Relation between dominance rank, prior agonistic intensity and subsequent aggressive levels in winners and losers of dyads of male Green swordtail fish (*Xiphophorus helleri*)

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Version 30/11/01 14:38:55

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Abstract

Aggressive scores obtained in a mirror test 1h before an encounter were found to be a good predictor of victory in male *Xiphophorus* dyads showing less than 5% size differences. Out of 36 dyad members showing higher aggressive scores at pre-test, 28 obtained victory in the subsequent encounter. It was found that future winners were more aggressive than future losers to their own image in mirror tests before their encounter. Initial individual aggressive levels in mirror tests were also found to be a function of the rank the individuals occupied in their home hierarchies. The higher the rank, the higher was the individual aggressive level as measured by mirror pre-tests, as well as by post-tests. This relationship applied to future winners, as well as to future losers. The level of aggression reached during agonistic encounter was not a function of the social ranks the opponents occupied in their home hierarchies. Males in dyads composed of two omegas fought as fiercely as males in dyads of two alphas or two betas. No significant relationship was noted between the initial individual aggressive scores at mirror pre-test and the levels of aggression reached during encounters. We found in winners the existence of a significant correlation between the aggressive level they reached during agonistic encounter and a subsequent *increase* in aggressive levels at mirror tests 1h and 24h after victory. The more intense the agonistic encounter, the more important the subsequent increase in aggressive level in winners; an increase which was still detectable 24h after victory. However, prior alpha winners were apparently not as sensitive as prior betas and prior omegas to the aggressive level reached during the encounter since their mirror scores obtained after victory did not change when compared to their baseline at pre-test. After defeat, losers did not show any significant change in aggressive scores in mirror tests. Moreover, it was found that encounters in which a 1h resident met an intruder were in general less aggressive than encounters between two intruders. Experiential effects are discussed as instances of learning and generalisation.

Keywords: Agonistic experience; Aggressive behaviour; Dominance; Subordination; Mirror test; Green swordtail fish; *Xiphophorus helleri*

Introduction

In many species of animals including fish, victory in a first agonistic encounter facilitates victory in a subsequent one, while prior defeat would have the contrary effect (Frey & Miller, 1972; Zayan, 1975a; Francis, 1983; Beaugrand & Zayan, 1985; Beacham & Newman, 1987; Beacham, 1988; Beaugrand, Payette & Goulet, 1996; Hsu & Wolf, 1998).

But what is the nature of victory or defeat experience? Is it simply a categorical state as e.g., being "prior-dominant" or "prior-subordinate" as it has usually been treated in the ethological literature, or is it a continuous property which comes with various values or quantities, and eventually measurable? Winning and losing experiences most likely come in various types and possibly degrees. In different contests, a winning individual would receive a given amount of dominance experience, while another one would receive a different amount. The same condition would prevail for a losing experience, which could vary according to defeated individuals from different encounters. Early indications for the existence of a continuum in an agonistic experience rather than of qualitative states came from Ginsburg & Allee (1942) and from Ratner (1961). Ginsburg & Allee (1942) have shown that there was a very good correlation between the initial rank of a hen in a small group and its propensity to win in a staged contest against a standard opponent. As for Ratner (1961), he found a direct relationship between the number of pecks received by a hen from a despot in a standard contest and its descent in the hierarchy once returned to its social group; the more it had been mistreated by the despot, the more it descended to a low rank.

More recently, Beaugrand & Goulet (2000) reported that *Xiphophorus* dyads composed of a prior-winner and a prior loser obtained through "rigged" contests were much more aggressive in subsequent encounters than pairs in which the dominant and subordinate could spontaneously self-select. Pairs to which prior experience had been imposed through their meeting with a much larger or smaller opponent recuperated more rapidly from handling, initiated contact earlier, took more time to assess each other and fought for a longer period of time than pairs in which the winner and loser self-selected as a spontaneous outcome of the encounter between well matched opponents. Prior-winners and prior-losers of the rigged condition more frequently relied on aggressive behaviour during contest than that of the self-selected condition. As a consequence, prior-winners and prior-losers of rigged pairs won equally the subsequent contest. On the contrary, prior-winners of the self-selected condition defeated their prior-loser opponent in a majority of cases. Beaugrand & Goulet (2000) tentatively explained their results by the following principle: winning or losing against a well matched opponent would provide more experience than winning over a much weaker opponent, or losing to a much stronger one. Their research reinforces the hypothesis that prior-experiences of victory or defeat are not qualitative states but come in various degrees and can be conceived as continuous variables.

The present research is concerned with the immediate determinants of experiential effects left by recent victory and defeat. Which individual prior states, and which events occurring during a given encounter determine the amount of experience one individual will register ? More particularly we examined the agonistic intensity of the encounter in which a victory or a defeat was experienced. As suggested by Beaugrand & Goulet (2000), it is possible that the higher the agonistic investment made during an encounter, the more important the experience recorded by the individual whatever the dominance outcome. At the level of prior individual states which might influence the amount of experience received, we examined the hierarchical status recently occupied by individuals; prior status might influence not only the intensity of agonistic encounters but also the way animals react to victory or to defeat. For instance, prior dominants may react more negatively to defeat than prior subordinates, which have nothing to lose anyway.

There is some evidence that prior status affects the fighting behaviour of male swordtails. Wilhelmi (1975) and Rohrs (1977) showed that rank order fights between omega males tend to be longer and more intensive, with significantly more circling and mouth-to-mouth fighting, than fights between alpha males coming from already stable hierarchies. Franck & Ribowski (1986) also found that high ranking males raised in heterosexual groups from birth behaved much less aggressively than low ranking males raised in a similar environment. The biting rates in mirror tests decreased systematically with increases in dominance position. Franck & Ribowski (1987) confirmed this by taking the two highest ranking males and the two lowest ranking males of already established hierarchies (6-14 mature males with females) and subsequently subjecting them to a mirror test for 15 min. They found that the biting rates of the low ranking males were 5-fold higher than those of the high ranking males. These results led them to conclude that aggressive scores to mirror tests were much higher in low ranking than in high ranking males. Such a result seems contrary to what is observed when *Xiphophorus* males are studied interacting in their own home hierarchies: high ranking males show much more aggressive behaviour than low ranking ones (Beaugrand, Caron & Comeau, 1984).

