

## Consequences of hyper-aggressiveness in Siamese fighting fish: cheaters seldom prospered

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**Abstract.** Zahavi's handicap theory, formalized by Grafen, suggests that 'cheaters' must be at a disadvantage if a communication system such as ritualized aggression is to evolve (Grafen 1991, In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 5–31. Oxford: Blackwell Scientific). To determine whether cheating is disadvantageous in *Betta splendens*, we held a series of live interactions, after inducing hyper-aggression by socially isolating and then briefly 'priming' the fish. Primed isolates, which were no stronger than their rivals, 'cheated' by escalating rapidly to tailbeating and biting. These cheaters, however, usually lost fights to non-isolated opponents. Unprimed isolates, i.e. socially isolated fish that were not primed, were not initially hyper-aggressive and thus did not cheat. They lost fewer fights than the cheaters. Results suggested that cheaters lost because they exhausted themselves by their hyper-aggressiveness, allowing their non-hyper-aggressive opponents to win. This result is consistent with the Zahavi–Grafen model of how an 'honest' level of ritualized aggression can be stabilized in a population.

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Animals usually perform ritualized aggression at an intensity that is predictable from their resource-holding potential (e.g. Davies & Halliday 1978; Clutton-Brock & Albon 1979; Dodson 1989). Why should evolution select for the honest communication of low resource-holding potential during a fight? Why not 'cheat', by displaying more intensely than normal, and increase the odds of driving off a rival?

Zahavi (1979, 1987) theorizing about the evolutionary stability of ritualized communication systems, hypothesized that all evolved communicative signals must be costly, so that their performance 'handicaps' a signaller. This idea was formalized by Grafen (1991), who argued that a stable communication system would evolve only if cheating on the convention (i.e. displaying at an intensity typical of a stronger individual) increased the handicap associated with that particular display. This extra handicap would increase with the degree of cheating. If an escalation in the cost did not exist, a cheater could gain an advantage over honest competitors, and either a predisposition to ignoring the 'cheatable'

signal would arise, or the 'cheater' strategy would invade the population. Since stable ritualized communication systems do exist, cheating must be costly, and honesty must pay.

In many cases, it is easy to discover physical constraints that would make cheating on aggressive display conventions costly; to perform more intensely than a rival, an individual must be stronger. The Zahavi–Grafen theory suggests that the handicap principle ought to apply to all cases. Not all aggressive displays have a large energetic cost, however. Although measurements have shown that some aggressive displays do require considerable energy, others do not (Horn et al. 1995). Moreover, determining which displays are energetically expensive cannot always be based on simple physics. For example, even though the vocal apparatus of song birds is highly acoustically efficient compared to that of crowing of roosters, song birds use much more energy for singing than roosters do for crowing (Horn et al. 1995). Furthermore, the evidence on whether animals lose by cheating during ritualized fights offers little support for the Zahavi–Grafen model. Studies in which animals were selected for atypical threat intensity, or manipulated into threatening unusually strongly, showed that the

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hyper-aggressive animals tended to win their interactions. Harris sparrows, *Zonotrichia querula*, that had been painted like dominants and injected with testosterone to make them behave aggressively rose in dominance status (Rohwer & Rohwer 1978). Male blue gouramis, *Trichogaster trichopterus*, that were classically conditioned to display aggressively to a light and then were shown this light at the start of an interaction, began the encounter already displaying and tended to win (Hollis 1984). This result seems consistent with the earlier conclusion of Barlow et al. (1986) that Midas cichlids, *Cichlasoma citrinellum*, win fights partly by prowess but partly by daring. Furthermore, defenceless, recently moulted stomatopods, *Gonodactylus bredini*, can often drive off hard-shelled opponents by performing a standard meral spread threat display (Adams & Caldwell 1990). Moreover, fighting animals often match each other's displays, so it is often difficult to predict the winner from behaviour performed at the beginning of a contest. This difficulty could be taken as evidence that animals bluff at least sometimes (Ribowski & Franck 1993).

