

Resolution of agonistic conflicts in dyads
of acquainted Green swordtails
(*Xiphophorus helleri*): A game with perfect information

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Abstract

Conflict resolution of familiar opponents was compared to that of unfamiliar ones in *Xiphophorus helleri* males. Under the *Familiar condition*, the two males which met had settled a contest against each other in a previously staged encounter in another aquarium. Thus one opponent was the previously dominant pair member, the other its previously subordinate. Under the *Unfamiliar condition*, two males met which were not acquainted with each other but had independently undergone previous experience of victory or defeat. We tested the hypothesis that familiar pairs would conform to some behavioural predictions of an «*asymmetrical game with perfect information*». As for unfamiliar pairs, being uninformed of asymmetries at a contest onset, they would have to acquire information on these during the course of interaction («*asymmetrical game with assessment*») or alternatively would have to persist for a certain time or cost («*war of attrition*»). All expectations derived from an «*asymmetrical game with perfect information*» applied to familiar pairs but not to unfamiliar ones. In familiar pairs, all prior roles were reinstated without any escalation. Though prior winners predominantly defeated prior losers under both conditions of cognizance, this difference was more extreme in familiar dyads than in unfamiliar ones. This suggests that the respective roles were less clearly identified in the latter. The costs of conflicts both in terms of aggressive behaviours used and in time were also higher in unfamiliar pairs than in familiar ones. Unacquainted individuals required a longer period to assess each other. In addition, they had to rely on more pugnacious behaviour to settle disputes in comparison to acquainted pairs. As expected also, familiar pairs being already cognizant of initial respective roles were more characterized in terms of the behavioural patterns typical of each of these roles. Differences between ultimate winners and losers were more clear in acquainted pairs, and appeared earlier during conflict. It was also possible earlier during contest to discriminate and to predict ultimate winners from losers of acquainted pairs using behavioural interactions. In most unacquainted pairs, ultimate winners could be forecasted using multivariate discriminant analyses, mainly by their offering «resistance» to future losers. A «war of attrition» did not fit to unacquainted pairs.

1. Introduction

Contests in which there is perfect information available to both contestants at conflict onset have been successfully modelled by Maynard Smith and Parker (1976) and Hammerstein (1981). In such contests, with unequal «*resource holding power*» (*RHP*: Parker, 1974) and with perfect information available to both contestants, there was found to exist two possible «*evolutionary stable strategies*» (*ESS*: Maynard Smith, 1974). The combatant in one of the two roles is treated invariably as the winner and the other as the loser. Contestants that recently had the opportunity to settle conflict and that meet again, upon recognizing each other, use the original asymmetry to rapidly settle the new dispute (Maynard Smith and Parker, 1976). These contestants can be considered as being in a situation of perfect information about their respective roles and solutions must be *ESSs* according to Selten's theorem (Selten, 1980). We can expect that familiar pairs rely on knowledge already available about their opponent and of their own position to settle conflict without the need for further assessment, probing or fighting. In such a situation, the contest is truly asymmetric and the use of bluffing is very unlikely (van Rhijn and Vodegel, 1980).

In the present paper, we compare conflict resolution of familiar pairs to that of unfamiliar ones. We formulate the hypothesis that familiar pairs will conform to some behavioural predictions of an «*asymmetrical game with perfect information*» (Hammerstein, 1981). These are games with the following properties (Maynard Smith, 1982): (i) Every contest is between a pair of individuals in which one is in role *A* (e.g. 'owner', 'larger', 'older') and the other in role *B* (e.g. 'intruder', 'smaller', 'younger'); (ii) both contestants know for certain which role to occupy; and (iii) the same strategy set (e.g. escalate, retaliate, display, etc.) is available to both contestants. The solutions must be *ESSs*, in which the individual in one role rapidly gets victory and its opponent in the other role, defeat. As for unfamiliar pairs, being uninformed on asymmetries at contest onset, they have to rely on alternate «games». One game would be to acquire information on asymmetries during the course of interaction (Enquist and Leimar, 1983; Leimar and Enquist, 1984). Another game would be to persist for a certain time or cost of which the value is higher for the animal in the winning role (e.g. «*war of attrition*»; Hammerstein and Parker, 1982).

Four classes of hypotheses are available from «*asymmetrical games with perfect information*» to contrast familiar to unfamiliar pairs. A first class concerns contest outcome that is expected to be more extreme in familiar dyads than unfamiliar ones. Familiar pairs should conform to the initial dominance relationship while in unfamiliar pairs role confusion should be more probable. A second class of hypotheses concerns the costs of conflict. Familiar pairs should settle disputes more economically than unfamiliar ones. This should be reflected by shorter contest length and by the use of less dangerous behaviour. A third class regards behavioural differences appearing during conflict and reflecting initial roles. It is to be expected that familiar pairs, being already cognizant of their respective roles, will be more characterized in terms of the behavioural patterns typical of these roles. In other words, differences between future winners and losers ought to be more pointed in familiar pairs than in unfamiliar ones. Finally, using behaviour, it should be possible to discriminate and to predict earlier during a contest future winners from future losers in familiar pairs than in unfamiliar ones.

In order to avoid undue repetitions, specific models, hypotheses and their empirical expectations will be presented in the Result section.

2. Methods

2.1 Subjects and material

A pool of more than 1,200 adult Green swordtail fishes, *Xiphophorus helleri* (*X.h.*), was constantly available in the laboratory. They were bought from the breeder Florida Fish Pounds (Tampa, Florida, USA). We maintained them in heterosexual groups of 100-150 individuals in nine large communal tanks of 165 litres (90 x 50 x 40 cm). When needed for the experiment, adult males were netted randomly from these communal tanks. All 40 pre-experimental and experimental glass aquariums (30 x 15 x 15 cm) were identical and contained 13.5 litres.

2.2 Size measurements

We took three size measurements on each fish: (1) its total length, from the snout to the end of the caudal fin; (2) its flank height, from the base of the dorsal fin to the origin of the gonopodium; and (3) its sword-length, from the distal end of the middle rays of the caudal fin to the tip of the sword. A precision of 0.5 mm was used throughout. We paired males according to differences in their lateral surface (*LS*). *LS* was obtained by adding sword-length to the product of total length and flank height. Calculated in this way, Beaugrand and Zayan (1985) found that *LS* showed a 5% mean error when compared to lateral surfaces measured using a planimeter. Moreover, these authors have shown that *LS* was significantly more correlated to dyadic dominance outcome than standard length in *X.h.*

Size measurements were obtained before the formation of pairs. We used a specially designed aquarium to measure the fish. Using a mesh partition that we could move freely, the fish was gently cornered and immobilized against the front glass. We then rapidly indicated its length, height and sword length on the front glass with a soft pen. After having released the fish, we measured distances between markings left on the glass using a ruler. Fish did not participate more than once in the present research.

2.3 Design

Two samples comprised originally of 30 pairs were formed. Each was assigned under one of the two independent experimental conditions. Conditions were rigorously the same, except for familiarity with the opponent.

Under the *Familiar condition (Fam)*, two males, which had settled contest against each other in a previously staged encounter in another aquarium met. One opponent was thus the prior dominant pair member (referred herein as the α), the other being its prior subordinate (ω).

Under the *Unfamiliar condition (Unf)*, pairs of males, which were not acquainted to each other but had independently undergone different prior experiences acquired elsewhere met. One fish had acquired prior victory experience (α) against an unfamiliar opponent in a pre-staged contest while its opponent had experienced a prior defeat experience (ω) in a similar contest.

All fish met in unfamiliar aquariums. They were paired according to their ratio in lateral surfaces. Only fish showing less than 10% difference were retained for pairing in both pre-experimental and experimental phases. This range of ratios between lateral surfaces corresponds to a zone in which Beaugrand et al. (1991) have shown that outcome was determined by prior experiences of dominance and subordination rather than by size differences.

2.4 Procedure

The experiment was divided into two phases that were completed within two consecutive days for each pair.

The pre-experimental phase served to measure the fish and to attribute prior experiences to the individuals to form a pair. The fish were netted from the various communal tanks, measured and their external appearance noted to insure proper recognition by the observer.

We isolated the fish for two hours in separate pre-experimental aquariums, then carried out the encounter by simultaneously introducing two opponents into a third aquarium where they stayed together for the next 18 hours. The first and last 3 hours of this period were used to identify the winner and loser of each pair. Behavioural observations were carried out from behind hides. The encounter was cancelled at the end of these 18 hours when no dominance relationship had clearly established. Fish from such unsettled encounters did not participate in the next phase.