Franck & Ribowski (1987) also investigated whether escalated fighting activities and the associated experience of winning or losing a fight could change an animal’s aggressiveness and its chance of winning a subsequent aggressive encounter. They first subjected swordtail fish males to a mirror pre-test. Then, 72h later 9 escalated fights of 10 min duration over a period of 3 days were imposed on the fish. In none of the encounters did the subjects have the final experience of winning or losing the fight. They found that biting rate significantly increased from mirror pre-test to the post-test more in experimental than in control fish who had only been pre- and post-tested but had not received the experience of fighting. Paradoxically, in their study, less aggressive controls were found to significantly defeat more aggressive experimental fish, leading these authors to conclude that probably escalated fighting activities did not improve the chance of winning subsequent fights and could even reduce this ability.

Franck & Ribowski (1987) also investigated the effect of victory or defeat upon measures to mirror tests passed approximately 1.5h before an agonistic encounter, and immediately after that encounter, and 24h later. They found that the biting rates of prior winners immediately increased after the first fight and those of losers drastically decreased. The biting rates of winners and losers were much nearer to the pre-experimental level 24h after the fight, but a significant difference was still present.

Though Franck & Ribowski (1987) report divergent effects upon subsequent aggressive levels due to prior experience of victory or defeat, they did not look specifically for a possible relationship between the intensity of agonistic exchanges in the preceding fight and the subsequent aggressive level. Moreover, the apparently incoherent results they reported concerning increased aggressive levels diminishing chances of subsequent victory requires clarification. It is possible that there exists an interaction between the initial hierarchical status of opponents, the level of aggression which they attain during encounter, and the subsequent importance of winner and loser effects, aspects which the present research will investigate.

Methods

Subjects and material

We had at our constant disposal in the laboratory about 1,000 adult males of the species *Xiphophorus helleri* bought at least one month earlier from the same breeding farm (5D Tropical Inc., Plant City, Florida, USA). These males were distributed in 9 batches of 100-150 individuals into large 165 litre tanks measuring 90x50x40 cm each. The fish were fed twice a day and kept under a 12:12 light-dark cycle initiated at 0900h.

The engagement of pairs, as well as their existence in small hierarchies composed of three individuals necessitated throughout the experiment the use of 40 identical glass aquariums measuring 30x30x15 cm and containing 13.5 litres of water each. The bottom of each aquarium was covered with 2 cm of gravel and assorted objects (shells, pieces of plastic, coloured rocks) which were spread out unevenly over the gravel in order to encourage the eventual recognition of the fish's milieu. The mirror tests lasted 5 min and were carried out in a smaller aquarium (15x15x30cm) divided in its middle by an opaque plastic separator which could be raised by the researcher at will. A 14x14cm glass mirror was placed inside the aquarium at the extremity of one of thus defined sections of the aquarium while the fish to be tested was confined to the alternate section of the aquarium behind the opaque separator. When the separator was raised, the fish could see its own image reflected by the mirror, approach it, and display to it.

Size measurements

We took three measurements of each fish (to a precision of 0.5 mm): (1) Body length - the distance between the tip of the snout and the tip of the caudal fin; (2) Sword length - the distance between the tip of the caudal fin and the outside of the sword; and (3) Flank height - the greatest distance between the root of the dorsal fin and the root of the gonopodium. These measurements were taken before triad formation and measurements were obtained while the fish remained in the aquatic environment. With the aid of a mobile mesh partition, the fish was gently immobilized against the inside glass wall of the aquarium. The anatomical positions, which correspond to the aforementioned measurements, were rapidly marked on the glass with a felt marker. After the fish was freed, a ruler was used to measure the distance between the marks left on the glass. We paired males according to differences in their lateral surface (*LS*). *LS* were obtained by adding the sword-length to the product of total length and flank height. Calculated in this way, Beaugrand & 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* had a significantly greater correlation with dyadic dominance outcome than the standard length in *Xiphophorus*.

Behaviour observations

Agonistic behaviour units of *Xiphophorus helleri* have been amply described (see e.g., Beaugrand & Zayan, 1985). The following behaviours were retained to be noted in the present research.

Unilateral attack: charge, butt or bite the opponent, or charge or bite the mirror.

Unilateral menace: lateral sigmoid display or tail-beating in front of the opponent or in front of the mirror.

Mutual attack: mutual charge, mutual biting, mouth-fight.

Mutual menace: mutual lateral sigmoid-display or mutual tail-beating.

Chase: unilateral attack followed by either fleeing or by adoption of a submissive posture by the opponent.

At the moment of analysis, these units were regrouped into larger behavioural categories:

Menaces: all unilateral and mutual menaces.

Attacks: all unilateral and mutual attacks.

Aggressive behaviour: all unilateral and mutual menaces and attacks.

Dominance criterion. We considered a dominance relationship as being established when one fish (dominant) was successful in chasing its opponent on six occasions without having been threatened, attacked or bitten in turn. Such a criterion has been validated by Beaugrand & Beaugrand (1991).

Welfare. 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 fulfilled. Neither detectable injury nor death occurred during the experimentation.

This research comprises two experiments which were carried out in succession during the same summer months in 1996.

The establishment of triads in home hierarchies

Before commencing any experimentation, fish were first established as triads and their hierarchy determined. Adult males were randomly caught from communal tanks, individually measured, and carefully described. The fish to form a triad had to be distinguishable from each others in order to be recognizable by the researcher. They had to be of similar morph, to show the same degree of sexual maturity, and to have size variations within a 20% range. Forty such triads were thus established in 15x15x30 cm aquariums and left undisturbed for one week before the beginning of any experimental manipulation. In the meanwhile, these fish established dominance hierarchies which became known to the researcher who inferred their respective ranks from the daily observation of their agonistic behaviour. Fish from triads whose hierarchy was not clearly known or stabilized after 7 days were not used in the rest of the experiment. In this paper "home hierarchies" will refer to triads which remained stable during the whole period of experimentation. Alpha, beta and omega fish will refer to individual fish respectively occupying the first, second and third rank in home hierarchies. At the end of experiment 1 and after each test carried out in experiment 2, the fish were returned to their home hierarchy and their position in the home hierarchy was monitored for any change in rank.