Thus, experimental evidence suggests that displaying more intensely than the norm sometimes confers an advantage rather than an immediate disadvantage. This evidence, however, is not strong enough to reject the Zahavi-Grafen model. These experiments were not designed to test the Zahavi-Grafen model directly, and some had possible confounds or small sample sizes. In the present study, we wanted to determine in our test species, *Betta splendens*, whether hyper-aggressive individuals win their fights.

Halperin et al. (1992) developed a non-intrusive manipulation to create hyper-aggressive 'cheaters' as well as controls that were similar but not hyper-aggressive. The method of recalibrating ritualized aggressive behaviour was as follows. Fish were first socially isolated. Social isolation makes *Betta* unresponsive to the first social stimuli they see (Halperin et al. 1992; see also Heiligenberg 1974). Socially isolated, attack-depressed *Betta* become hyper-aggressive, however, after being presented with social stimuli for several minutes (Halperin et al. 1992). A little-understood process associated with seeing aggression-relevant social stimuli lifts the transient unresponsiveness and moves the fish into a hyper-aggressive phase. We call this process 'priming'.

Thus, unprimed isolated fish are not hyper-aggressive, but primed isolates are. Since the fish's true resource-holding potential is unlikely to have been altered by a few minutes of priming, the hyper-aggressiveness of the primed isolates can be called 'cheating'. The unprimed isolate fish do not 'cheat' because they have not entered the hyper-aggressive phase when their fights begin. Fish that are only minimally primed can therefore serve as controls for the effects of social isolation per se. We call them unprimed isolates, although the fish we used, as described below, received a brief priming to lift them from the phase of extremely depressed attack readiness. We could therefore determine whether the primed isolate 'cheaters' lost more fights than did the non-cheating unprimed isolates, as predicted by the Zahavi-Grafen model.

## METHODS

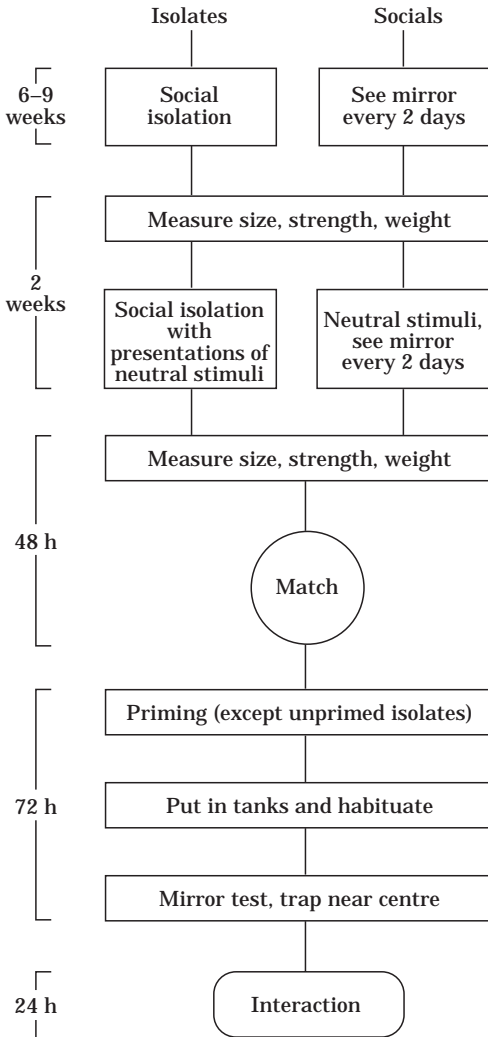
### Subjects and Housing

We obtained 262 adult male *B. splendens* from a local wholesaler. Of these, 49 well-matched pairs were eventually used in live interactions. Each fish was housed in a 2-litre jar of water and maintained on a 12:12 h light:dark cycle at 25–27°C. Sheets of white paper placed between jars reduced internal reflections and prevented the fish from viewing their neighbours. Fish were fed TetraMin flake food, *Daphnia pulex*, and live, brown *Tubifex* sp.

### Grouping and Isolation

We measured the distance between the mouth and the base of the tail on each fish (standard length; Hubbs & Lagler 1958) and the longest distance between dorsal and ventral body surfaces. These were multiplied to give a size score. We divided the fish into two groups, matched for size. Half the fish in each group were red, and the other half were blue. One group was socially isolated; fish in the other group (socials) occasionally saw social stimuli under conditions described below (Fig. 1).