The experimental phase began by imposing 3 hours of isolation to the fish. Subsequently, they were both netted and simultaneously introduced into another unfamiliar tank. Under the *Fam* condition, the same two fish, which had met and settled dominance at the previous phase encountered again. Under the *Unf* condition, they were unfamiliar to each other but had independently acquired opposite prior experiences of dominance. In this case, new pairs were formed by recombination

of opponents having experienced prior experience of dominance or subordination at the previous phase. Again, pair members had to show a ratio in lateral surfaces within $\pm 10\%$ difference and to originate from different communal tanks, as well as to be unfamiliar to the future test tank.

The fish were observed interacting until one clearly dominated its opponent or for a maximum of 30 minutes, whatever came first. In the latter case, the unsettled encounter was not considered for analysis in the sample.

In both phases, the selection of fish to form pairs was computer assisted. A program also randomly attributed pairs to the various available aquariums.

2.5 Behavioural observations

Observations were carried out from behind hides by two observers not cognizant of experimental conditions and randomly assigned to the recording of the behaviour of only one of the opponents of each pair. We used two Tandy C101 hand-held computers whose internal oscillators had been synchronized.

The two observers had been intensively trained together and their degree of agreement was systematically verified at various steps of the research. The Cohen's kappa (Cohen, 1960) was used and never fell below 0.8.

All relevant individual behavioural acts were coded live from the moment both fish were introduced into the test tank, until the attainment of the dominance criterion. Several behaviour units were directly encoded and were marked with an asterisk in the following list. These units facultatively contributed, at the moment of analyses, to broader categories.

Offensive behaviour (off). This category includes *attacking** (att) and *biting** the opponent. *Attacking* entails the sudden acceleration of an individual toward its conspecific; the initial distance being at least equal to the length of the initiator. This unit may be followed by *biting*, which consists in grasping with the mouth such anatomical parts of the other individual as the flank, the ventral or pectoral fins, the gonopodium ("fin-grips" of Ribowski and Franck, 1993), or even the mouth of the opponent (*mouth-fight**).

Menacing behaviour (men). This category includes *tail-beating** and *lateral-display**. *Lateral-display* consists of the spreading of all fins with the exception of the ventral fins which are kept close to the body. The body presents, most often, a typical sigmoid posture (*S-drohen*). The orientation of the individual is usually perpendicular to and in front of the conspecific, or parallel to it, when both fish are mutually displaying. In *tail-beat*, the initiator adopts a *lateral-display* posture, curves its body sharply, and rhythmically beats with its tail at a frequency of 2-10 units per minute. *Tail-beats* are administered in the direction of the opponent, as if water current was aimed at its head, flank or tail.

Chase. A *chase* is an interactive behaviour. It was defined as the initiation of either a *menace*, *offence*, or *approach* behaviour by a given contestant, and its concomitance with, or immediate succession, by a *defensive behaviour* or *flight* by the other contestant.

*Approach**. This is a slow movement of a fish toward its conspecific. It is initiated from a distance exceeding approximately twice the total length of the initiator.

Defensive behaviour (def). This category includes *flight** and adopting a *folding posture**. *Flight* is associated with an *approach*, *attack*, *bite*, *lateral-display*, or *tail-beat* unit initiated by the opponent. The threatened fish rapidly avoids the charging opponent or escapes its presence by a sudden acceleration to separate them. *Flight* is sometimes accompanied or followed by a *folding posture*. The *folding posture* consists of the immobile or slowly moving fish lowering its dorsal and caudal fins and spreading its ventral ones. Sometimes, the fish also tilts on the side and will adopt a vertical position (*head-up picket**) in a corner of the aquarium upon being approached. The defensive unit is an interactive pattern since it entails the concomitant initiation of an aggressive act by an opponent.

*Flutter**. The fish is oriented perpendicularly against one of the sides of the aquarium and swims laterally or up and down as if trying to get out of the aquarium.

*Bottom immobility**. The immobile fish touches the bottom of the aquarium with its belly or sword for a period longer than one second. *Rising** from the bottom was also noted when the fish left the substrate for more than one second.

*Eating**. The fish grazes on the sides of the aquarium, or feeds on the bottom or at the surface.

*Breaking the surface**. The fish goes to the surface to gulp air or to skim.

Aggressive behaviour (agg). This category includes offensive and menacing behaviour units.

Dominance criterion. We considered that a dominance relationship had been established when one fish (the winner: W) was successful in chasing its opponent (the loser: L) on six occasions without being threatened, attacked, or bitten in turn. Such an extreme behavioural asymmetry is significant to a Binomial test ($x:6, N:6, P.0156$).

Welfare. No detectable injury nor death occurred during experimentation itself. At the experimental phase, we took care to separate contestants or to return them to communal tanks as soon as the dominance criterion had been reached.

2.6 Data reduction and analysis

The chosen mode to capture behavioural observations also automatically records the moment of occurrence of each unit since contest onset. Identification of the initiator and facultative target fish was implicit since each observer had to follow and record the behaviour of a single opponent.

The two files of observations recorded for each complete contest, one for each opponent, were collapsed into a single interaction file by synchronizing common recordings of timing events. When two events had been encoded simultaneously they were randomly placed in sequence.

For sequential analyses, a time limit of three seconds was imposed beyond which a behaviour act was considered independent of the preceding intra-subject or inter-subject act. A «*pause*» was thus inserted in such cases between the two successive acts or repetition of the same act. This criterion was chosen following examination of the pooled distributions of intervals separating all types of behaviour including repetitions, both for intra-subject and inter-subject transitions, as well as after examination of the logarithmic curves of their survival values (Beaugrand, 1980; Slater and Lester, 1982).

High order patterns of behaviour transitions were obtained using *SYNTAX*, a behavioural parser developed by Beaugrand et al. . These patterns will be noted as in e.g. « X_{act_1} and Y_{act_2} », where X is the initiator of the first *act* (e.g. men, off, agg, etc.) and Y , the initiator of *act*₂ which followed within 3 seconds; else, *act*₂ is a «*pause*» (ex: « X_{act} and $X\&Y_{pause}$ »). In first order auto-transitions initiated by the same fish, Y will be replaced by X , as in e.g. « X_{act_1} and X_{act_2} ». Repetitions of the same act will be indicated by putting the repeated act within accolades as in e.g. « $\{X_{act_1}\}$ and X_{act_2} », meaning that *act* was repeated a certain number of times by X before being followed by *act*₂.

In the present research, all contest records ended with the occurrence of the first defensive behaviour, which was part of the six leading to the satisfaction of the dominance criterion. Acts occurring after this first occurrence were thus not considered for analysis, because we estimated that the «*decision*» to concede victory had already been taken by the loser on its first flight part of the criterion.

The behaviours of a pair of contestants were not considered as independent data, but systems influencing each other. All statistical tests comparing within the same sample winners to losers on behavioural frequencies, proportions, or rates were thus always of the paired or correlated measurements type.

3. Results

Out of the 60 originally staged contests, five did not reach the dominance criterion at the second step of the experiment and were thus discarded. Four came from the *Fam* sample and one from the *Unf*. Some 55 complete dyadic records will thus analysed, 26 forming the *Fam* sample, and 29, the *Unf* one.

Data analysis was guided by the following general comparative hypothesis:

M1 An asymmetrical game with perfect information would apply to a contest of *Fam* pairs, but not to *Unf* ones that were only very imperfectly informed on asymmetries.

It was hypothesized that *Unf* pairs being uninformed on asymmetries at contest onset would settle according to either one of

the following «games»:

M2 An asymmetrical game with imperfect information and assessment or,

M3 a «true» war of attrition.

In order to obtain working hypotheses, it was also not unrealistic to admit the following postulates:

P1 Recent dominance experience increases RHP of the individual, while recent experience of subordination decreases it.

This postulate is grounded in ample empirical study (e.g. Braddock, 1945; Frey and Miller, 1972; Zayan, 1975; Francis, 1983; Beaugrand and Zayan, 1985; Beacham and Newman, 1987).

P2 Contests were symmetrical with respect to size/strength. In the present experiment, size asymmetries were kept minimal in order to let other asymmetries play. This was checked *a posteriori*. As expected from Beaugrand et al. (1991), within the range of size differences chosen, pair members showing the larger lateral surface did not more frequently win contest in comparison to their smaller opponents (Anova, $F = 0.89$, $df = 1/25$, *ns*). The contests can thus be considered symmetrical on that aspect.

P3 Resources had on the average the same value for both pair members. *X.h.* males apparently fight for high ranking, which gives them preference by females (Beaugrand et al., 1984; Franck and Ribowski, 1988). In the present study, we have no reason to think that resources had systematically more value for one opponent than for the other. Contests were always staged in unfamiliar aquariums thus eliminating prior residency effects and prior cognizance of available resources of the meeting site. Fish contested in the absence of females and food. All males had been subjected to the same general rearing conditions of food availability and of heterosexuality.

