.

Grosenick, L., Clement, T.S. & Fernald, R.D. (2007). Fish can infer social rank by observation alone. — Nature 445: 429-432.

Heg, D. & Bachar, Z. (2006). Cooperative breeding in the Lake Tanganyika cichlid *Julidochromis ornatus*. — Environ. Biol. Fish 76: 265-281.

Hert, E. (1984). Individual recognition of helpers by the breeders in the cichlid fish Lamprologus-Brichardi (Poll, 1974). — J. Comp. Ethol. 68: 313-325.

Hsu, Y., Earley, R.L. & Wolf, L.L. (2006). Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. — Biol. Rev. 81: 33-74.

Huntingford, F.A. & Turner, A.K. (1987). Animal conflict. — Chapman & Hall, London.

Hurd, P.L. (1997). Cooperative signaling between opponents in fish fights. — Anim. Behav. 54: 1309-1315.

Jakobsson, S., Brick, O. & Kullberg, C. (1995). Escalated fighting behaviour incurs increased predation risk. — Anim. Behav. 49: 235-238.

Johnstone, R.A. (1997). Recognition and the evolution of distinctive signatures: when does it pay to reveal identify? — Proc. Roy. Soc. Lond. B: Biol. Sci. 264: 1547-1553.

Jordan, L.A., Avolio, C., Herbert-Read, J.E., Krause, J., Rubenstein, D.I. & Ward, A.J.W. (2010a). Group structure in a restricted entry system is mediated by both resident and joiner preferences. — Behav. Ecol. Sociobiol. 64: 1099-1106.

Jordan, L.A., Wong, M.Y.L. & Balshine, S. (2010b). The effects of familiarity and social hierarchy on group membership decisions in a social fish. — Biol. Lett. 6: 301-303.

Kemp, D.J. & Wiklund, C. (2001). Fighting without weaponry: a review of male–male contest competition in butterflies. — Behav. Ecol. Sociobiol. 49: 429-442.

Konings, A. (1998). Cichlids in their natural habitat. — Cichlid Press, El Paso, TX.

Koops, M. & Grant, J. (1993). Weight asymmetry and sequential assessment in convict cichlid contests. — Can. J. Zool. 71: 475-479.

Krause, J. & Ruxton, G.D. (2002). Living in groups. — Oxford University Press, New York, NY.

Kuwamura, T. (1986). Parental care and mating systems of cichlid fishes in Lake Tanganyika — a preliminary field survey. — J. Ethol. 4: 129-146.

Leiser, J.K. (2003). When are neighbours 'dear enemies' and when are they not? The responses of territorial male variegated pupfish, *Cyprinodon variegatus*, to neighbours, strangers and heterospecifics. — Anim. Behav. 65: 453-462.

Maynard-Smith, J. & Harper, D. (2003). Animal signals. — Oxford University Press, Oxford.

Mboko, S. & Kohda, M. (1999). Piracy mating by large males in a monogamous substrate-breeding cichlid in Lake Tanganyika. — J. Ethol. 17: 51-55.

Mowles, S.L., Cotton, P.A. & Briffa, M. (2010). Whole-organism performance capacity predicts resource-holding potential in the hermit crab *Pagurus bernhardus*. — Anim. Behav. 80: 277-282.

Neat, F.C., Taylor, A.C. & Huntingford, F.A. (1998a). Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. — Anim. Behav. 55: 875-882.

Neat, F.C., Huntingford, F.A. & Beveridge, M.M.C. (1998b). Fighting and assessment in male cichlid fish: the effects of asymmetries in gonadal state and body size. — Anim. Behav. 55: 883-891.

O'Connor, C.M., Rodela, T.M., Mileva, V.R., Balshine, S. & Gilmour, K.M. (2013). Corticosteroid receptor gene expression is related to sex and social behaviour in a social fish. — Comp. Biochem. Physiol. A 164: 438-446.

Parker, G.A. (1974). Assessment strategy and the evolution of fighting behaviour. — J. Theor. Biol. 47: 223-243.

Parker, G.A. & Rubenstein, D.I. (1981). Role assessment, reserve strategy and acquisition of information in asymmetric animal conflicts. — Anim. Behav. 29: 221-240.