Isolates received no social stimuli for 6–9 weeks. They saw no red or blue objects during this isolation period, since these colours are found in aggression-releasing stimuli. Sensory deprivation



**Figure 1.** Flow diagram of isolation and test procedures. Time line on left indicates time required for each step.

was prevented by showing the fish neutral objects, such as strips of paper blown by a fan, by occasionally giving them live food, and by letting them see their care-givers during daily feeding and occasional jar cleaning (Halperin et al. 1992). We kept socials in the same room, under identical conditions, except that they were shown a mirror for 2 min at a random time every second day. These brief presentations simulated social contact while minimizing the difference between socials and isolates.

### Controlled Stimulation and Matching

Following the initial isolation versus social contact period, we selected a set of 12 fish, consisting of the six isolates and six socials that would be tested 3 weeks later. We chose fish of approximately equal size using the measurements taken at the beginning of the experiment. We measured these fish carefully and weighed them on a Sartorius electronic scale. An unspecified combination of physical strength, strength of motivation and tolerance of disturbance was tested by measuring the cumulative distance they swam against a 4 cm/s current in 1 min. Although this current speed was slow, it was adequate to differentiate performance levels. For simplicity, we refer to this measure of performance as 'strength'.

For the following 2 weeks, these fish were maintained as before, except that we added a standardized regime of stimulation to prevent further sensory deprivation and to habituate the fish thoroughly to being observed. We presented 12 neutral stimuli, in random order and at random times, twice daily, 6 days per week. Neutral stimuli ranged from 2.5 to 14 cm in height, and had only shades of brown, green, black and white. Stimuli included pieces of clear plastic hose, black plastic mesh, gastropod shells, green pieces of cardboard, white patterns on black backgrounds and black patterns on white backgrounds. These objects did not elicit aggressive displays.

At the end of the 2 weeks, we again measured this set of 12 fish carefully for size, strength and weight to determine whether there was a differential increase between groups and to provide data for matching. From these six isolates and six socials, we selected the three matched pairs that would fight the following week (four pairs were used in later runs). We always paired a red fish with a blue fish for ease of identification during the live interactions. Since fighting ability varies with colour, we balanced groups for colour, so that an equal number of red and blue fish were either socials or isolates.

We initially created three interaction types: (1) primed isolate versus social ( $N=15$ ); (2) social versus social ( $N=13$ ); and (3) primed isolate versus primed isolate ( $N=13$ ). We ran a fourth interaction type in the last 8 weeks of the experiment, unprimed isolate versus social ( $N=8$ ). We never re-used fish.

### Priming

Priming involves the presentation of stimuli that could elicit social behaviour in a responsive animal. With the exception of the unprimed isolates, each fish was primed over 2 days using mirrors, as well as models of male *Betta* that were approximately the same size as the fish. Stimuli were presented for 5 min each, except for the last *Betta* model, which was shown for only 1 min. Presentations were separated by 9-min breaks.

The first model presented on the first day was a neutral stimulus, a black plastic star. This stimulus was followed by one of the following four sets of priming stimuli, which were chosen to allow later assessment of the effectiveness of various priming-stimulus feature combinations: (1) a red male *Betta* model followed by a green plastic plant; (2) a green male *Betta* model followed by a red plastic plant; (3) a green plastic plant followed by a red male *Betta* model; (4) a red plastic plant followed by a green male *Betta* model. A mirror was the last stimulus presented on day 1.

On the second day, there were two presentations of a mirror followed by a red *Betta* model. The final priming stimulus was presented the day before interactions, when all the fish, including the unprimed isolates, saw a mirror for 3 min, as described below.

### Interactions

Live interactions were staged in large tanks ( $2.4 \times 0.45 \times 0.15$  m deep), divided in half by two removable opaque partitions. Many rocks, shells, plastic plants, plant pots and plastic 'walls' were in each half and provided hiding places for the fish. Tanks and objects were cleaned between interactions, and water was aged at least 36 h before fish were introduced to the tank.

