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Cooperative signalling between opponents in fish fights

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Abstract. Cichlids of the species *Nannacara anomala* employ several colour displays during fights which do not seem to signal either fighting ability or motivation. How should these colour displays be interpreted when winning is reliably predicted by weight asymmetries? Medial Line colour displays were associated with, and predicted, tail-beating, while Vertical Bar colour displays were associated with mouth-wrestling. I suggest that these colour displays are used to facilitate the transmission of assessment information within a fight, and that they are an example of cooperative signalling between opponents. The results support the idea that the structure of fights contains strong cooperative aspects.

Winning access to resources is ultimately determined by the ability to inflict costs on other competitors. Individuals fighting over a resource have opposing interests with respect to that resource, but may share a far larger common interest in avoiding injury (Geist 1974; Enquist & Leimar 1990). Theoretical treatments (Leimar & Enquist 1988; Enquist et al. 1990) of animal fights as a cooperative effort to determine who would win an all-out fight, were one to take place, are well supported by empirical data (Enquist et al. 1990; Leimar et al. 1991; Keeley & Grant 1993; Koops & Grant 1993). When the contestants are comparably motivated, the winner is the individual capable of inflicting the greater cost upon the opponent. It is easy to conclude mistakenly that behaviours that reduce contest costs to the mutual benefit of the contestants would not be evolutionarily stable.

Size is usually the decisive factor in cichlid fights: winners may be reliably predicted by weight asymmetries as small as 2% (Barlow et al. 1986; Enquist & Jakobsson 1986). Virtually all the agonistic displays and behaviours of these species have the potential to provide receivers with information about the signaller's weight (Baerends & Baerends-van Roon 1950; Enquist et al. 1990; Beeching 1992; Keeley & Grant 1993). These behaviours are all performance displays, signals that individuals differ in their ability to perform. Performance signalling has also been termed unambiguous signalling (Maynard Smith 1982), assessment signalling (Maynard Smith & Harper 1988) and revealing handicaps (Grafen 1990).

Examples of performance displays used by the cichlid *Nannacara anomala* are lateral displays, tail-beating and mouth-wrestling. A lateral display, in which a fish poses side-on to its opponent, is unbluffable. Although all fish may attempt to look as large as possible, small fish will look smaller than large fish. Such visual assessment is known to be used during the early stages of cichlid fights (Enquist et al. 1987; Beeching 1992). While tail-beating, a fish directs a jet of water towards its opponent, the force of which provides tactile cues as to the fish's weight (Baerends & Baerends-van Roon 1950; Jakobsson et al. 1979; Enquist et al. 1990; Keeley & Grant 1993). A small or weak fish is physically incapable of generating as much force as a large fish. Mouth-wrestling fish lock jaws and attempt to push each other backwards (Baerends & Baerends-van Roon 1950; Jakobsson et al. 1979; Enquist et al. 1990); smaller fish cannot indicate any strength they choose, but will be constrained to signal their weaker state by pushing with less force than a larger fish can.

In direct contrast to performance displays are those signals that all individuals are capable of making. Such signals may cost different amounts for different individuals to employ (e.g. handicapped signals, Grafen 1990), but their use is an

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option available to all individuals, and so are in principle 'cheatable' displays. *Nannacara anomala* employ several colour displays during fights which appear to be of this type. The use of such cheatable signals in aggressive interactions has always seemed problematic (Dawkins & Krebs 1978; Caryl 1979; Hinde 1981; Maynard Smith 1982). If contestants with greatly conflicting interests have the option of exaggerating their motivation or their intentions to escalate, it would appear that they ought to do so to the maximum possible degree.

As in most cichlids, *N. anomala* fights escalate through phases in which different behaviours are used (Baerends & Baerends-van Roon 1950; Jakobsson et al. 1979; Barlow et al. 1986; Koops & Grant 1993). Theory suggests that more escalated behaviours impart more accurate information, but at a higher cost (Enquist et al. 1985; Leimar & Enquist 1988). In *N. anomala*, escalation proceeds through the phases lateral display, tail-beating, mouth-wrestling and circling (Enquist & Jakobsson 1986; Enquist et al. 1990). While these agonistic behaviours have been well studied, the colour signals used in these interactions have received much less attention.