Experiment 1

The objective of the first experiment was to determine whether differences existing between opponents on measures of aggression obtained from a mirror pre-test could predict dominance outcome in a subsequent agonistic encounter.

A single sample composed of 36 pairs of *Xiphophorus* males was used. Pair members came from different home hierarchies in which they occupied similar ranks. They were thus unfamiliar with each other and with the meeting place. They had to show similar sexual maturity and morph. They were also carefully matched on size which showed less than 5% difference.

Members to form a pair were first simultaneously and independently subjected to a mirror test of a duration of 5 min. Menaces and attacks initiated towards their own reflected image were counted. Each fish was then isolated for a 1-hour period in another unfamiliar tank after which period pair members met in a still unfamiliar aquarium. Agonistic behaviour was used to determine which pair member dominated the other. The agonistic encounters lasted until the dominance criterion was reached or 30 min, whichever came first. Fish were then returned to their home hierarchies.

Experiment 2

The second experiment had several objectives. The first objective was to identify the nature of the relationship existing between the quality / intensity of agonistic encounters and subsequent measures of aggression in winners and losers. More specifically, we were expecting that more intense agonistic encounters would have more drastic and divergent effects on subsequent aggressive levels in winners and losers. A second objective was to obtain the relationship existing between the ranks occupied by males in their home hierarchy and the aggressive levels measured by mirror tests before and after agonistic encounter. A third objective was to identify the relationship existing between previous ranks in home hierarchies and the level of aggression reached during the subsequent dyadic encounter.

The experiment comprised two samples originally composed of 50 pairs each. The first sample (RI) corresponds to the condition in which familiarity with the meeting place was used as an asymmetry to induce agonistic variability within the encounters. These conditions consisted of encounters between a 1h prior resident and an intruder. The other sample (II) was composed of pairs of unfamiliar intruders encountering in an unfamiliar aquarium. Each sample was subdivided into 3 levels in which opponents occupied similar ranks in their respective home hierarchies: both opponents were either alphas, betas, or omegas. Each pair member was subjected to four mirror tests, 24h (pre-1) and 1h (pre-2) before the agonistic encounter, and 1h (post-1) and 24h (post-2) after the agonistic encounter.

Except for the prior residents which had spent 1h in the meeting place, all other fish were unfamiliar with the meeting place. Fish to form a pair had to show similar sexual maturity and morph. They were also carefully matched on size, which had to show less than 5% difference. Fish were returned to their home hierarchies after pre-1 and post-1. One hour before the agonistic encounter, pair members were recaptured from their home tank and introduced singly into an unfamiliar aquarium. After one hour, the fish to form a pair were netted, placed in a small plastic container for 5 min and then simultaneously introduced into the aquarium where they encountered. In 50 cases selected at random, one fish of the pair was returned to the aquarium where it had been previously isolated for 1h, thus becoming a prior-resident. Fish were left to interact with each other for 30 min, and all agonistic behaviours were noted.

Results

Experiment 1

Winners were not larger than losers in lateral surfaces (winners=524$_{mm2}$, losers=522, Anova F=.004, df= 1 / 70, *P*=.95).

Figure 1 illustrates the results for agonistic behaviour. As can be seen, future winners were systematically the more aggressive of the pairs in the mirror test carried out 1h before encounter. On the average, during mirror test, winners used menaces more frequently than losers (winners=4.55, losers=2.33, F=8.82, df=1 / 70, *P*=.004), and they attacked their own image more frequently (winners=4.50, losers=1.89, F=15.66, df=1 / 70, *P*=.002). The same applies to the sum of menaces and attacks, winners being superior to losers in that respect also (winners=9.00, losers=4.2, F=17.39, df=1 / 70, *P*<.001).

Of the 36 winners, 26 had superiority of menaces, 29 of attacks, and 28 were superior in the use of both aggressive behaviours, which is significant to a binomial test (min Z-Binomial test, p=.5, x=26, n=36, *P*<.006).

Thus one may conclude that winners were in general more aggressive to their own image reflected in a mirror than losers which they encountered in a subsequent experiment.

Experiment 2

Comparison of winners to losers on mirror test scores

In most cases only the results for the total number of aggressive acts will be presented since they perfectly reflect the results obtained for menaces and attacks.

Results obtained at the four successive mirror tests are illustrated at Figure 2. It is noteworthy to recall that the two first mirror tests were passed 24 (Pre-1) and 1h (Pre-2) before agonistic encounter, and that the two other tests were passed 1h (Post-1) and 24h (Post-2) after the encounter.

As revealed by Figure 2, future winners were systematically more aggressive (mean total number of aggressive acts) in the mirror tests before encounters than future losers (Pre-1: t=4.43, df=186, *P*<.001; Pre-2: t=3.95, df=186, *P*<.001) thus confirming the results of Experiment 1. Repeated testing at pre-test conducted to a significant diminution in aggressive levels from Pre-1 to Pre-2 in both future winners and losers. (winners: t=2.04 , df=93, *P*=.044; t=2.19, df=93, *P*=.031). This probably corresponds to habituation.

In general, winners remained more aggressive than losers after the agonistic encounter. Thus in 76 of the 94 pairs, the winner was the more aggressive member of the pair after the two successive post-tests, which is highly significant (Z-Binomial test, p=.5, x=76, n=94, *P*<.0001).

In winners, aggressive levels increased after victory (t= -3.0, df=93, *P*<.003) and were still of a higher level 24h after victory (Wilcoxon Z=-2.09, *P*=0.036). The diminution between Post-1 and Post-2 was not significant in winners (t=-1.33, df=93, *P*=.187).

In losers, defeat did not have any significant effect on subsequent aggressive levels. When compared to their pre-test level, aggressive levels of losers remained unchanged 1h (t=0.22, df=93, *P*=.45) and 24h (t=-1.27, df=93, *P*=.45) after defeat. There was no difference between Post-1 and Post-2 in losers (t=0.84, df=93, *P*=.40), and the slight increase noted on Fig. 2 24h after was not significant (Pre-2 to Post-2: t=-1.17, df=93, *P*=.25).