One fish was placed in each half of a tank by an associate. The coded labels on the tanks did not indicate which group each fish came from, so investigators recording behaviour were blind as to which type of interaction they were recording.

The fish were left for 48 h to habituate to the new tanks. During this period, they were also habituated to people sitting near the tanks who were holding event recorders or manipulating the dividers. We repeatedly inserted and removed peripheral dividers 30 cm from the central divider and moved one central partition at a time, so that

each fish could habituate to the removal of the partition without viewing its opponent.

We allowed each fish, including the unprimed isolates, to display to a mirror for 3 min. This brief priming was designed to bring the unprimed isolates out of the intense depression of attack readiness that very long isolation can cause. All fish were immediately trapped within 30 cm of the central divider by clear Plexiglas peripheral dividers to ensure that the opponents would see each other soon after the removal of the central dividers. The live encounter began the next morning. Once the fish displayed aggressively and moved towards each other, we gently removed the peripheral dividers.

We allowed interactions to continue for 24 h. Although fighting in *B. splendens* typically involves bites directed towards the large flowing fins, bites are seldom directed at the body. If fighting became too intense, or if it appeared that a fish's body was bitten, we terminated the interaction. Despite the use of large tanks with plenty of cover to which a loser could withdraw, intense fighting did occur once.

We observed the first 45 min of an interaction, and thereafter for 15-min periods at 4 h and 18 h after the removal of the central divider. We also made frequent spot checks to determine whether to terminate interactions. At the end of the 24-h period, we determined a winner. A fish was considered the winner if it exclusively used a distinctly larger portion of the tank, or if its aggressive displays resulted in its opponent fleeing, turning pale, sinking to the bottom or freezing with fins closed.

### Statistics

We examined the durations of aggressive behaviours (biting, tailbeating, approaching opponents with opercula extended, and broadside posture with fins raised; Simpson 1968). To combine different types of aggressive behaviour, durations for each behaviour were initially ranked separately. We then summed these ranks and performed non-parametric statistical tests on the summed ranks (Siegel & Castellan 1988).

## RESULTS AND DISCUSSION

### Cheaters Usually Lost

The primed isolate cheaters usually lost their interactions with socials. Of the 13 social versus

primed isolate interactions with decided outcomes, 11 were won by socials (Binomial test,  $P=0.011$ ). Unprimed isolates were not significantly disadvantaged in interactions with socials, winning three of five settled encounters (Binomial test,  $P=0.50$ ). This result confirmed earlier studies (J. R. P. Halperin, unpublished data) suggesting that unprimed isolates have no clear advantage or disadvantage when encountering socials. Thus, socials were more likely to beat a primed isolate than an unprimed isolate ( $\chi^2_1=5.02$ ,  $P=0.026$ ).

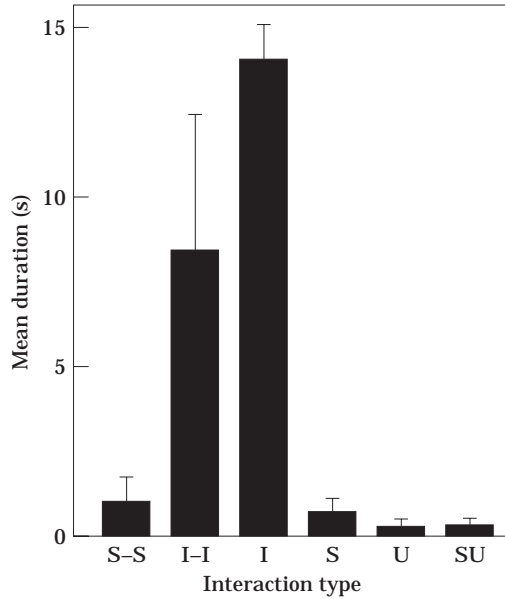
We next confirmed that the fish had behaved as planned in the experimental design, checking that cheaters did indeed cheat (i.e. that the primed isolates were hyper-aggressive). We then evaluated several alternative hypotheses that could have explained why the cheaters lost. We also provided data on the closeness of matching, since this is relevant to estimating statistical effect size.