From this, several expectations were searched for into the data; the first one pertained to contest outcomes.

3.1 Contest outcomes

e1 Since in Fam pairs, individuals were already in possession of unambiguous information on their respective roles, they would conform again to these initial roles upon meeting again. The previously dominant pair member (α) should remain the dominant (W), and its subordinate (ω) rival should remain the subordinate (L).

Expectation e1 is confirmed: out of 26 contests, prior members of *Fam* pairs systematically dominated their prior rivals in 100% of cases. This extreme result is evidently significant ($x: 0$, $N: 26$, Bin $P < 0.001$).

e2 In the Unf sample, prior α pair members would significantly defeat their prior ω opponents. This is explainable by the fact that winners (W) were advantaged by prior α experience over their losing (L) opponents, and that the latter were disadvantaged by prior ω experience. In addition, either under M2 they were to assess each other or, under M3, prior α s would be prepared to accept higher costs than prior ω s.

Expectation e2 is confirmed: in *Unf* pairs, 21 out of the 29 fish having received α experience defeated their ω rival. This is highly significant to a Binomial test ($x: 21$, $N: 29$, $P < 0.012$).

e3 In Unf pairs, since information was at best very imperfect at contest onset, role (or) confusion would be more prevalent than in Fam pairs, which were already perfectly informed. Thus, we could expect that α pair members of Fam pairs would defeat their ω rivals more often than in Unf pairs.

Expectation e3 is confirmed by significant Fisher exact probability ($P < 0.003$) and X^2 tests ($X^2 = 8.39$, $P < 0.004$).

3.2 On the costs of contests

Costs can be reflected by contest length or by the degree and frequency with which "dangerous" behaviour is used. We can reasonably assume that

P4 «displaying», fighting, obtaining and giving information have energetic costs. Time spent in contest also has costs.

P5 The relative cost of behavioural patterns part of the fish repertoire can be postulated as being a direct function of: (1) the probability that the action pattern leads to injury; (2) the level of excitement exhibited during action; and (3) the energy expenditure required for its completion (Riechert, 1979). It can thus be postulated that, within the aggressive behaviour repertoire of *X.h.*, offensive behaviour patterns (*off*: biting, mouth-fighting, attacking/charging) represent a higher cost than menacing behaviours (*men*: lateral display, tail-beating).

H1 *Fam* pairs being already informed on respective roles would settle at a much lower cost than *Unf* ones. The latter had under M2 no reliable initial information on respective roles and had to gain some; or under M3 *Unf* had to «display» until one pair member gave up by attrition.

This hypothesis can be supported by several empirical evidences based on persistence, on choice of behaviour and on their relative frequency.

3.2.1 Costs of persistence

The record of each contest was subdivided into several phases. A *Preliminary phase* was defined as the period starting with the introduction of the opponents into the test tank and lasting until the first occurrence of any aggressive behaviour (*men* or *off*). This first phase could facultatively be followed by a *Menacing phase*, which began with the first occurrence of any menacing behaviour (*lateral-display* or *tail-beat*) and ended with a first offensive behaviour or with the first defensive behaviour part of the dominance criterion. The *Menacing phase* was dominated by *lateral display* and *tail-beating*. Facultatively also, came next an *Offensive phase* that began with the first occurrence of any behaviour of the offensive type. This phase was dominated by *bite*, *mouth-fight*, or *attack/charge*. It ended with the occurrence of the first defensive behaviour.

Since it was of interest to compare their given importance under each condition to assessment, the *Menacing* and *Offensive phases* of each contest were concatenated to form an *Assessment phase*. It was plausible to assume that assessment occurred in the period between the occurrence of the first menacing behaviour and the first defensive behaviour.

Following H1, above, it could be expected that

e4 the duration of the *Assessment phase* would be significantly shorter in *Fam* pairs than in *Unf* ones.

The mean durations of the various contest phases are presented in Table 1.

Contests between *Fam* and *Unf* pairs were of equal total duration. Its The mean durations of the *Offensive* and *Assessment* phases were much shorter in *Fam* pairs than in *Unf* ones.

e5 It was expected that the number of assessment phases still continuing after a certain point in time, would differ in *Fam* pairs in comparison to *Unf* ones.

Table 1
Mean duration of conflicts

Contest type	Phase duration (mins)				
	N =	Pre	Men	Off	Ass
Familiar	26	4.44	1.89	0.42-↓	2.31-↓
Unfamiliar	29	4.88	1.29	5.02-↑*	6.31-↑*

Pre: preliminary phase; Men: menacing phase; Off: offensive phase; Ass: assessment phase.

* $P < 0.01$ to T -tests and Kruskal-Wallis Anovas.

As shown by Fig. 1, survivorship curves of *Fam* and *Unf* pairs (based on percentages in survival) differed from each other when compared with a Kolmogorov-Smirnov test ($D=0.47$, $P<0.001$). The cumulative persistence times of *Unf* pairs can be described as a negative exponential distribution ($Y=1.594435*\exp(-0.2031*X)$; $R^2=0.91$, $F=206.$, Durbin-Watson = 0.336). However, the line was best fitted by a logarithmic function ($Y=1.117-0.365*\log(X)$; $R^2=-0.983$, $F=561.3351$, Durbin-Watson = 1.027) that can also be a Poisson process.

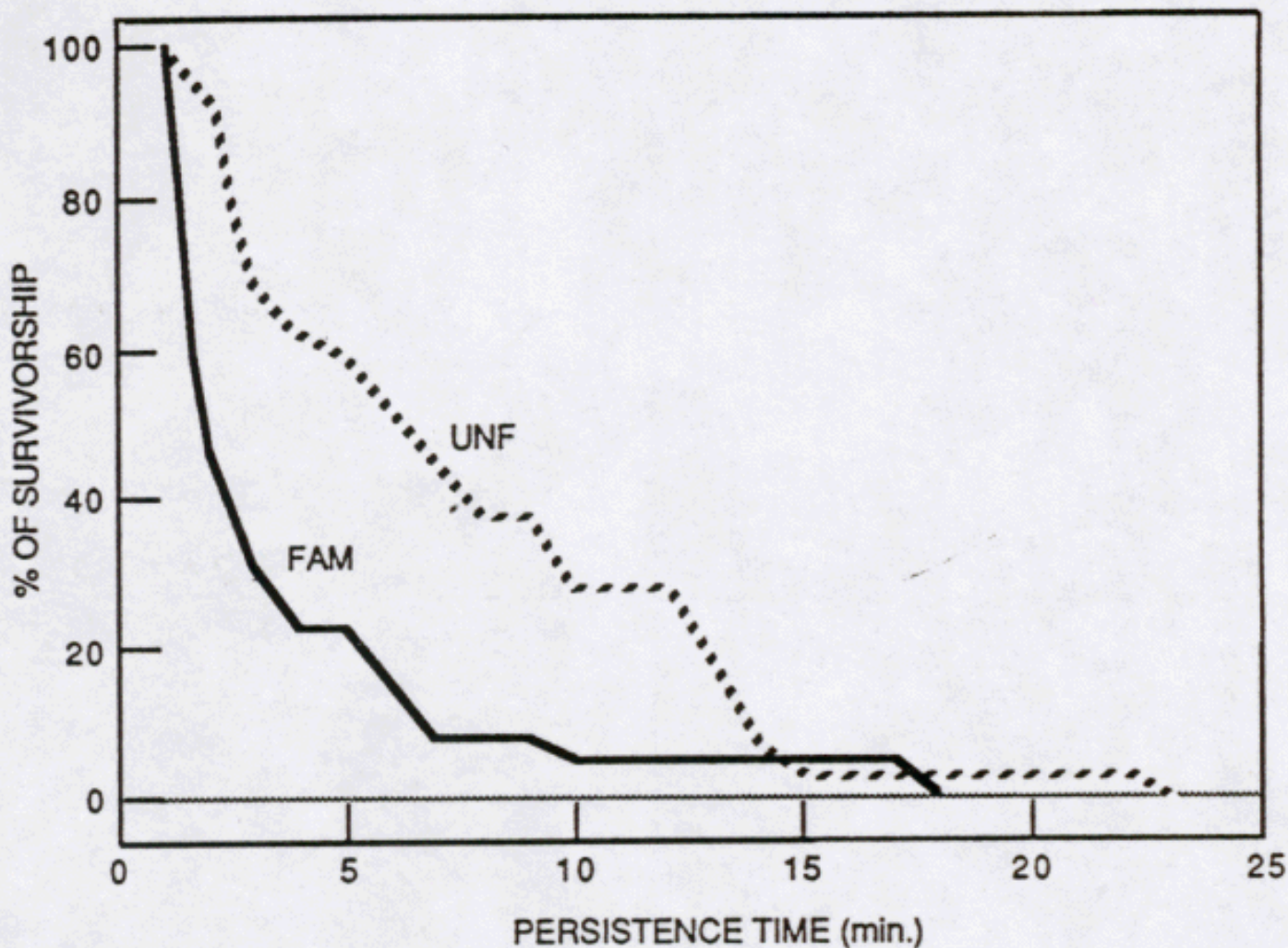


Fig. 1. Survivorship plots of cumulative persistence times (the percentage of contests still continuing after a certain point in time).