Thus, based on comparisons of the aggressive levels measured before and after confrontation, it appears that only winners were affected by the subsequent victory and this effect was still significant 24h later. On the contrary, losers did not seem to be affected by their defeat.

Influence of agonistic intensity upon subsequent aggression levels at post-test.

One main objective of the present research was to find any relationship existing between aggressive levels noted during encounter, and the subsequent aggressive levels as measured by the two post-tests.

The difference between the number of aggressive acts initiated by the winner and loser within each pair, divided by the total number of all unilateral and mutual aggressive acts noted during each encounter was used as an index of agonistic intensity which occurred during a given encounter. This index varied between 1 and 70 with a mean of 18.1 [$CI_{.95}$: 15.13 to 21.09]. Several other indexes were tried as well, but calculated in this way, it gave the best correlations with changes in aggressive level from Pre-test to Post-test. Figure 3 presents correlations thus calculated between the chosen index and changes in aggressive levels. It can be seen that in general correlations were higher for the winners than for the losers. The highest correlation was obtained for changes between Pre-2 and Post-1 for winners (r=0.5, df=93, 2-tail $P< .001$).

Thus, the more intense the agonistic encounter, the more important was the subsequent increase in aggressive levels in winners. This increase was still detectable 24h after victory (r=.36, df=93, $P<.001$). In losers, there was apparently some increase (r=.26, df=93, P<.01) but far less important than for winners. It is clear that winners increased more after the encounter than losers did (t-test for correlated data=-3.14, df=93, $P<.002$). The slopes of the corresponding regression lines illustrated at Figure 4 visually confirms this. The lines on this figure were obtained for winners and losers by linearly regressing level of aggression reached during encounter onto the change in aggressive levels between the pre-test 1h before the encounter and the post-test 1h after encounter. The regression equation is highly significant for winners (Anova F=30.22, df=1/91, $P<.001$), but nonetheless significant for losers (F=6.82, df=1/91, $P<.01$). Similar results were obtained for indexes of aggression calculated in various manners as well. Similar results were obtained for indexes of aggression calculated in various manners as well.

Relationship between initial aggressive levels to pre-tests and aggressive levels reached during encounter

No systematic or significant relationship was found between initial individual aggressive levels of pair members and the aggressive level they reached during their encounter. This applies to menaces, and attacks as well as to their combination. For instance, the highest correlation obtained was between the scores at the first mirror pre-test and frequency of attacks initiated by the future winner; but it was not significant (r=0.05, df=93, *P*=.64).

Importance of prior status in home hierarchies

Another major objective of the present research was to examine the relationship between prior hierarchical status and aggressive levels in mirror tests and during agonistic encounter. In this experiment, the rank each opponent occupied in its home hierarchy was known and equalized within pairs. Thus 32 pairs were composed of an alpha meeting another alpha, 29 of a beta meeting another beta, and 32 were of two omega opponents. Figure 5 presents the mean aggressive levels showed at Pre-1 and Post-1 as a function of the social rank of winners and losers. Several interesting tendencies can be recognized on this figure.

First, again it can be seen that pre-test aggressive levels were in general higher in future winners than in future losers. This is confirmed by statistical analysis (Total aggression: Anova F=15.47, df=1/186, *P*<.001).

Second, within the category of future winners and future losers, aggressive levels followed more or less the social rank of the individuals, being higher in alphas, intermediate in betas and lowest in omegas. Analyses using orthogonal components indicates that the linear trend is significant for winners, for losers, and for winners and losers combined into a common trend (min F =27.60, df = 1 / 182**,** *P*<.001 for the linear component). Post-hoc Scheffé tests were used to locate significant differences in aggressive levels according to initial rank. Alphas who were to win were at Pre-1 and Pre-2 more aggressive to their own image than betas and omegas which were to lose. They more frequently menaced (min F=8.65, df=2 / 185, *P*<.003, Scheffé: 8.92, *P*<.003) and attacked (min F=3.11, df=2 / 185, *P*<.05, Scheffé: 4.89, *P*<.05) and their total aggressive level was higher (min F=5.82, df=5 / 182, *P*<.001, Scheffé winner-alpha / loser-beta : 23.75, *P*<.001; Scheffé winner-alpha / loser-omega: 18.94, P<.02) . Other differences were not strong enough to reach statistical significance.

Third, the ordering principles just mentioned also applied to aggressive scores taken 1h after agonistic encounter, and to a lesser degree 24h after. In this case also the overall linear trend was significant (F = 28.52, df= 1 / 182 *P*<.001).

Fourthly, as mentioned previously, in general aggressive levels of winners increased from pre-test to post-test. But the significant increase was only due to betas and omegas (t-2.86, df=60, *P*<.006), not to alphas for which no difference was found between mirror tests Pre-2 and Post-1 (t=-1.37, df=31, *P*<.179).

In losers, no significant change occurred in aggressive levels after agonistic encounter. Prior alpha losers did not change in aggressive level (t=-.03, df=31, *P*=.98), omega losers slightly increased but not significantly (t=-1.29, df=31, *P*=.205), while betas almost significantly decreased (t=2.03, df=28, *P*=.052).

Relationship between prior ranks and agonistic intensity during fight

Pairs composed of two alphas were not more or less systematically aggressive during agonistic encounter than pairs composed of two omegas or two betas (F=.04, df=2 / 92, *P*=.96).

Effects of prior residence

In the present research it was possible to compare the behaviour of the 47 encounters between a resident and an intruder (RI), to the 48 encounters between two intruders (II).