The use of colour displays to indicate a generally aggressive state has been noted in several species of fish (Barlow 1963; De Boer 1980; Muske & Fernald 1987; Dawkins & Guilford 1993; Beeching 1995). Vertical Bars are associated with aggressive behaviour in several species of cichlid (Baerends & Baerends-van Roon 1950; Hulscher-Emeis 1991, 1992; Nelissen 1991), and swordtails (Zimmerer & Kallman 1988; Morris et al. 1995), but is apparently a submissive signal in at least one species of cichlid (Beeching 1995). Many authors of descriptive studies have concluded that Longitudinal Lines signal escape and Vertical Bars signal attack (see Hulscher-Emeis 1992 for a review). Hulscher-Emeis (1992) found no strict relationship between any colour pattern and either attack or escape in *Tilapia zillii*. There was, however, a correlation between Vertical Bar intensity and the act of chasing an intruding male (Hulscher-Emeis 1992) and mouth-wrestling (Hulscher-Emeis 1991).

I reanalysed videotaped *N. anomala* fights to test the hypothesis that colour signals are used to coordinate assessment signals within fights. Changes in colour displays should be associated with, and predict, performance signals.

METHODS

I obtained all the data used in this study by reanalysing fights originally recorded on videotape and used by Enquist et al. (1990). I used 20 fights (40 fish) in which the lighting quality was sufficiently good to allow analysis of colour displays throughout the interaction.

I identified two distinct transient colour displays for analysis; Medial Line and Vertical Bar (Fig. 1). The Medial Line display consists of a black line running along the length of the fish. A wider white line runs above the black line when the dark line is most fully expressed. The Vertical Bar display consists of a number of dark vertical lines between the pectoral fin and tail, most heavily expressed towards the tail. I used a third category 'None' to categorize all other colour displays. When the colour of a fish could not be determined, usually because it was behind its opponent, or was backlit, I classified the colour as 'unknown'. I scored the following gross behaviours: tail-beat, mouth-wrestle, mouth-wrestling attempt (a mouth-to-mouth grip that was not subsequently used in a wrestling bout) and bite. When a fish performed a tail-beat it was said to have 'sent' a tail-beat, and the other fish was said to have 'received' it.

I considered interactions to start when both fish had raised their dorsal fins and had bright eye colour, or had approached each other and used an aggressive display. I considered them to end when one fish lowered its dorsal fin, turned pale and fled from its opponent. I measured the length of tail-beating phases from the start of the interaction to the beginning of the first mouth-wrestling bout. The mouth-wrestling phase was defined as everything that followed the first mouth-wrestle.

RESULTS

Figure 2 shows behaviours and colour displays used during a typical fight. At first glance it appears that Medial Line display is associated with tail-beating, and Vertical Bar display is associated with mouth-wrestling. I now test and examine these relationships.

Medial Lines and Tail-beating

I observed 109 Medial Line displays (each fish performing from 0 to 12) with a median duration