### Cheaters Did Cheat (Primed Isolates were Hyper-Aggressive)

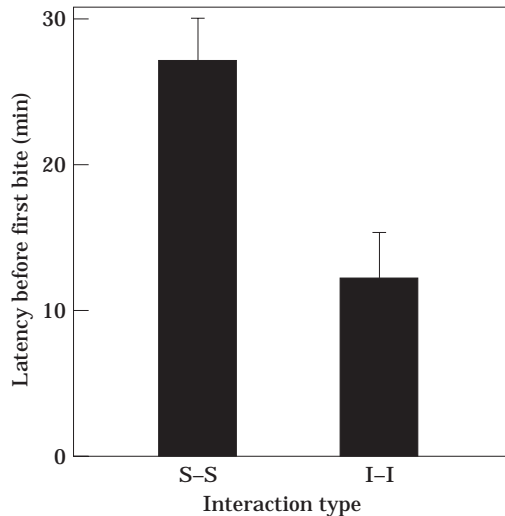
Our method of priming did induce 'cheating' in the primed isolates, meaning that they were more aggressive than would be expected. During the first 10 min of the social versus primed isolate interactions, the primed isolates spent more time tailbeating and biting than the socials did (Wilcoxon signed ranks test:  $P=0.047$ ; Fig. 2). Primed isolate versus primed isolate fish also spent more time tailbeating and biting than social versus social pairs, over the same period (Mann-Whitney  $U$ -test:  $U=137.5$ ,  $N_{1,2}=10$ ,  $P=0.006$ ). The latency to the first bite was shorter for primed isolate versus primed isolate pairs than for social versus social dyads ( $U=139$ ,  $N_{1,2}=10$ ,  $P=0.005$ ; Fig. 3). No significant difference was found between opponents in the social versus unprimed isolate interactions.

### Matching and Contests Settled

Primed isolates won only two of the 15 encounters with socials, but socials won 11, suggesting that cheating gives a fish a huge disadvantage. In assessing the magnitude of the cost paid by cheaters, however, information is necessary about how well-matched the fish were. Several lines of evidence suggest that our matching was quite good, even though pairs were always mis-matched for colour.



**Figure 2.** Mean duration of tailbeat and biting behaviours during the first 10 min of interactions. S-S=social versus social interactions; I-I=primed isolate versus primed isolate interactions; I=primed isolate of social versus primed isolate interaction; S=social of social versus primed isolate interaction; U=unprimed isolate; SU=social of social versus unprimed isolate interaction.



**Figure 3.** Latency before first bite. Legend as in Fig. 2.

Three variables allowed us to create closely matched pairs. By chance, the primed isolates were slightly larger, heavier and stronger than

**Table I.** The number of interactions with a clear winner

Interaction	<i>N</i> with clear winner	<i>N</i> with no clear winner	Total <i>N</i>	Binomial probability
Social–primed isolate	13	2	15	0.004
Primed isolate–primed isolate	7	6	13	0.500
Social–social	8	5	13	0.291
Social–unprimed isolate	5	3	8	0.363

Data include pairs for which more detailed behavioural observations were not taken.

**Table II.** Alternative hypotheses tested to determine why 'cheaters' lost

Hypothesis	Test/comparison	Was hypothesis supported?
Debilitating effect of social isolation?	Both unprimed and primed isolates were socially isolated, but primed isolates lost more often. Isolates grew as much as socials. Primed isolate dyads fought as vigorously in the first 10 min of interactions as in the last 10 min	No
Hyper-fearful?	Only one case of hiding or fleeing. Primed isolates did not reduce aggression when socials began biting.	No
Massive retaliation?	Socials versus primed isolates did not have a higher peak biting rate than social versus social fish.	No
Zahavi–Grafen hypothesis?	Primed isolates initially were hyper-aggressive and did not compensate by reducing other behaviours. Socials conserved energy at the beginning of fights. Socials retaliated moderately after primed isolates performed strength-indicating behaviours.	Yes

their social opponents, although this difference was not significant ( $F_{2,95}=0.224$ ,  $P<0.8$ ).