Residents defeated intruders in 29 out of 47 pairs, which approaches significance (Z-Binomial test, p=.5, x=29, n=47, $P<.072$). It was found that within RI pairs, residents were not significantly more aggressive than their intruder opponents, nor in their use of menaces, attacks, or both (max F=2.34, df=1/91, $P=.13$). However, comparing RI to II for aggressive levels during encounter, it was found that encounters between two intruders were more aggressive than encounters between a resident and an intruder (F=15.01, df=1/91, $P<.002$ for total aggression). Winners and losers of II pairs were systematically more aggressive than winners and losers of II pairs in their use of both menaces and attacks (min F=6.29, df=1/91, $P<.014$). They used menaces more frequently (mean: 23 versus 11, F=7.49, df=1/91, $P<.001$) and attacked three times more frequently than RI pairs (mean: 20 versus 7, F=21.46, df=1/91, $P<.001$). The latency of the first attack was also longer (Mann-Whitney U-test, $Z=-1.951$, $P<0.05$) in II pairs than in RI ones. In RI pairs, first attack was the initiative of the resident in a great majority of cases (Z-Binomial test: p=.5, x=37, n=47, $P<.001$).

Thus, although 1h prior residence did not significantly change the probability that the resident individual defeated the intruder, it nonetheless *reduced* the amount of aggressive behaviour necessary to reach outcome, as compared to that of control encounters in which both pair members were unfamiliar to the meeting place.

Discussion

Relationship between scores at mirror pre-test and subsequent dominance outcome

One objective of this research was to determine whether differences existing between opponents on measures of aggression obtained from a mirror pre-test could predict dominance outcome in a subsequent agonistic encounter. We found that future winners were more aggressive than future losers to their own image in mirror tests passed before encounter. Future winners used menaces and attacks more often than future losers. In a significant majority of pairs, 28/36 in the first experiment and 70/93 in the second, the male showing a higher aggressive score in both of the 5 min mirror pre-tests was to win the subsequent encounter.

Such a finding is particularly interesting since aggressive levels measured using mirror tests could represent an appreciation of the initial basic fighting ability or aggressiveness of the individual, or of its initial aggressive motivation. These intervening variables are useful to represent the biological function which internally controls the readiness to show aggression and which ensures that aggression will occur at appropriate times, and at the appropriate level. Motivation to show aggressive behaviour is often treated as part of a balance system between aggressive and fear tendencies (as in e.g., Archer, 1988). If mirror tests can be considered as a measure of fear in front of an unfamiliar opponent, then our results are consistent with that of Rasa (1969) who found that a low index of fearful behaviour at the beginning of a fight was correlated with subsequent victory in conflicts between pairs of juvenile pomacentrid fish.

In their model of determinants of dominance in *Xiphophorus,* Beaugrand and Zayan (1985) had identified that prior experiences of victory and defeat, and familiarity with the meeting place, could together explain more than 87% of dominance outcomes in dyads in which size differences were less than 5%. Later these factors were studied in interaction with larger size differences (Beaugrand et al., 1991, 1996). However, when combined these factors could not explain more than 75% of outcomes when size differences between opponents were less than 20%. Basal individual aggressive levels, as measured through a mirror test, could allow to increase the predictive and explanatory powers of future models.

Franck & Ribowski (1987) have found that the reproducibility of the mirror test was really excellent with male *Xiphophorus*, with extremely high correlations between a first and a second test, even when after one or two months between testing. We confirm such a general appreciation, though we are conscious that a mirror test is quite different from being equivalent to an agonistic encounter, that the fish rapidly habituate to it, and that a single test passed right before an agonistic encounter can sensitise the subject, thus increasing its aggressive behaviour in the subsequent encounter. One major problem with mirror tests is that the mirror image never initiates menace or attack and never flees.

Relationship between prior ranks in home hierarchies and scores at mirror tests

Initial individual aggressive levels in mirror tests were found to be function of the rank the individuals occupied in their home hierarchies. The higher the rank, the higher the individual's aggressive level as measured by mirror pre-tests, as well as by post-tests. This relationship applied to future winners, as well as to future losers. This finding is not surprising since motivation to defend ones rank should depend upon the rank already occupied. Beaugrand et al. (1984) have clearly shown that in stabilized tetrads of male *Xiphophorus* maintained with females, mean frequencies of aggressive acts were proportional to the hierarchical status of the initiating individual, with the alpha male having neat superiority in 70% of cases. It is not surprising that scores in mirror tests passed 30 min only after having been retrieved from their home hierarchies still reflected the aggressive levels these fish had to maintain in order to defend their rank in their home hierarchies.

However, this result is absolutely contrary to what Franck & Ribowski (1986, 1987) have reported in similar experiments. In mirror tests they have found that high ranking males raised in small heterosexual groups from birth behaved much less aggressively than low ranking males. The biting rates to the mirror tests decreased systematically with increasing dominance position. In one of the experiments published by Franck & Ribowski (1987) the two highest ranking males and the two lowest ranking males of already established hierarchies (6-14 mature males with females) were isolated for 18h in a test aquarium to be subsequently mirror tested for 15 min. The biting rates of the low ranking males were 5-fold higher than those of the high ranking males. These authors concluded that aggression scores in mirror tests of males from long-term stabilized groups were much higher in low ranking than in high ranking males. In order to verify whether biting rates would change according to a change in status, they re-arranged groups in such a way that high ranking males dropped and low ranking ones ascended in the social hierarchy. They found that social improvement resulted in a decrease, and social worsening in an increase of biting rates in the mirror test. In still another experiment, they tried to extinguish the rank order experience by a 30-day period of social isolation flanked by two mirror tests. Again, in the first test, alpha males were by far less aggressive than omega males. In the second test, the prior alpha males were more aggressive and the prior omega less aggressive than before, the difference between biting rates having disappeared (only N=9 were used under each condition). As we shall discuss later, social isolation could explain the discrepancy between their results and the present ones.

Absence of relationship between prior social rank and intensity of agonistic encounters.

Though winners showed higher aggressive scores than future losers at pre-test, and since prior alphas had higher aggressive scores than prior betas and omegas, one could have expected that two alphas would reach higher aggressive levels in the subsequent encounters than two omegas. This is not the case. The level of aggression reached during encounter was not a function of the social ranks the opponents occupied in their home hierarchies. Two omegas fought as fiercely as two alphas or as two betas. Since both opponents in the present research always occupied the same rank (i.e., two prior alphas, two betas, two omegas), we cannot eliminate the possibility that the aggressive level reached was due to the presence of only a minimal rank asymmetry within each pair. Future research staging the encounters of mirror pre-tested opponents occupying various hierarchical ranks could clarify this.