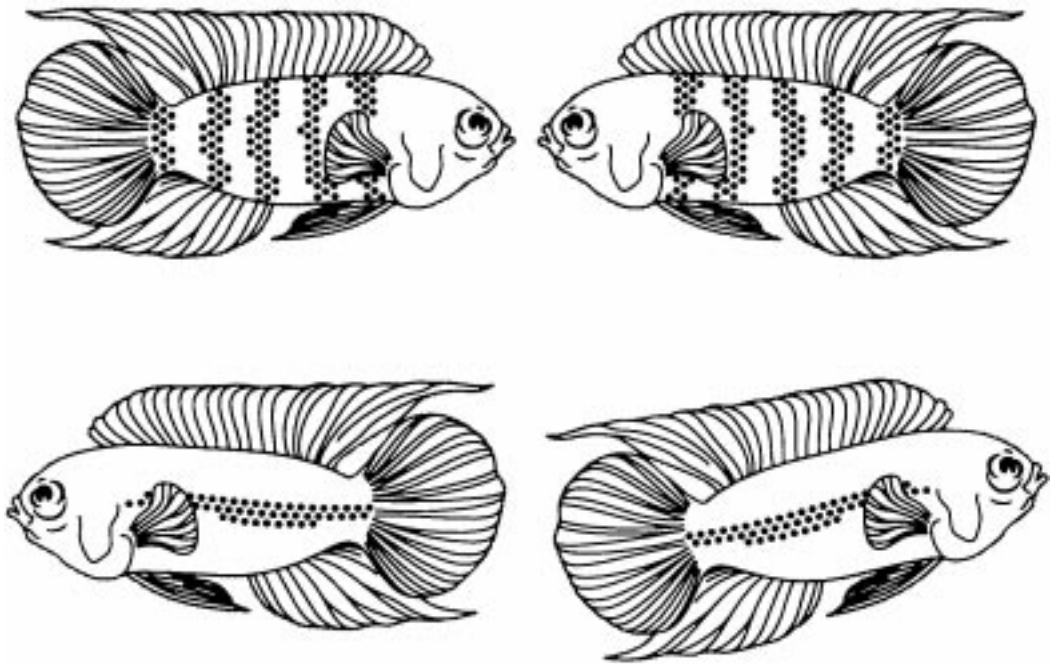

Figure 1. The colour displays of *Nannacara anomala*. The upper pair of fish are showing the Vertical Bar display, and the lower pair the Medial Line display.

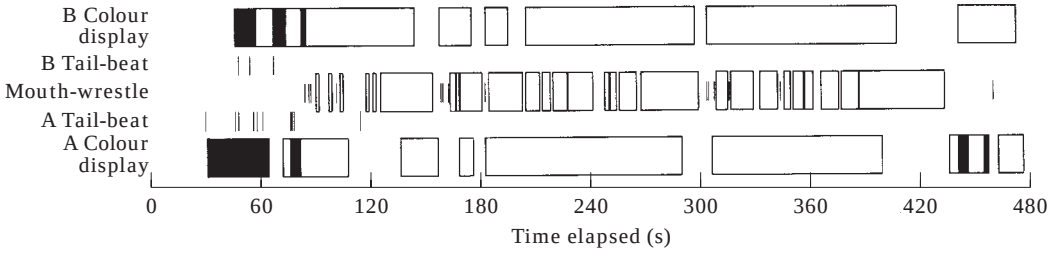

Figure 2. The structure of a typical *Nannacara anomala* fight. The colour displays, tail-beats, mouth-wrestling bouts and mouth-wrestling attempts are shown for a typical fight (fight no. 1). The onset and duration of colour displays for fish A and B are marked in the 'A Colour display' and 'B Colour display' rows, respectively. □: Vertical Bar displays; ■: Medial Line displays. Boxes in the 'mouth-wrestle' row denote the onset and duration of mouth-wrestling bouts, vertical dashes in that row denote mouth-wrestling attempts (contact that did not go on to mouth-wrestling). Vertical lines in the tail-beating rows denote the occurrence of tail-beats.

of 16 s (range 2–299 s). There was no correlation between body weight and total time spent showing Medial Lines ($r = -0.13$, $N = 40$, NS). Winners and losers did not differ in the total time they spent displaying Medial Lines (Wilcoxon signed-ranks test: $T = 67$, $N = 19$, NS), although winners tended to show them less than losers. Within the tail-beating phase, tail-beating rates were higher when the sender was displaying a Medial Line, for both eventual winners and losers (both $P < 0.05$, sign test on 15 of 20 fights; Table I).

I tested whether tail-beats that occurred when only one of the two fish was showing a Medial Line were sent more than received by the fish showing the Medial Line. If the probabilities of both Medial Lines and tail-beats increase during the tail-beating phase because of some underlying third factor, then tail-beats should be sent as often

Table I. Rates of tail-beats (no./s) sent in relation to colour display of sender