In regards to the survivorship of *Fam* pairs, it was best fitted by a power function ($Y=1.7921 \cdot X \cdot \exp(-1.2768)$; $R^2=0.955$, $F=317.84$, Durbin-Watson = 0.82).

These results on survivorship and durations of assessment clearly suggest that major differences exist regarding the costs involved in durations of contest between *Fam* and *Unf* pairs.

3.2.2 Costs of aggressive behaviour

In general, Fam pairs will be less aggressive than Unf ones. Aggressive behaviour (especially of the dangerous type) will

be less frequently used by Fam pairs than by Unf ones.

Examination of Table 2A clearly indicates that aggressive behaviour was systematically much less frequent in contests between *Fam* pairs than between *Unf* ones. The comparison of winners and losers indicates that this global difference in aggression reflects itself by more frequent use of menacing and offensive behaviours by both members in *Unf* pairs in comparison to *Fam* ones.

e7 Among aggressive acts initiated by Fam pairs, the proportion of behaviours of the menacing (ritualized) type should be greater than that of the offensive (more dangerous) type.

The expectation is confirmed by noting that 85% of all aggressive behaviours manifested by *Fam* pairs were ritualized (*menaces*). The difference in proportion is significant (Z test, $P < 0.01$).

In regard to the proportion of dangerous vs ritualized behaviours that were used by *Unf* pairs, we were not in a position to make a clear forecast. It is nevertheless interesting to note that within aggressive acts initiated by *Unf* pairs, the proportion of behaviours of the dangerous type was greater than that of the ritualized type. Only 33% of aggressive behaviour were ritualized. The excess of offensive behaviours over menacing ones was found statistically significant (Z test, $P < 0.01$).

e8 Fam pairs should less frequently use mutual offenses than Unf ones.

Expectation e8 is confirmed. As shown in Table 3, pairs of sample *Fam* almost never used mutual offenses, *i.e.* «*X_off* and *Y_off*», as compared to *Unf* ones.

e9 Fam pairs should less frequently use mutual menaces than Unf ones.

The hypothesis is supported. Mutual menaces, *i.e.* «*X_men* and *Y_men*», were significantly less frequently used by *Fam* pairs than by *Unf* ones (Table 4).

e10 Defensive behavioural patterns should appear after quantitatively less aggression in contests of Fam pairs than of Unf ones.

The expectation is confirmed: losers of *Fam* pairs signalled their defeat before the 10th aggressive act initiated by their opponent (7.62 acts after being menaced or 1.65 acts after being attacked) while ultimate losers of *Unf* pairs required, on the average, 74.34 aggressive acts before showing the first sign of defeat.

These results, on the use of dangerous behaviour and on its relative intensity, support the hypothesis that contests between *Unf* pairs were much more costly than contests between pair-members, already acquainted to each other, which only had to confirm a previously established dominance relationship.

Table 2

Action pattern	Familiar pairs		Unfamiliar pairs	
	Winner	Loser	Winner	Loser
(a) Mean frequencies of aggressive and defensive action patterns initiated by future winners and losers				
Tail-beat	5.15 ^w	1.19 ^b	15.83	9.62
Lateral-display	2.46	1.85 ^b	14.55	9.93
Attack	0.81 ^w	0.08 ^b	5.76	6.52
Bite	0.85 ^w	0.12 ^b	37.21	48.38
Flutter	0.42 ^w	4.85	0.62 ^w	6.69
Flight	0.00 ^w	1.08	0.03 ^w	1.17
(b) Mean latencies and superiorities of aggressive and defensive action patterns initiated by future winners and losers ^a				
Latencies (mins)				
1st agg	7.39 ^w	19.43 ^b	5.64	7.61
1st 2 agg	11.45 ^w	21.24 ^b	6.76	10.64
1st 3 agg	13.09 ^w	24.69 ^b	6.92	10.73
1st flutter	28.23 ^w	18.86	25.20	12.93
1st flight	30.00 ^w	9.22	29.00	10.87
Superiorities (frequencies)				
1st agg	18 ^z	6	18	10
1st 2 agg	15	9	8	10
1st 3 agg	15 ^z	5	16	10
1st flutter	2 ^z	12 ^b	4 ^z	18
1st flight	0 ^z	26 ^b	0 ^z	29

^a Latencies are in minutes lapsed since conflict onset. Superiorities correspond to the frequency that a given pair member was the initiator, the first, the first 2 acts or the first 3 acts.

^b Significant between samples difference between *both* future winners and losers; Kruskal–Wallis Anova and *T*-test for independent samples, $P < 0.01$.

^w Significant within sample difference between future winners and losers; Wilcoxon matched-pairs signed-ranks test and *T*-test for correlated data, $P < 0.01$.

^z Significant to a Binomial test, $P < 0.02$.

3.3 Behavioural differences according to roles

It was to be expected that, since *Fam* pairs already knew their respective roles right from or near contest onset, major behavioural differences reflecting the cognizance of these roles will show up in analyses. In *Unf* pairs, if fish assess each other, we can expect that their roles will become clear for them by the end of the contest itself. Indeed, it is to their advantage to concede victory as soon as reliable information is obtained on the asymmetry. On the other hand, if no assessment occurs and fish settle according to a process of attrition, it is to be expected that no reliable difference will appear between future winners and losers. Indeed, fish should not behave in such a way as to assist their opponent, if this in turn can cause a loss to the signaller by revealing their readiness to persist (Maynard Smith, 1982; Dawkins and Krebs, 1978). In any case, we could expect that behavioural differences would appear earlier during contests of *Fam* pairs than that of *Unf* ones.

Two behavioural measures were used to verify the existence of this differential characterization. Firstly, differences between opponents were searched for by examination of total behaviour frequencies. The second measure took time into consideration and were examined throughout contest.

3.3.1 Total behavioural differences

e11 It was expected that, in *Fam* pairs, α would have the almost exclusive use of offensive behavioural patterns since such a use is part of their repertoire as the dominant fish in pairs of *Xiphophorus* males that form stable dyads (Beaugrand et al., 1984; Beaugrand and Beaugrand, 1991)

Expectation e11 is confirmed (see Table 2A). Although rarely used, offensive behaviours, i.e. *biting* and *attacking* behaviours, were nevertheless more frequently used by winners than by losers of familiar pairs. This would contrast with

e12 *Unf* pairs in which both members would equally resort to offensive behaviours. In this case, roles as α or ω are not clear.

Winners and losers of sample *Unf* have equally used offensive behaviour against their rival (Table 2A), thus confirming expectation e12.

e13 α pair members of *Fam* pairs would almost exclusively resort to unilateral aggressive acts (i.e. not responded to by a behaviour of the same category). This asymmetrical pattern is characteristic of a dominance-subordination relationship that is already clearly established and is in its maintenance phase (Beaugrand et al., 1984; Beaugrand and Beaugrand, 1991).

The expectation was confirmed in several aspects. In *Fam* pairs, the winner was more frequently the initiator of aggressive acts not responded to with aggression by its subordinate opponent («*X_agg and X&Y pau*»; Table 3). The same pattern was also found for intra-subject repetitions of aggressive behaviours («*X_agg and X_agg*», Table 3). The winner was also systematically the first one to initiate the first three aggressive behaviours (Table 2B).

Table 3
Mean frequencies of agonistic sequences

Interaction pattern	Familiar pairs		Unfamiliar pairs	
	Winner	Loser	Winner	Loser
<i>X_men & Y_men</i>	0.62	0.88 ^b	3.97	4.34
<i>X_men & Y_off</i>	0.00	0.08 ^b	9.17 ^w	1.93
<i>X_off & Y_off</i>	0.04	0.00 ^b	21.52	22.28
<i>X_off & Y_men</i>	0.12	0.12 ^b	3.45 ^w	10.38
<i>X_agg & X_agg</i>	4.73 ^w	0.62 ^b	23.52	26.90
<i>X_agg & pause</i>	2.77 ^w	1.12 ^b	9.66	7.34
<i>X_agg & Y_def</i>	1.04 ^w	0.00	1.55 ^w	0.17
<i>Warning</i>	0.81 ^w	0.12 ^b	3.24	2.76

Comparisons between unfamiliar and familiar pairs. men:

menace; off: offensive behaviour; agg: men or off; def: defensive behaviour. *X*: initiator; *Y*: target.