Peake, T.M. & McGregor, P.K. (2004). Information and aggression in fishes. — Learn. Behav. 32: 114-121.

Qualls, C. & Jaeger, R. (1991). Dear enemy recognition in *Anolis carolinenis*. — J. Herpetol. 25: 361-363.

R Development Core Team (2012). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, available online at: http://www.R-project.org/.

Reddon, A.R., Balk, D. & Balshine, S. (2013). Probing aggressive motivation during territorial contests in a group-living cichlid fish. — Behav. Proc. 92: 47-51.

Reddon, A.R. & Hurd, P.L. (2009). Differences in aggressive behavior between convict cichlid color morphs: amelanistic convicts lose even with a size advantage. — Acta Ethol. 12: 49-53.

Reddon, A.R., Voisin, M.R., Menon, N., Marsh-Rollo, S.E., Wong, M.Y.L. & Balshine, S. (2011). Rules of engagement for resource contests in a social fish. — Anim. Behav. 82: 93-99.

Reddon, A.R., O'Connor, C.M., Marsh-Rollo, S.E. & Balshine, S. (2012). Effects of isotocin on social responses in a cooperatively breeding fish. — Anim. Behav. 84: 753-760.

Riechert, S.E. (2013). Maynard Smith & Parker's (1976) rule book for animal contests, mostly. — Anim. Behav. 86: 3-9.

Rubenstein, D.R. & Kealy, J. (2010). Cooperation, conflict, and the evolution of complex animal societies. — Nature Educ. Knowl. 1: 47.

Sapolsky, R.M. (2005). The influence of social hierarchy on primate health. — Science 308: 648-652.

Sopinka, N.M., Fitzpatrick, J.L., Desjardins, J.K., Stiver, K.A., Marsh-Rollo, S.E. & Balshine, S. (2009). Liver size reveals social status in the African cichlid *Neolamprologus pulcher*. — J. Fish Biol. 75: 1-16.

Stiver, K.A., Dierkes, P., Taborsky, M. & Balshine, S. (2004). Dispersal patterns and status change in a cooperatively breeding fish: evidence from microsatellite analyses and behavioural observations. — J. Fish Biol. 65: 91-105.

Stiver, K.A., Fitzpatrick, J.L., Desjardins, J.K. & Balshine, S. (2006). Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. — Anim. Behav. 71: 449-456.

Taborsky, M. (1984). Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. — Anim. Behav. 32: 1236-1252.

Taborsky, M. & Limberger, D. (1981). Helpers in fish. — Behav. Ecol. Sociobiol. 8: 143-145.

Taves, M.D., Desjardins, J.K., Mishra, S. & Balshine, S. (2009). Androgens and dominance: sex-specific patterns in a highly social fish (*Neolamprologus pulcher*). — Gen. Comp. Endocrinol. 161: 202-207.

Taylor, P.W. & Elwood, R.W. (2003). The mismeasure of animal contests. — Anim. Behav. 65: 1195-1202.

Temeles, E.J. (1994). The role of neighbors in territorial systems — when are they dear enemies. — Anim. Behav. 47: 339-350.

Tierney, A.J., Andrews, K., Happer, K.R. & White, M.K.M. (2013). Dear enemies and nasty neighbors in crayfish: effects of social status and sex on responses to familiar and unfamiliar conspecifics. — Behav. Proc. 99: 47-51.

Umbers, K.D.L., Tatarnic, N.J., Holwell, G.I. & Herberstein, M.E. (2012). Ferocious fighting between male grasshoppers. — PloS ONE 7: e49600.

Wilson, E.O. (1975). Sociobiology: the new synthesis. — Harvard University Press, Cambridge, MA.

Wong, M.Y.L. & Balshine, S. (2011a). The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher*. — Biol. Rev. 86: 511-530.

Wong, M.Y.L. & Balshine, S. (2011b). Fight for your breeding right: hierarchy re-establishment predicts aggression in a social queue. — Biol. Lett. 7: 190-193.

Wong, M.Y.L., Munday, P.L., Buston, P.M. & Jones, G.P. (2008). Fasting or feasting in a fish social hierarchy. — Curr. Biol. 18: 372-373.