The fact that fights between prior alphas were not more aggressive than between prior betas or omegas reinforces the hypothesis than mirror tests do not furnish the same measure of aggressive potential as fights.

Still, such results contradict those published by Wilhelmi (1975) and Rohrs (1977). These authors had reported that rank order fights between omega *Xiphophorus* males tended to be more aggressive than between prior alpha males. They fought longer and more intensively, with significantly more circling and mouth-to-mouth fighting. Again, their fish were isolated immediately prior to encounter, a procedural difference which could explain the discrepancy between their results and ours.

Absence of relationship between aggressive scores at mirror pre-tests and aggressive levels reached during encounter

One could have also expected that the higher aggressive levels at pre-test shown by two fish forming a pair, the more their subsequent fight would have been protracted and highly aggressive. Such an expectation did not confirm itself. No significant relationship was noted between the initial individual aggressive scores at pre-test and the levels of aggression reached during encounter. Again, such a result asks about the concurrent validity of scores given by mirror tests and that given by agonistic encounters.

Nonetheless, such a result is perfectly in agreement with that prescribed by game theory. Animals may be initially of different fighting potentials, a difference which it is to their interest to advertise to their opponent, but they should not reveal to the opponent to what extent they are willing to continue displaying or fighting (Maynard Smith, 1982). Thus they display with uniform and typical intensity (Morris, 1957). Indeed, many studies have shown the difficulty to distinguish between the behaviour of the eventual winner and loser except near the end of a contest (Simpson, 1968; Dow et al., 1976; Jakobsson et al., 1979; Beaugrand, 1997). Natural selection, Maynard Smith argued, would favour a sharp switch at a threshold level of motivation. As long as the motivational balance stills favours attack, it should occur at full intensity, but once the threshold level is reached, there should be a sudden change to escape behaviour in the future loser.

Relationship between aggressive levels reached during encounter and subsequent scores at mirror tests

Another major objective of the present study was to identify any relationship existing between aggressive levels noted during encounter, and the subsequent aggressive levels as measured by the two mirror post-tests. The present study found in winners the existence of a significant correlation between the aggressive levels they reached during agonistic encounter and a subsequent *increase* in aggressive levels during mirror tests 1h and 24h after victory.

The more intense the agonistic encounter had been, the more important was the subsequent increase in aggressive level in winners, an increase which was still detectable 24h after victory. However, prior alphas were apparently not as sensitive as prior betas and prior omegas to the aggressive levels reached during encounter since their mirror scores at post-test did not change when compared to their baseline at pre-test. The highest correlations were thus obtained for changes between Pre-2 and Post-1 in winners when alphas were excluded from data to be analysed (r=0.53, df=61, P<.001), explaining 25% of variance.

Following the results obtained by Franck & Ribowski (1987), we were expecting that this correlation would be negative in losers, to account for the reduction in aggressive scores in mirror tests after defeat that they had reported in a similar study. Though the present result only partially confirms their finding it nonetheless bears some importance: victory experience at least would be a function of what happened during the proceeding encounter in which it was acquired, and it would be a function of the intensity of the agonistic exchanges which occurred while such an experience was acquired. The more intense the encounter in terms of aggressive levels reached, the more important the effect upon subsequent aggressive levels as measured in mirror tests in winners.

Franck & Ribowski (1987) found that the biting rates of winners immediately increased after the first fight and those of losers drastically decreased. The biting rates of winners and losers 24h after the fight were much nearer to the pre-experimental level but a significant difference was still present. In the same paper, these authors also investigated the problem of whether escalated fighting activities and the associated experience of winning or losing a fight could change an animal’s aggressiveness and its chance of winning a subsequent aggressive encounter. In the experiment they made, *Xiphophorus* males were first subjected to a mirror test. Then 72h later, they imposed 9 escalated fights of 10 min duration over a period of 3 days on the fish. In none of the encounters did the fish have the final experience of winning or losing the fight (the fight was interrupted before decision; those fight which resulted into decision were eliminated from the sample). The fish were left in isolation for 18h in the future meeing place. Then, by raising a partition each experimental male was confronted with one ‘control’ male, which had not experienced fighting activity, and the winning and losing individuals were determined. They found that biting rate significantly increased from one mirror test to the other in both experimental and control fish which had only been pre-tested to the mirror test and had not received experience in fighting. However, the biting rate of the experimental sample was significantly higher than in the controls. They concluded that repeated fighting activities had increased the aggressive motivation of their males at least for a period of 18h spent in isolation (since the last agonistic experience held 18h before final mirror test). They used N=13 experimental animals and 13 control fish (thus they made only 13 fights). In the subsequent fight between E and C fish, 10 out of 13 C fish defeated E fish which seemed clearly in contradiction with their previous conclusion about aggressive motivation since the fish which had shown lower levels of biting rates in the prior mirror test were the ones which won the most fights (Binomial test: n=13, x=10, p=.5, $P < .05$). They laconically concluded that "probably escalated fighting activities do not improve the chance of winning fights against other opponents. On the contrary, frequent escalated fighting activities could even reduce the ability to be victorious in later encounters. " (p. 228).

That the more aggressive individuals do not necessarily obtain victory is not surprising at all. Several studies (Thinès & Heuts, 1968; Frey & Miller, 1972; Zayan, 1975a) clearly state that there is not an obligatory relationship between aggressive behavioural levels and dominance outcome. In *Betta splendens*, the fish showing a higher level of aggressive display does not necessarily win the encounter (Simpson, 1968). As we shall discuss later, only 'bites' were used by Franck & Ribowski (1987) to assess the aggressive levels of their fish.

Victory is not apparently reached in *Xiphophorus* through a brute superiority in the number of "bites", but through the exertion of a more subtle evaluative process which Beaugrand (1997) has just begun to describe. He used interaction patterns (X menaces, Y attacks) rather than individual patterns (attacks, or bites) as is usually used to describe fights in *Xiphophorus.* His results indicate that future winners are recognizable essentially by two characteristics: first, they have the initiative in the use of threatening behaviour; in that respect, they lead of the encounter; but the opponent responds as well. Second, future winners are less prone to retaliate by offensive behaviour (attack, bite) to the offensive behaviour they receive from the opponent. Instead, they offer resistance to the opponent when it retaliates with menaces or attacks. Resistance takes the form in these fish of "not responding", or of responding by a behaviour of lower agonistic intensity (by a menace to an offence).