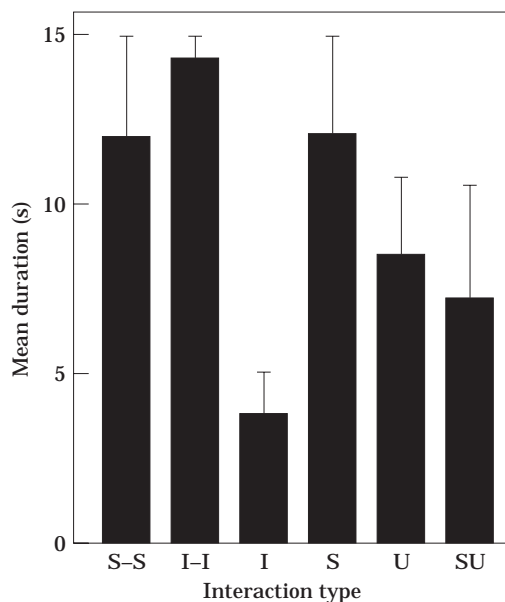
The low rate of settling dominance in the primed isolate versus primed isolate interactions and the social versus social pairs also suggests that matching was good (Table I). Enquist et al. (1990) showed that fight duration is correlated with symmetry between opponents. In fact, only six of our 13 primed isolate pairs had clear winners, as did eight of the 13 social versus social dyads and five of the eight social versus unprimed isolate interactions. In previous experiments using *Betta*, outcomes were determined fairly quickly (range of mean time to decision=29.7–78 min; Meliska & Meliska 1976; Haller 1991, 1992). Bronstein (1984) reported settling of matches within at most 6.5 h. Fish used in these and other studies, however, were paired at random (Haller 1991, 1992, 1994), or matched using a single variable, such as size (Meliska & Meliska 1976) or display reaction to a mirror (Bronstein 1984). It is possible that, in

those experiments that matched individuals using a single variable, a mismatch in some other variable resulted in faster determinations of dominance. The equality of our pairs is thus supported by the fact that so many interactions were still undecided after 24 h.

There was a clear winner in most of the social versus primed isolate interactions (13 of the 15 interactions had a clear winner; binomial test:  $P=0.004$ ). The large number of settled outcomes in social versus primed isolate pairs suggests that something unique about this interaction mismatched these pairs. Table II summarizes the hypotheses considered as candidates to explain why the cheaters lost.

#### Testing for Debilitating Effects of Social Isolation

We checked whether the social isolation procedure could have been debilitating. If this were the case, then the fact that socials had an



**Figure 4.** Mean duration of tailbeat and biting in the last 10 min of interactions. Legend as in Fig. 2.

advantage over primed isolates compared to unprimed isolates might have been explained by the unprimed isolate fish having some quality that counteracted the debilitating effect of isolation. However, a comparison of size–strength–weight data from two tests, separated by 2 weeks, showed that the isolates grew just as fast as the socials during this interval. Thus, it is highly unlikely that the socials became any larger, stronger or heavier than the primed isolates in the 4 days between matching and encounter. Furthermore, the primed isolate dyads fought as vigorously in the last 10 min of the recorded interactions as in the first 10 (Figs 2 and 4), which suggests that they were strong and motivated.

### Testing for Hyper-fearfulness

We examined the possibility that the primed isolates were hyper-fearful as well as hyper-aggressive. Halperin et al. (1992) and Halperin & Dunham (1993) suggested that hyper-fearfulness could result from social isolation. Only one instance of fleeing and hiding behaviour, however, was observed in all 49 interactions. Also, primed isolates did not immediately reduce their aggressive behaviour once their social opponents began

intense biting (Fig 5). In the 9 min prior to the peak rate of biting by the socials, both isolates and socials increased the time they spent biting, as shown by a comparison of two 5-min intervals (minutes  $-9$  to  $-5$  versus minutes  $-4$  to  $0$ , Wilcoxon signed-ranks test:  $P=0.0313$ ; Fig. 5). Finally, primed isolates fighting primed isolates showed no signs of being intimidated by their hyper-aggressive opponents. They performed just as much tailbeating and biting in the last 10 min of their interactions as in the first 10 min (Wilcoxon signed-ranks test:  $P>0.5$ ).