^w Significant within sample difference between future winners and losers; Wilcoxon matched-pairs signed-ranks test and *T*-test for correlated data, $P < 0.01$.

^b Significant between samples difference between *both* future winners and losers; Kruskal–Wallis Anova and *T*-test for independent samples, $P < 0.01$.

e14 *In contrast, it was expected that pair members of Unf contests would more equally and more frequently use unilateral as well as mutual aggressive acts than Fam ones.*

The hypothesis was (in general) confirmed. As can be seen from Table 2A, the winners and losers of *Unf* pairs more frequently and more equally used aggressive behaviour than pair members of the *Fam* condition did. However, subtle differences were found to exist between the winners and losers of sample *Unf* in their behavioural interactions. For instance, losers more frequently answered menaces with offensive behaviours than winners did («*X_men and Y_off*», Table 3). Offensive behaviours initiated by losers were also more frequently answered by menaces by future winners («*X_off and Y_men*», Table 3).

e15 *Defensive behaviours such as fluttering, going to the surface when menaced, or adopting a folding posture when approached will have shorter latencies for future losers of Fam pairs than for future winners thus confirming pre-established roles in Fam pairs.*

All *flights* in *Fam* pairs were exclusively initiated by the future losers and prior subordinates (W: 0 vs L: 28, Binomial: $P < 0.001$). Future losers also *fluttered* significantly more often on the average than winners (L: 4.85 vs W: 0.42, t&w: $P < 0.01$). In addition, losers of *Fam* pairs were significantly the first ones to initiate the first three flutters (L: 12 vs W: 2, Binomial: $P < 0.006$).

As for *Unf* pairs, defensive behavioural patterns were also of shorter latencies for losers than for winners. For instance, future losers of *Unf* pairs were significantly the first ones to initiate the first three *flutters* (L: 18 vs W: 4, Binomial: $P < 0.002$).

In *Fam* pairs, knowledge about each other's role was supposed to be perfect. Conflicts were then truly asymmetric and bluff, very unlikely (Van Rhijn and Vodegel, 1980). It could thus be expected that

e16 *since Fam pair members were able to recognize their respective roles, warnings would be the privilege of the α individual of the pair, rather than that of the ω .*

A «*warning*» was defined as a suite of *menaces* initiated by one member, *menaces* that were always ignored, *i.e.* followed by a *pause*, a «*stay*», or not responded to by any aggressive or defensive behaviour by the opponent. These sequences of «*{X_men and X&Y pause}*» could be repeated a certain number of times but were eventually followed by a dangerous behaviour that was directed toward the warned individual, *i.e.* «*{X_men} and X off*».

The expectation is confirmed. Whilst *warnings* were not found to occur very often in *Fam* pairs, winners were nevertheless more frequently the initiators than losers (Table 4).

e17 *In Unf pairs, warnings would equally be initiated by both pair members.*

The hypothesis was globally confirmed. Winners and losers of *Unf* pairs equally served *warnings* (W: 3.24 vs L: 2.76, t&w:

ns).

3.3.2 Behavioural differences developing throughout contest

In the context of the present study, we could expect that

H2 individual behaviour during the course of contest would indicate differences between ultimate winners and losers especially in Fam pairs, and that these differences would appear earlier in Fam contests than in Unf ones.

For each individual behaviour unit, two measures were calculated. First, individual «*current accomplishment*» during a contest was obtained by integrating the surface below the curve defined by the cumulative frequencies for a given behaviour for each contestant. Each contest was divided into 100 equal intervals, and current accomplishment was calculated at the end of each interval. Although contests did not have the same total duration, values in current accomplishment corresponding to each percentile or interval were summed across contest within a given sample. Anovas and Wilcoxon tests were used to compare relative accomplishment of winners and losers at each given moment during contest. We report as significant only the differences reaching the $P < 0.01$ significance level to *both* the Anova and the corresponding distribution-free test.

A second measure of change during contest was provided by individual «*rate of accomplishment*». This was calculated by dividing the individual frequency of a given behaviour during a given time interval by the duration of the corresponding interval. Each contest was thus separated into five successive «*rounds*» each corresponding to 20% of total contest duration. Rates of accomplishment for all behavioural acts were then calculated for each of these five rounds. Contest rates, obtained for to-be winners and losers or for s and s, were compared using Anovas with successive rounds as repeated measures. In *a posteriori* comparisons, Tukey's honestly significant difference test (Kirk, 1968) and Wilcoxon matched-pairs signed ranks tests were used to localize rounds for which the difference in rate between members reached significance. Unless specified, we report significant differences in rates that reached at least the $P < 0.05$ level in both tests.

Differences between winners and losers in total accomplishment, rate of menacing behaviour (*lateral-display*, *tail-beating*), and offensive behaviour (*biting*, *attacking*) became respectively significant at the end of the 3rd and 4th rounds. They remained significant thereafter. Future losers *fluttered* at a greater rate than winners from the 3rd round until the end of contest, and they also went to the surface at a greater rate during the 3rd and 4th rounds. The fact that behavioural differences appear during contest is thus amply supported in the case of *Fam* pairs.

Differences were noted to develop during contest but were less clear in *Unf* pairs than in *Fam* ones. The following differences were nevertheless found when the analyses were carried out on the five rounds: By the end of contest, winners (either prior or) of *Unf* pairs had more frequently approached their opponent and had been more frequently the first ones to do so ($P < 0.01$). Although overall accomplishments in aggressive behaviour were equivalent for both *Unf* winners and losers, the former showed higher menacing and attacking rates during the last round. In general, losers more frequently fluttered and were also systematically the first ones to initiate the first three *flutters*. They *fluttered* at a greater rate during the first round (significant only to a Wilcoxon, $P < 0.05$) and kept on until the end of contest (t&w, $P < 0.01$). Within sample comparisons indicate that future winners and losers behaved differently; this applies to *Fam* as well as to *Unf* pairs. However, it will be noted that the behavioural patterns that could be used to distinguish opponents were not necessarily the same in the two kinds of encounters.

3.4 Predicting winners and losers

Being able to distinguish on a behavioural basis winners from losers during the course of the contest entails that one can predict contest outcome. For further we cross-validated the existence of differences using behavioural sequence patterns (e.g. «*X_off and Y_men*»). Our hypothesis was that

H3 significant statistical prediction of outcome would become possible earlier in contests between Fam pairs than in Unf ones.

To test this several successive discriminant analyses (Jennrich, 1977; Pimentel and Frey, 1978) were performed using SPSS. The direct method of inclusion was used; all variables being entered simultaneously in the analysis. Each contest record was partitioned into the three phases defined above, *i.e.* Preliminary, Menacing, and Offensive phases. Each of the three phases was in turn subdivided into five rounds corresponding to 20% of the duration of the phase for a total of 15 rounds per

contest. We postulated that the fish had memories of what they had accomplished since contest had begun. Fifteen successive and cumulative sequential analyses were thus performed; each starting with contest onset and terminating with the end of the corresponding round.

For each behaviour sequence pattern and fish, the following proportion $P(\cdot)$ was calculated:

$P(\text{own}) = S(\text{own}) / [S(\text{own}) + S(\text{opponent})]$ where $S(\cdot)$ is the current accomplishment for that behaviour interaction initiated by one individual or by its opponent.

Discriminant analysis requires the classification of the various sets of data that are statistically independent. Each sample was thus divided into two independent sub-samples. Each contest record contributed to the data set, either for a difference between the data of the winner minus that of the loser, or vice versa, but not to both sets at the time. A first sub-sample was thus composed of half of the future winners minus the future losers, and the other, of half of the future losers minus future winners that were part of the original sample. The classificatory analyses had to properly discriminate winners from losers using these differences in individual accomplishment with a discriminant function obtained following a within sample analysis.

Progressive hits are presented in Fig. 2. The analyses indicate a gradual increase of successful classification as contests proceeded. Comparing the three frames of Fig. 2, it is apparent that hits concerning *Fam* pairs grew faster than hits for *Unf* ones.