Differences in the way behaviour was noted could also account for discrepancy between our results and that of Franck & Ribowski (1987).

As mentioned above, this increase in scores in mirror tests from pre-test to post-test was significant only when opponents were prior betas or prior omegas. Individuals which had occupied the alpha position in their home hierarchy were apparently not influenced by their recent victory since their scores to mirror tests did not vary from pre-test to post-test. In addition, the effect was not found in losers: defeat did not induce any significant change in aggressive levels subsequent to fighting as had been first reported by Franck & Ribowski (1987). Though a slight decrease was noted in betas, it did not reach the required 5% level of significance.

It is thus possible that a range effect occurred in the present research. Such an effect manifests itself when the variable being observed reaches an upper value limit (ceiling effect) and cannot increase further, or reaches a lower value limit (floor effect) and cannot decrease further. For instance prior alphas could have already reached their maximum before victory and could not increase their aggressive scores further after victory, contrary to prior betas and omegas. Similarly, losers could have already been at their minimum before encounter and could not lower further their aggressive levels after defeat.

Encounters between a resident and an intruder were less aggressive

A rather unexpected result is that pairs in which a resident met an intruder (RI) were in general less aggressive than pairs composed of two intruders (II). Thus, although 1h prior residence did not significantly change the probability that the resident individual defeated the intruder, it nonetheless *reduced* the amount of aggressive behaviour necessary to reach outcome, as compared to that of control encounters in which both pair members were unfamiliar to the meeting place.

Recall that in the present research the resident and intruder fish were equally handled and had not been socially isolated for more than 1h. Thus, prior residence corresponds to familiarity with the meeting site for a very short period of time. Fish pairs composed of a resident and of an intruder were compared to a control sample composed of two intruders. Beaugrand & Zayan (1985) and Beaugrand & Beaugrand (1991) have used such control groups but their emphasis was on dominance outcomes rather than on agonistic behaviour. Surprisingly, such a control group is lacking from all other studies we have examined and in which prior residence was studied.

It is usually assumed that prior residence increases aggressiveness in the resident, and thus increases its chance of dominating an intruder of similar size (Braddock , 1949; Jenkins, 1969; Frey & Miller, 1972; Myrberg, 1972; De Boer & Heuts, 1973; Zayan, 1975a, b). Thus the fact that, in the present study, RI encounters generated significantly less aggressive behaviour than the II control group suggests that future researches use such a control group to compare the behavioural units used in these two kinds of encounters, and to compare sequences in which they are used, rather than simply comparing the behaviour of a resident with that of an intruder within a unique group.

RI pairs showed less aggressive behaviour than II pairs, whilst not clearly favouring the dominance of residents in RI pairs. One explanation is that residents are in general less shy than intruders. As confirmed in the present study, they usually were the first to initiate contact, display, and attack in RI pairs (Frey & Miller, 1972; Zayan, 1975b), thus bringing rapidly the encounter to a high level, leading to rapid assessment and settlement. In encounters between intruders, one can presume that the fish were more equally matched, and thus were more prudent. They displayed more to each other, and mutually attacked more often before being able to reach decision.

Tentative of conciliation with Franck & Ribowski (1987)

Since the present research was in a great part based on the results published by Franck & Ribowski (1987) on the same species of fish, it seemed important to compare the two studies in order to make an attempt to conciliate our results and theirs. Quite evidently, answers are suggested from the comparison of the procedures and methods followed by each study. Though the paper of Franck & Ribowski (1987) is generous in experiments (5 experiments are presented in their paper), one cannot equally qualify their paper in regards to given procedural details, which are essential in any effort to identify discrepancies between studies.

One nonetheless notes that, in the 5 studies reported, all fish were systematically isolated for periods of 18-24h and sometimes up to 72h before the completion of any mirror test, as well as before encounters. This was done to allow the fish some acclimatization before the subsequent test. In the 2nd experiment of the present research, fish were never socially isolated more than 2h. They were netted directly from their home hierarchies, allowed 15 min in isolation to settle down or given 1h to develop prior residence. Then a mirror test was administered or the fish met an opponent which had been similarly handled. Moreover, fish were returned to their home hierarchies immediately after the first and the last mirror test. Franck & Ribowski (1987) do not clearly mention what was done with their fish in between tests. Apparently, in some of their experiments fish stayed in the experimental tanks for several hours instead of being returned to their home group. For the present authors, the major difference resumes to a question of isolation which in their case was sufficient to obliterate the previous social experiences of their fish. Such a radical suppression of previous experience seems to produce specific effects on the aggressive state. For instance, a period of social isolation of only a few hours contributes to an increase in aggression in fish (Braddock, 1945; McDonald et al., 1968; Thinès & Heuts, 1968; Frey & Miller, 1972; Goldenbogen, 1977; Wilhelmi, 1975). A short period of isolation is even frequently used to "prime" agonistic behaviour, a procedure already used on *Xiphophorus* by Braddock (1945). The fact that, in the Franck & Ribowski (1987) study, lower ranking fish showed up more aggressive than high ranking ones after isolation suggest that fish of various prior hierarchical statuses might not react to the same way to short periods of isolation. This could be examined in future research.

One may think that an isolation period will eliminate any immediate social experience of submission, as was suggested by Braddock (1945) and by Frey & Miller (1972). The positive correlation which seems to exist between isolation and subsequent aggression cannot be taken to imply that the more aggressive individuals are necessarily the ultimate dominants as shown by Thinès & Heuts (1968) and Zayan (1975a). Moreover, a number of researchers have pointed to the similarity between the behaviour of isolated, prior alphas or prior winners in male mice (Benton & Brain, 1979; Puglisi-Allegra et al., 1989), and in *Xiphophorus* (Beaugrand & Zayan, 1985). Unpublished results from this laboratory indicate that fights between two *Xiphophorus* males which have been isolated for 18-24h are as protracted and aggressive as that between two prior winners. As noted by Beaugrand & Zayan (1985), the frequency of sexual behaviour is significantly higher in encounters in which at least one opponent has been isolated for 18-24h.