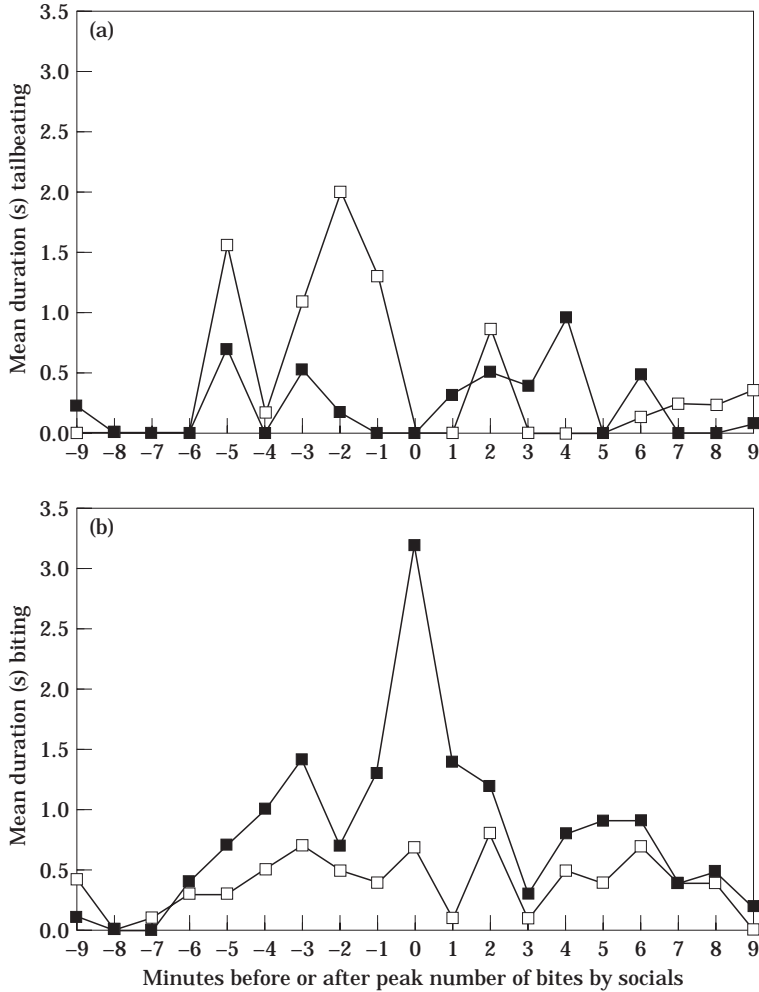
To see how primed isolates responded to retaliation by socials, we examined the time each spent tailbeating and biting within the 5-min periods immediately before and after the 1 min in which the socials performed the peak number of bites. The decrease in time spent tailbeating and biting was not significant (Wilcoxon signed-ranks test:  $P=0.1250$ ). We cannot conclude that the primed isolates matched the socials' biting once the socials had escalated, and they certainly did not manage to effectively counter-retaliate, but neither did their behaviour indicate hyper-fearfulness.

### Did Socials Massively Retaliate?

We then wanted to examine what happened when the socials defeated the cheaters. For example, winning through massive retaliation would not support the Zahavi–Grafen model. Massive retaliation would itself be energetically very costly, and should re-balance the pair even if energetic costs of aggressive behaviour were initially significant.

We first tested whether the socials retaliated massively by calculating the durations of tailbeating and biting in the last 10 min of the 45-min observation period (Fig. 4). Although the socials' mean looked higher than that of their primed isolate opponents, the difference was not significant (Wilcoxon signed-ranks test:  $P=0.1094$ ). More importantly, the mean for the socials fighting primed isolates was close to the mean of socials fighting other socials ( $U=105.5$ ,  $N_{1,2}=10$ ,  $P>0.5$ ). The mean duration of tailbeating and biting by socials fighting primed isolates was not significantly different from that in the hyper-aggressive primed isolate dyads ( $U=123$ ,  $N_{1,2}=10$ ,  $P=0.0952$ ).