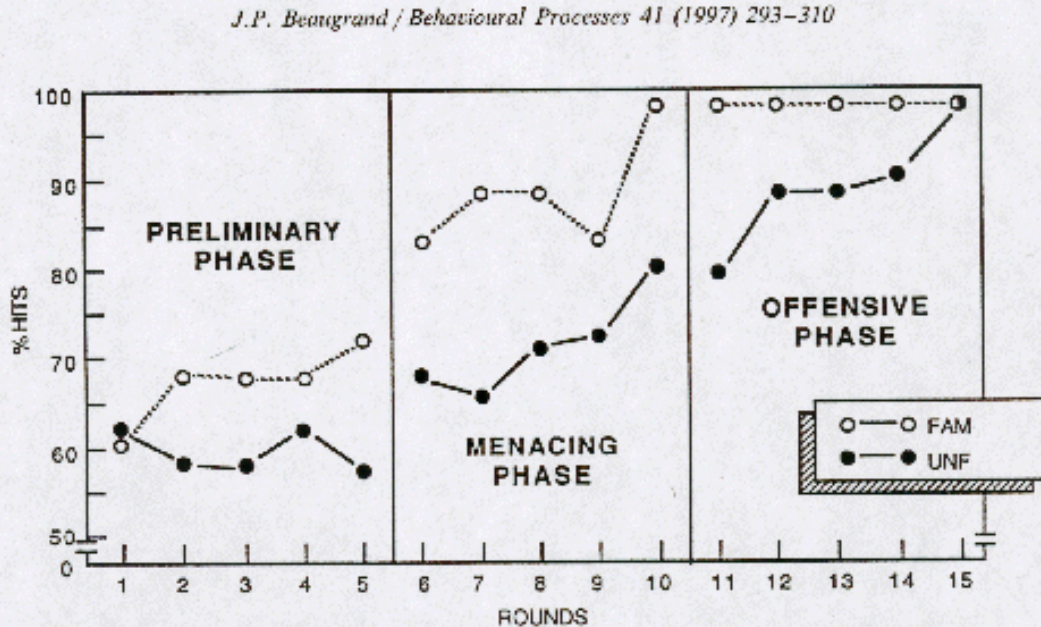


Fig. 2. Success of classification of winners and losers using discriminant analyses performed on cumulative proportions of accomplishment in behavioural interactions.

Using a Z test for proportions (Siegel and Castellan, 1988, p. 43), hits given by each discriminant analysis were roughly checked against chance. Hits for *Fam* pairs were significant, at least at the 1% level right from round 5 through round 15. As for *Unf* pairs, hits started to be higher than by chance alone from round 6 up to the end. At rounds 7, 10 and 11, hits were higher for *Fam* pairs than for *Unf* ones (Fisher test, $P=0.03$). However, that difference gradually faded out as the *Offensive phase* progressed. Examination of successive canonical correlations also indicates that outcome in *Fam* pairs could be forecasted earlier than that of *Unf* ones during contest. For instance, by the end of the *Menacing phase* (round 10, see Table 4), canonical correlation was 0.934 ($P<0.01$) for the *Fam* pairs, and 100% of cases could be correctly classified. This contrasts with the canonical correlation of sample *Unf* that was only 0.758 and with the fact that none of the sequence patterns correlated significantly with outcome. The corresponding discriminant function still made correct classification in 79% of cases, suggesting a multivariate contribution.

Table 4

Discriminant results for familiar and unfamiliar pairs by the end of the *Menacing phase* (round 10)

Familiar pairs		Unfamiliar pairs	
Eigenvalue	6.81	Eigenvalue	1.366
Canonical R	0.934	Canonical R	0.758
Hits	100.00%	Hits	79.17%
<i>X_men</i> & <i>X_men</i>	0.3790*	<i>X_men</i> & <i>Y_close</i>	0.3259
<i>X_men</i> & <i>pause</i>	0.3275*	<i>X_men</i> & <i>X_off</i>	0.3073
<i>X_men</i> & <i>X_off</i>	0.2960*	<i>X_men</i> & <i>Y_flu</i>	0.2579
<i>X_men</i> & <i>Y_men</i>	-0.2071*	<i>X_men</i> & <i>Y_flu</i>	0.2579
<i>X_men</i> & <i>Y_sur</i>	0.1625*	<i>X_men</i> & <i>X_flee</i>	-0.1824
<i>X_men</i> & <i>Y_eat</i>	-0.1625*	<i>X_men</i> & <i>X_close</i>	-0.1824

Pooled within-groups correlations between discriminating variables (behaviour patterns) and canonical discriminant function. The variables are ordered by their importance of correlation with the canonical function.

* $P < 0.01$ to univariate Anova.

Reciprocal behaviours that contributed most to the canonical discriminant function in *Fam* pairs essentially confirmed already mentioned results. At the end of the *Menacing phase*, winners had the advantage of: (i) repeated *menaces* («*X_men* and *X_men*», where *X* is the future winner), (ii) retaliation to *menaces* initiated by the future loser («*X_men* and *Y_men*», where *X* is the future loser), and (iii) escalation initiated by the future winner, *i.e.* a switch to offensive behaviour right after having given a threat («*X_men* and *X_off*», where *X* is the winner). *Menaces* were more frequently not responded to, or more frequently followed by, *flutter* or by *going to the surface* when initiated by the prior member of a pair («*X_men* and *X&Y_pause*»). All these patterns were significant to univariate Anovas comparing winners to losers of *Fam* pairs.

In *Unf* pairs, similar behavioural interactions were also noted by the end of the *Menacing phase*, but none of them reached significance to univariate Anovas and the overall discriminant function was also not significant. Lack of space prevents the examination in details of discriminant results obtained for successive rounds of the offensive phase. However, they essentially confirmed what has been already mentioned. It should be clear that winners of *Fam* pairs could be forecasted earlier than future winners of *Unf* ones. This gives sufficient support, for the moment, to the expectation that differences develop during contest. These differences between winners and losers appear earlier when opponents are already acquainted

to each other, than when they are strangers.

4. Discussion

Our results are coherent with those prescribed by an «*asymmetrical games with perfect information*» as applied to familiar pairs but not to unfamiliar ones. Contestants that recently had the opportunity to settle conflict and meet again, upon recognizing each other, use the original asymmetry to rapidly settle disputes (Maynard Smith and Parker, 1976). These contestants can be considered as being in a situation of perfect information about their respective roles and solutions must be ESSs according to Selten's (1980) theorem. This could be reflected in the present data by the fact that all prior roles were reinstated, without any escalation. Though, prior winners systematically defeated prior losers under both conditions of cognizance, contest outcome was more extreme in familiar dyads than in unfamiliar ones. *Fam* individuals conformed to and reinstated their initial dominance relationship while, in *Unf* pairs, respective roles were less clearly identified. The costs of conflicts were also higher in *Unf* pairs than in *Fam* ones. Though total contest lengths did not significantly differ, unacquainted individuals required a longer period to assess each other, and had to rely on more pugnacious behaviours to settle disputes as compared to *Fam* individuals. As expected also, *Fam* pairs, being already cognizant of initial respective roles, were more characterized in terms of the behavioural patterns typical of each of these roles. Differences between future winners and losers were more obvious in *Fam* pairs, and appeared earlier during conflict. Therefore, it was possible earlier during contest to discriminate and to predict future winners from future losers of *Fam* pairs using behaviour interactions.

Though the main objective of the present work was not to identify which strategy was more appropriate to account for conflict resolution of unfamiliar pairs, some of our results nonetheless suggest that not a «*war of attrition*», but an «*asymmetrical game with assessment*» would apply. Most *Unf* pairs relied on dangerous behaviour and escalation to settle conflict and by definition in a «*true*» war of attrition, opponents rely on displays to settle the dispute. That *X.h.* rely on protracted fights to settle disputes is well known (Franck, 1964; Beaugrand and Zayan, 1985; Franck and Ribowski, 1989; Beaugrand et al., 1991; Ribowski and Franck, 1993a). These fights are very stressful, as indicated by drastic changes in corticoid concentrations which appear especially in losers right after conflict resolution (Hannes et al., 1984). Unfamiliar opponents allotted more time to what could correspond to a period of assessment. Moreover, future winners and losers did not use exactly the same patterns of behaviour during assessment. For instance, by the end of the Menacing phase (i.e. at round 10, ending with the use of the first dangerous behaviour), 79% of unfamiliar conflicts were characterized by more «*initiatives*» taken by future winners than by future losers (see Table 4). By «*initiatives*» is meant first menacing the opponent and then: (i) letting it approach (*X_men and Y_close*), (ii) escalating (*X_men and X_off*) immediately, or (iii) simply provoking it (*X_men and X&Y_pause*). At round 13, during the offensive phase, 90% of winners could also be predicted by their «*initiative*» in using either menaces or attacks. For instance the following patterns contributed significantly to the canonical correlation (0.82) at round 13: *X_off and X_men*, *X_men and Y_off*, *X_men and X&Y_pause*, *X_off and Y_men*, where *X* is the future winner and *Y*, the future loser. Future winners thus seemed to have the «*lead*». In a war of attrition, it is postulated that there is no exchange of information or communication, nor direct or indirect influence by one opponent that could change the behavioural trajectory of the other. Opponents should display with typical intensity (Morris, 1957; Maynard Smith and Parker, 1976) and keep in step with the adversary, giving sign of distress only at the very end of the contest as an indication of capitulation (Simpson, 1968; Dow et al., 1976; Jakobsson et al., 1979; Caryl, 1979). When escalation occurs in a (generalized) war of attrition, it is that «*escalation*» is not really dangerous since the winner is determined by its persistence time rather than by its risky use of weapons (Parker and Rubenstein, 1981).