Fight	Winners				Losers			
	Medial Line display		All other colour displays		Medial Line display		All other colour displays	
1	0.21	(8/38)	0.04	(1/26)	0.16	(3/26)	0	(0/38)
2	0.16	(9/56)	0	(0/45)	0.16	(8/49)	0	(0/52)
3	0.02	(5/220)	0.01	(1/200)	0.03	(9/345)	0	(0/75)
4	0.06	(7/115)	0	(0/18)	0.19	(20/105)	0	(0/28)
5	0.06	(4/65)	0.09	(4/45)	0.08	(5/64)	0	(0/46)
6	0.12	(10/82)	0	(0/41)	0.12	(3/25)	0.03	(3/98)
7	0.57	(4/7)	0.02	(4/199)	0.08	(8/92)	0.01	(1/114)
8	0.04	(3/83)	0.03	(5/175)	0.05	(9/193)	0	(0/65)
9	0	(0/0)	0.06	(3/52)	0.11	(2/19)	0.03	(1/33)
10	0	(0/0)	0.02	(6/304)	0.17	(15/90)	0.03	(6/214)
11	0	(0/11)	0.07	(4/59)	0.11	(6/53)	0.06	(1/17)
12	0.06	(2/35)	0.02	(3/134)	0	(0/0)	0.05	(8/169)
13	0.19	(29/153)	0.01	(2/217)	0.07	(8/114)	0.01	(3/256)
14	0.18	(6/33)	0.13	(4/30)	0.11	(1/9)	0.09	(5/54)
15	0.03	(2/77)	0.01	(1/69)	0	(0/0)	0.02	(3/146)
16	0.23	(16/70)	0	(0/18)	0	(0/0)	0.03	(3/88)
17	0.11	(2/19)	0	(0/79)	0.03	(1/31)	0	(0/67)
18	0.08	(3/38)	0.06	(8/135)	0	(0/14)	0.07	(11/159)
19	0	(0/0)	0.04	(5/128)	0	(0/0)	0.02	(3/128)
20	0.36	(17/47)	0.11	(17/150)	0.10	(20/195)	0	(0/2)

Only tail-beats that occurred within the tail-beating phase are shown. The numbers in parentheses are the number of tail-beats sent in a Medial Line display/the summed duration (s) of the display.

as they are received by the individual showing the Medial Line. Tail-beats occurred more often when only the sender was showing a Medial Line than when only the receiver was; 130 and 56 times, respectively ($\chi^2_1 = 29.4$, $P < 0.001$).

Figure 3 shows the incidence of tail-beating after a switch to a Medial Line display and Table II shows the distribution of tail-beats sent with respect to the onset of the Medial Line display. Tail-beats were significantly more likely to be sent in the 5 and 10 s following the onset of the Medial Line display than in the same amount of time preceding the display onset in both winners and losers (sign tests: winners $P < 0.05$ on 11 of 12 and 10 of 12 fights, losers $P < 0.005$ on 13 of 13 and 12 of 13 fights, 5 and 10 s respectively). The Medial Line display was therefore associated with, and predicted, tail-beating, for both eventual winners and losers.

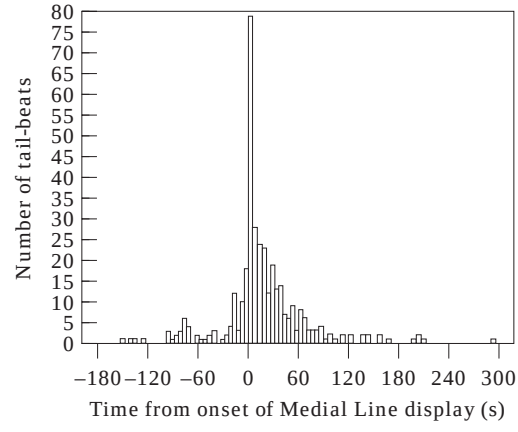

Figure 3. The elapsed time between acquisition of a Medial Line display by the sender and initiation of tail-beating. If the sender of a tail-beat was not showing a Medial Line, then the shortest time interval (forward or back) to acquisition of a Medial Line was counted, producing negative times in some instances. An additional six tail-beats with negative lag times of greater than 10 min (all from the same fish), and one positive greater than 10 min are not shown.

Vertical Bars and Mouth-wrestling

I recorded 179 Vertical Bar displays, with each fish using the display up to 21 times (median three

Table II. The number of tail-beats of winners and losers prior to and after the onset of the Medial Line display

	Winners				Losers			
	Prior		After		Prior		After	
Fight	0–10 s	0–5 s	0–5 s	0–10 s	0–10 s	0–5 s	0–5 s	0–10 s
1	1	1	3	3	0	0	2	3
2	0	0	1	3	0	0	2	2
3	0	0	0	0	0	0	2	3
4	1	1	1	1	3	1	4	7
5	0	0	0	0	0	0	3	3
6	0	0	1	1	1	0	1	3
7	0	0	4	4	0	0	2	4
8	0	0	1	1	0	0	0	0
9	0	0	0	0	1	0	1	1
10	0	0	0	0	4	4	7	10
11	0	0	0	0	1	0	3	4
12	0	0	4	4	1	1	1	3
13	0	0	6	8	1	0	2	2
14	2	2	1	1	3	1	2	2
15	0	0	1	2	0	0	0	0
16	4	4	5	5	0	0	0	0
17	2	1	1	2	0	0	0	0
18	4	1	3	3	0	0	0	0
19	0	0	0	0	0	0	0	0
20	8	5	11	19	0	0	1	3