In Fig. 5b, the peak biting rate of socials facing primed isolates was high compared to the biting



**Figure 5.** Mean duration of (a) tailbeating and (b) biting in each minute around the minute in which each social reached its peak biting rate. 0 refers to the minute in which each social performed its peak number of bites. The data are thus zeroed on the biting peak of each social fish (■ social; □ primed isolate).

rates of their partners. This graph represents the peak biting rate for each social independent of the time at which this occurred, so it does not indicate massive retaliation. We constructed a similar graph for the social dyads, zeroed on the minute when biting peaked for one of the partners chosen at random. Socials facing primed isolates did not have a significantly higher peak biting rate than fish in social dyads ( $U=112$ ,  $N_{1,2}=10$ ,  $P>0.3$ ) or in primed isolate dyads ( $U=102$ ,  $N_{1,2}=10$ ,  $P>0.5$ ). This result suggests that the socials won without massive retaliation.

### The Zahavi–Grafen hypothesis

We considered two frameworks that deal with costly communication, the ‘war of attrition’ model from game theory and Zahavi’s and Grafen’s handicap theory that some physical constraint should limit the success of a cheating strategy in any evolved communication system such as ritualized aggression (Grafen 1991). It should be possible to analyse our results by generalizing the asymmetrical war of attrition model (Enquist & Leimar 1987), because in a war of attrition,

there must be some cost with respect to which attrition occurs. Assigning a specific interpretation to the hyper-aggressiveness produced by social isolation, however (for example, by suggesting that the primed isolates may estimate that they have a higher V/K ratio than warranted), awaits further studies of how isolation increases aggressiveness.

We therefore examined the possibility that the isolates' hyper-responsiveness was energetically 'costly' in the Zahavian sense. The primed isolates may have nearly always lost because they tired as a result of the intensity of their initial display. The exhaustion due to hyper-aggression may have made the delayed retaliation by the socials particularly successful. Swimming involving marked changes in direction and speed is energetically expensive ('routine swimming'; Boisclair & Tang 1993). We therefore assumed that tailbeating and biting actions were energetically expensive, since they also involve sudden fast movements through water. (Mouthfighting is also presumably energy-intensive, but it is by definition carried out by both fish, so it is irrelevant to a hypothesized unequal energy expenditure.)

We had already shown that the primed isolates tailbeat and bit significantly more than their social partners. The energetic expense of tailbeating and biting, however, at the beginning of the fight could have been balanced if the primed isolate fish performed fewer moderately costly behaviours. We therefore checked whether the primed isolates fighting socials spent less time approaching with opercula extended, facing with opercula extended, and in broadside posture with fins raised. There was actually a non-significant trend for the primed isolates to perform more of these behaviours in the first 10 min of interactions (Wilcoxon signed-ranks test on total duration:  $P=0.085$ ). Therefore, primed isolates were not saving energy by reducing the performance of moderately aggressive behaviours.

We looked for evidence that the socials might have retaliated only after the primed isolates were exhausted. Social peak biting tended to follow a bout of tailbeating by the primed isolates, and tailbeating may have communicated information about the cheaters' waning energy levels. The primed isolates showed a non-significant tendency to tailbeat more in the 5 min before the socials' peak than in the 5 min afterwards (Wilcoxon signed-ranks test:  $P=0.0625$ ; Fig. 5).

The disadvantage to cheating appears to depend upon the strategy used by the primed isolates' opponents at the beginning of the interactions, when they displayed little, consistent with their expressing a cautious, honest assessment that they might be weaker than their apparently vigorous opponent. If the socials had matched the primed isolates' aggression levels throughout the interaction, both would have tired at about the same rate, and fewer interactions would have been decided. This is presumably what occurred in both the primed isolate versus primed isolate and social versus social pairs. The social fish in the social versus primed isolate interactions used a fighting strategy we termed 'smart boxer'. By not matching the initial aggression levels of the primed isolates, the socials did not tire at the same rate as the isolates during the early stages of the fight. The results suggest that a mismatch in strength may have been created, allowing the socials to retaliate effectively once it was apparent the isolates were tiring. Thus, the cost of aggression was paid most heavily by cheaters, as predicted by the Zahavi-Grafen model (Grafen 1991).

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