Persistence time in *Unf* pairs (as determined by the time or energy expenditure the loser is willing to invest) was found to be a negative exponential distribution that could have been generated by a Poisson process. Though a war of attrition implies a distribution of persistence times conforming to a Poisson process (Parker and Thompson, 1980), finding that persistence times distribute accordingly (as a negative exponential) is not a particularly strong evidence for a mixed ESS, since all that is needed to generate such a distribution is that individuals have a constant probability of giving up per unit of time (Maynard Smith, 1982).

The game played by unfamiliar individuals was clearly asymmetric since most α s defeated ω s. Recent victory is known to increase RHP and recent defeat to decrease it. One must assume that, at the start of contest, asymmetries in experience were not perceptible because familiar and unfamiliar pairs would have behaved similarly, which was not the case. In addition, we must assume that the victory gains (*V*) assessed by opponents were on the average the same for both pair members. In

unfamiliar pairs, some information about asymmetry in *RHP* probably became available during contest and progressively tended toward a situation of optimal assessment (Parker and Rubenstein, 1981; Austad, 1983). In such a case the *ESS* is to persist indefinitely when in α role and to withdraw immediately when in the complement ω role. Even if assessment is less than perfect, then contest will also occur, but individuals in one role will persist longer. In the present research, the time required for assessment was longer in unfamiliar pairs, thus inversely correlated with the accuracy of initial assessment. As expected also, imperfect role assessment in *Unf* pairs generated more escalation (Parker and Rubenstein, 1981). Conversely, in *Fam* pairs, most contests settled entirely peacefully because reliable estimates of *RHP* were already available upon recognition of the opponent and, presumably, after quick assessment of resource value.

An alternative model, called the sequential assessment game (Enquist and Leimar, 1983; Leimar and Enquist, 1984) could also apply well to *Unf* and to *Fam* pairs of the present research. The model begins with the assumption that behavioural interactions serve progressively to inform and to obtain information on relative *RHP* of the combatants. An animal's decision to continue or to quit the contest is then determined by this information. *Fam* pairs upon recognizing each other would have been suddenly in a position to rapidly settle conflict because of no need for further assessment. As for unfamiliar pairs, they would have had to assess each other much longer in order to obtain stabilized information on mutual asymmetries, with increased costs and duration. The sequential assessment game would also have been in a position to make qualitative predictions based on asymmetries. However, the model was too much in advance quantitatively compared to our capacity to measure and control variables in the present situation and its possibilities would have been largely unexploited by the present data, as compared to its application to the fighting in the Bowl and doily spider (Leimar et al., 1991).

Behavioural asymmetries between future winners and losers of *Unf* pairs appeared during the course of contest and were strongly correlated with outcome. This eliminates that a «*true war of attrition*» applied in this case (Bishop and Cannings, 1978), unless these asymmetries were significant only to human observers (aided with statistical multivariate analysis and computing) and not strategically significant to the opponents themselves.

RHP is usually regarded as including differences in intrinsic features (*e.g.* size, strength, weaponry, etc, which might be called together «*fighting ability*») and differences in extrinsic features (*e.g.* postural differences to do with the relative placing of the two opponents) that would enable an individual to win an escalated contest (Maynard Smith, 1982). Functional models are not concerned with specifying which cues are used in the recognition and assessment of *RHP*. However, it is implicit that weapons, body size and information about previous encounters with that opponent (*i.e.* individual recognition) are the principal indicators of *RHP* (Archer, 1988). In his 1974 paper, Parker immediately recognized that successful fighting experience markedly increased the readiness for escalation (*e.g.* in mice and rats, Scott and Fredericson, 1951), an effect which he explained in terms of experience increasing *RHP*. One important question to answer is how prior experience (as a fraction of *RHP*) can influence dominance outcome.

Beaugrand and Zayan (1985) and Beaugrand et al. (1991, 1996) examined the question of how two or three factors that potentially contribute to individual *RHP* interact, especially when they are antagonistic. Their answer is that asymmetries such as size and prior experience simply add or cancel algebraically to each other. However, reality gets more complex when prior residence interact with prior experience and size. For instance Beaugrand et al. (1996) suggested that familiarity with the meeting site would have more a important comforting effect in prior losers than in prior winners, and that it could even cancel a disadvantage in size in such a case.

Asymmetries in resource (incentive) value *V* also play a major role in determining the outcomes of contests in animals (Parker and Rubenstein, 1981; Leimar et al., 1991) in functional models. During contests, it is presumed that both *RHP* and *V* are mutually assessed and compared by the opponents to take decisions concerning the course of conflict. However, an approach in terms of mechanism must admit that the animal possess the neural capacity to integrate and to compare all these factors and use the result to decide whether to retreat or to perform aggressive acts at any given moment during conflict. Maynard Smith and Riechert (1984) have proposed and tested a model based on the classical ethological hypothesis that agonistic behaviour is proximally determined by a balance between two conflicting tendencies, attack and flight. Such a model could help in bridging functional explanations with proximate causal ones. A similar effort has been made by Beaugrand et al. (ms3) in reducing several factors known to contribute to *RHP*, prior experience of victory and defeat, prior residency, size asymmetries and their interactions into a single continuum variable, which they called «*confidence*». Such a reduction did not diminish predictive power as compared to the use of the original variables, and insured some gain in proximal explanation.

The original expectation of early game theory models was that the behaviour of ultimate winners and losers were

indistinguishable until shortly before the end of confrontation (Maynard Smith, 1982). Only costly behavioural activities which are difficult to fake are expected to provide true information on RHP and not on their «intentions». In the Blue gourami (*Trichogaster trichopterus*), fin-tugging was the only aggressive pattern which could help in distinguishing ultimate winners from losers, with more fin-tugging in ultimate winners (Frey and Miller, 1972). Significant behavioural differences between winners and losers were reported to exist toward the end of fights in cichlids by Jakobsson et al. (1979), and by Mosler (1985). Turner and Huntingford (1986) report that in the cichlid fish *Oreochromis mossambicus* «circling around» and «tail-beat» could predict victory even from the first quarter of the contests onwards. Riechert (1978) also found that in the funnel-web spider *Agelenopsis aperta* the behaviour of the ultimate winners was less stereotyped before contest escalated. In unfamiliar *X.h.* pairs Ribowski and Franck (1993) report that «a significant characteristic of loser behaviour is that the Biting rates are higher before and after escalation. Conversely, Fin Grips are more frequent in ultimate winners than the losers. However, such behavioural differences are very poor predictors of the outcome of the fight from the viewpoint of a single individual during contest. Correct forecasts did not exceed 67%». This research has approached the same problem with the help of multivariate classificatory (discriminant) analyses on current accomplishments and rates of individual (*e.g. menaces*) as well as on interactive behavioural acts (*e.g. «X_men and Y_men»*). Our results have been mentioned and showed a rather good predictive power.

Finally, the present results confirm the existence of individual recognition in *Xiphophorus* that had been first reported by Zayan (1974) using hybrids between *X. helleri* and *X. maculatus*, and integrated by Beaugrand and Zayan (1985) in their model of dominance in *Xiphophorus helleri*.

When the repertoires of familiar and unfamiliar opponents are compared, major differences are thus noted. It is found that familiar pairs very rarely use mutual offenses and engage into combat. This contrasts with a majority of unfamiliar pairs that rely not only on mutual menaces, but also on mutual offensive behaviours and on escalation in order to settle conflict.

These results, together with the fact that previous dominant pair members of familiar pairs always defeated their subordinate opponent, suggest that *Xiphophorus* possess the neural capacity corresponding to the elementary cognitive processes involved in individual recognition and assessment.