All tail-beats occurring within 10 s of a change to Medial Line display are included, regardless of the phase of the fight in which they occurred.

times). Vertical Bar displays ranged in length from 1 to 2051 s (median 20 s). There was no correlation between body weight and total time spent showing Vertical Bars ($r = -0.09$, $N = 40$, NS). Winners and losers did not differ significantly in the total time they spent displaying Vertical Bars (Wilcoxon signed-ranks test: $T = 63$, $N = 19$, NS), although winners tended to show them less than losers. Table III shows the rate of onset of mouth-wrestling when both, one, or neither fish were showing a Vertical Bar display. I calculated rates by dividing the number of mouth-wrestle initiations by the time that Vertical Bars were displayed during the mouth-wrestle phase excluding the time spent mouth-wrestling. Mouth-wrestle initiation rates differed significantly, being higher when Vertical Bars were shown (Friedman two-way analysis of variance by rank (Siegel 1956): $\chi^2_{r2} = 15.27$, $N = 11$, $P < 0.001$).

DISCUSSION

To obtain the most accurate information from tail-beating, fish have to coordinate their actions to some degree. There will be some optimum receiver position with respect to the jet of water for the receiver to be in; a receiver 1 cm away from this position may receive no useful information at all. Obvious coordination is similarly required when mouth-wrestling to get both fish to have their mouths at the same place at the same time.

Medial Lines indeed predicted tail-beating, and Vertical Bar displays also seemed to signal readiness to engage in mouth-wrestling. This relationship was by no means absolute, however: of 405 tail-beats, 54 were sent by a fish displaying Vertical Bars, and 20 of 481 mouth-wrestles were initiated when one of the fish was displaying a Medial Line. One mouth-wrestle was initiated when both fish were showing a Medial Line.

The use of colour displays to indicate a generally aggressive state has been noted in several species of fish (Barlow 1963; De Boer 1980; Muske & Fernald 1987; Dawkins & Guilford 1993; Beeching 1995), but this seems to be the first example of a fish signalling a specific agonistic behaviour within a fight. These signals are most likely to function as alerting components

Table III. The rates of initiation of mouth-wrestling as a function of whether both, one, or neither fish was showing Vertical Bars

Fight	Vertical Bar display		
	Both	One	Neither
1	0.27	0.12	0
2	—	0.10	0.07
3	0.10	0.08	0.05
4	0.11	0.02	0
7	0.02	0.03	0
8	0.06	0.07	0.02
9	0.11	0.06	0
10	0.11	0.01	0
11	0.15	0.19	0
12	0.25	0.07	0
13	2.0	0	—
15	0.04	0	—
16	—	0.08	0
17	0.11	0.09	0.10
18	0.12	0.08	0
19	0.11	0.06	—
20	—	0.12	0.20

Rates were obtained by dividing the number of mouth-wrestle initiations by the number of seconds within the mouth-wrestling phase that both, one or neither fish were showing Vertical Bars.

(Wiley 1983) or amplifiers (Hasson 1989) to the subsequent performance signals, facilitating the transmission of assessment information.

Hulscher-Emeis (1992) suggested that such displays indicate stress. The tendency for winners to express these colour displays less, particularly the Vertical Bar display, suggests their suppression may have some competitive value. This seems to be the case in at least one other cichlid (Barlow 1983).

While weight asymmetry determines the winner of a fight, coordinating displays may decrease the costs of fighting for both contestants. Fights that make use of performance signals are expected to maximize the efficiency of these displays (Leimar & Enquist 1988; Enquist et al. 1990). *Nannacara anomala* are probably not unusual in their use of such signals; they are to be expected whenever performance signals are used.

The outcome of a fight is more than winning or losing; it also encompasses the cost paid to determine a winner. This is another example supporting the idea that fighting behaviour may contain cooperative aspects.

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