Finally, the present work has some methodological implications when it comes to select a criterion that could serve as evidence that a species is capable of «individual recognition». The criterion must be doubly comparative. Pairs of acquainted individuals not only have to confirm or maintain their initial dominance status relationship but, in addition, they must at the same time manifest a much lower frequency of agonistic behaviour than that which is normally associated to the establishment of dominance relationship between unfamiliar opponents serving as a control. Invariance of the initial relationship is not sufficient since it could well reflect the fact that the *e.g.* larger or more aggressive individuals of each pair remain in a position to defeat their *e.g.* smaller or less aggressive opponents, without implying any individual recognition at all. The present research reproduces the findings of Zayan (1974) and shows that extreme differences are noted in the repertoire of individuals familiar to each other as compared to fish that are unfamiliar but that have received equivalent divergent experiences of dominance.

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References

- Archer, J., 1988. *The Behavioural Biology of Aggression*. Cambridge University Press.
- Austad, S.N., 1983. A game theoretical interpretation of male combat in the bowl and dolly spider (*Frontinella pyramitela*). *Anim. Behav.*, 31: 59-73.
- Beacham, J.L. and Newman, J.A., 1987. Social experience and the formation of dominance relationships in the pumpkinseed sunfish (*Lepomis gibbosus*). *Anim. Behav.*, 35: 1560-1563.
- Beaugrand, J.P., 1980. Observation directe du comportement. In: -- *Fondement et étapes de la recherche scientifique en psychologie* (M. Robert, Ed.). Paris: Maloine, pp. 165-218.

- Beaugrand, J.P. and Beaugrand, M., 1991. Prior residency and the stability of dominance relationships in pairs of green swordtail fish *Xiphophorus helleri* (Pisces, Poeciliidae). Behav. Proc., 24: 169-175.
- Beaugrand, J.P., Caron, J. and Comeau, L., 1984. Social organization of small heterosexual groups of green swordtails (*Xiphophorus helleri*, Pisces, Poeciliidae) under condition of captivity. Behaviour, 91: 24-60.
- Beaugrand, J.P., Goulet, C., Payette, D., 1991. Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri*: Effects of body size and prior dominance. Anim. Behav., 41: 417-424.
- Beaugrand, J.P., Payette, D. and Goulet, C., 1996. Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience, and prior residency. Behaviour, 133: 1-17.
- Beaugrand, J.P., Proulx, R. and Bégin, J., ms1. SYNTAX: a table driven parser for the recognition of behavioural patterns. (submitted)
- Beaugrand, J.P., and Zayan, R. (1985). An experimental model of aggressive dominance in *Xiphophorus helleri* (Pisces, Poeciliidae). Behav. Proc., 10: 1-52.
- Bishop, D.T. and Cannings, C., 1978. A generalized war of attrition. J. Theor. Bio., 70: 85-124.
- Braddock, J.C., 1945. Some aspects of the dominance-subordination relationship in the fish *Platypoecilus maculatus*. Physiol. Zool., 18: 176-195.
- Caryl, P.G., 1979. Communication by agonistic displays: What can game theory contribute to ethology ? Behaviour, 68: 136-161.
- Cohen, J., 1960. A coefficient of agreement for nominal scales. Educ. Psychol. Measurement, 20: 37-46.
- Dow, M., Ewing, A.W. and Sutherland, I., 1976. Studies on the behaviour of ciprinodont fish III. The temporal patterning of aggression in *Aphysemion striatum* (Boulenger). Behaviour, 59: 252-268.
- Enquist, M. and Leimar, O., 1983. Evolution of fighting behaviour: Decision rules and assessment of relative strength. J. Theor. Biol., 102: 387-410.
- Francis, R.C., 1983. Experimental effects on agonistic behavior in the paradise fish, *Macropodus operculatus*. Behaviour, 85: 292-313.
- Franck, D. 1964. Vergleichende Verhaltensstudien an lebendgebarenden Zahnkarpfen der Gattung *Xiphophorus*. J. Zool. Physiol., 71, 117-170
- Franck, D., Ribowski, A., 1987. Influence of prior agonistic experiences on aggression measures in the male swordtail (*Xiphophorus helleri*). Behaviour, 103: 217-239.
- Franck, D., Ribowski, A., 1989. Escalating fights for rank-order position between male swordtails (*Xiphophorus helleri*): Effects of prior-order experience and information transfer. Behav. Ecol. Sociobiol., 24, 133-143.
- Frey, D.F. and Miller, R.J., 1972. The establishment of dominance relationships in the blue gourami, *Trichogaster trichopterus* (Pallas). Behaviour, 42: 8-62.
- Hammerstein, P., 1981. The role of asymmetries in animal contests. Anim. Behav., 29: 193-205.
- Hammerstein, P. and Parker, G.A., 1982. The asymmetric war of attrition. J. Theor. Biol., 96: 647-682.
- Jakobsson, S. Radesäter, T. and Järvi, T., 1979. On the fighting behaviour of *Nannacara anomala* (Pisces, Cichlidae) . Z. Tierpsychol., 49: 210-220.
- Jennrich, R.I., 1977. Stepwise discriminant analysis. In: Statistical methods for digital computers (K. Enslein, A. Ralston and H.S. Wilf, Eds) New York: John Wiley, pp. 76-95.
- Kirk, R.E., 1968. Experimental design: Procedures for the behavioral sciences. Brooks and Cole.

- Leimar, O. and Enquist, M., 1984. Effects of asymmetries in owner-intruder conflicts. *J. Theor. Biol.*, 111: 475-491.
- Leimar, O., Austad, S. and Enquist, M., 1991. A test of the sequential assessment game: fighting in the bowl and doily spider *Frontinella pyramitela*. *Evolution*, 45: 862-874.
- Maynard Smith, J., 1974. The theory of games and the evolution of animal conflicts. *J. Theor. Biol.*, 47: 209-221.
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press.
- Maynard Smith, J., and Parker, G.A., 1976. The logic of asymmetric contests. *Anim. Behav.*, 24: 159-175.
- Maynard Smith, J., and Riechert, S.E., 1984. A conflicting-tendency model of spider agonistic behaviour: Hybrid-pure population line comparisons. *Anim. Behav.*, 32: 564-578.
- Morris, D., 1957. "Typical intensity" and its relation to the problem of ritualisation. *Behaviour*, 11: 1-12.
- Mosler, H.-J., 1985. Making the decision to continue the fight or to flee: an analysis of contests between *Haplochromis burtoni* (Pisces). *Behaviour*, 92: 129-145.
- Parker, G.A., 1974. Assessment strategy and the Evolution of fighting behavior. *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.
- Parker, G.A. & Thompson, E.A., 1980. Dung fly struggles: a test of the war of attrition. *Behav. Ecol. Sociobiol.*, 7: 37-44.
- Pimentel, R.A. and Frey, D.F., 1978. Multivariate analysis of variance and discriminant analysis. In: *Quantitative ethology* (P.W. Colgan, Ed.), New York: John Wiley. pp. 247-274.
- Ribowski, A. and Franck, D., 1993. Demonstration of strength and concealment of weakness in escalating fights of male swordtails (*Xiphophorus helleri*). *Ethology*, 93: 265-274.
- Riechert, S.E., 1979. Games spiders play. II. Resource Assessment Strategies. *Behav. Ecol. Sociobiol.*, 6: 121-128.
- Van Rhijn, J.G., Vodegel, R., 1980. Being honest about one's intentions: An evolutionary stable strategy for animal conflicts. *J. Theor. Biol.*, 85: 623-641.
- Scott, J.P. and Fredericson, E., 1951. The causes of fighting in mice and rats. *Physiol. Zool.*, 24: 273-309.
- Selten, R., 1980. A note on evolutionary stable strategies in asymmetric animal conflicts. *J. Theor. Biol.*, 84: 93-101.
- Siegel, S. and Castellan, N.J. Jr., 1988. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill.
- Simpson, M.J.A., 1968. The display of the Siamese fighting fish *Betta splendens*. *Anim. Behav. Monog.*, 1: 1-73.
- Slater, P.J.B. and Lester, N.P., 1982. Minimising errors in splitting behaviour into bouts. *Behaviour*, 79: 153-161.
- Turner, G.F. and Huntingford, F.A., 1986. A problem for game theory analysis: assessment and intention in male mouthbreeder contests. *Anim. Behav.*, 34: 961-970.
- Zayan, R.C., 1974. Le rôle de la reconnaissance individuelle dans la stabilité des relations hiérarchiques chez *Xiphophorus* (Pisces, Poeciliidae). *Behaviour*, 49: 268-312.
- Zayan, R.C., 1975. Défense du territoire et reconnaissance individuelle chez *Xiphophorus* (Pisces, Poeciliidae). *Behaviour*, 52: 266-312.