In mice, the effects of isolation following agonistic behaviour have been amply investigated. For instance Andrade et al. (1989) report that mice which had had the experience of winning recovered from the effects of defeat and could retaliate with attacks as little as 12h later when left in isolation. On the contrary, mice which had been defeated took at least three days of isolation to recover from their initial timidity. These, as well as more stringent effects following long term isolation, have led some authors to suggest that there is a "syndrome" induced by social isolation in the mouse (Valzelli, 1981; Puglisi-Allegra et al., 1989). Some of the effects of isolation are similar to those observed following a chronic stressful experience.

In the Franck & Ribowski (1987) study, the use of "control" males which were much smaller and had not experienced any fighting before is also questionable. Again, our understanding is that these "control" males were either long-term isolates, or repeatedly used, and not equally handled as the E fish which they subsequently encountered.

Another procedural difference between this experiment and that of Franck & Ribowski (1987) concerns the way fish were handled. In the present research, fish were routinely netted, put in small plastic transfer boxes and (re)-introduced into the test milieu. In Franck & Ribowski (1987) experiments, fish to encounter were left undisturbed in different compartments of the test aquarium, separated by an opaque partition; the partition was later raised, allowing the two fish to interact with each other or a given fish with its own image reflected in the mirror. However, their more civilized manner of handling the fish should have worked in favour of their showing a natural relationship with prior ranks, not against.

There were also differences between studies in the durations of the mirror tests. Franck & Ribowski (1987) mirror tests lasted 15 or 20 min, while ours were always of only 5 min duration. Our understanding of the performance of the fish in front of their own image is that it habituated, thus justifying the use of a rather short period cutting off the phase in which responding decreased. In the present research, the mean aggressive rates in the two pre-tests were of 15.97 and

14.05 units / min respectively. Their mean at mirror pre-test was of about 7.8 “bites” / min (estimated from their Fig. 5), which more or less corresponds to the mean frequency of ‘attacks’ in the present research. This brings us to another difference which concerns the behaviour units which were used to categorize behaviour in the two studies. In the present study, all menacing (lateral-spread displays, tail-beats) and offensive (attacks, bites) units were counted. At the moment of statistical analysis, these molecular units were usually aggregated into the more general category of “aggressive” behaviour. In the Franck & Ribowski (1987) study, only “bites” were noted and counted. These correspond to our “attacks”, charging the mirror and possibly “biting” the mirror image. Menaces, lateral-spread displays and tail-beats (Franck & Ribowski’s S-threats) were apparently not counted in their experiments with mirrors; at least they do not report about them. They write “But we regard the bites as the most relevant and direct measure of aggressiveness. The relation between S-threats and bites seems to be rather complex …“ (page 220).

Another additional difference concerns the maturity of the home hierarchies from which subjects came. In the present research, triads had been formed 168h before the experiment and only members coming from complete and stabilized triads were chosen to serve in the experiment. In the Franck & Ribowski (1987) research, fish were kept in small groups for “long-term stabilized groups” before serving in their experiments, and we have no indication on their degree of hierarchical completeness and stability when the time came to serve in experiments. Moreover, in the present research, triads were formed randomly and size differences within home hierarchies could vary up to 20%. In their research, size differences were apparently kept within a 5% difference.

Considering all these methodological differences between the two researches, one cannot be surprised that different results were obtained. The least these discrepancies can suggest is to replicate these experiments with systematic variation of social isolation levels, and of prior ranks of opponents.

Mechanisms underlying experiential effects

The precise nature of the process underlying the relationship between experiential factors and agonistic behaviour remains undetermined. A “soft” explanation can be obtained within the framework of associative learning or conditioning (Scott & Frederickson, 1951; McDonald et al., 1968; Scott, 1971).

Flanelly & Blanchard (1981) have suggested that the formation of a hierarchy was simply modifications of responsiveness following a consistent history of victories or defeats, these levels of responsiveness being more and more specific as inter-individual discrimination is learned by the individuals composing the group. When the group remains in time composed of the same individuals such a discrimination contributes to individual recognition, and to the installation of a stable hierarchy. But such a learning process is only possible if victory or defeat have reinforcing properties.

Aggressive displays in themselves seem to have reinforcing properties in *Betta splendens* which can be operantly trained to obtain its own mirror image as the reinforcer, at which it can subsequently display (Hogan, 1967; Bols, 1977; Hogan & Roper, 1978).

Several other studies, especially those using mice, also indicate that winning a fight increases subsequent readiness to attack (Ginsburg & Allee, 1942; Scott, 1946). Experiments by Tellegen et al. (1969), Legrand (1970) and Tellegen & Horn (1972) have shown that reinforcing properties of attacking a strange mouse depended on the subject's level of aggressive motivation. The nature of the reinforcement in such situations remains unclear. A first view, the negative reinforcement view, is that reinforcement comes from the cessation of an aversive state due to cessation of attack (the opponent flees or adopts a submissive posture). However, such a view is difficult to conciliate with the fact that animals will perform an operant response to obtain the opportunity to menace or attack an opponent. The other view is thus appetitive, i.e., positively reinforcing (Hinde, 1970; Rasa, 1976): the performance of aggressive behaviour in itself would procure some pleasure to the attacker. The problem with the reinforcing quality of attacks is that during a fight, both the future winner and future losers attack equally, keeping up in steps in terms of reinforcements until one of them capitulates. Decision must then play a crucial role into the nature of the reinforcing properties of the situation.

Our view is simply this: satisfaction would come primarily from the initiation of aggressive acts which are successful in inducing the rival to flee or at least to have it signal appeasement; dissatisfaction would come essentially from having to flee or to appease the attacker. Thus, the winner or to be dominant individual would be positively reinforced during the whole encounter by its own aggressive behaviour, but victory would bring much more satisfaction to the winner from the moment the loser would signal its capitulation. Each subsequent attack would be greatly reinforced by the winner seeing the loser fleeing or submitting. As for the loser, it would also be partly satisfied (positively reinforced) during encounter by the initiation of aggressive acts from its part. However, upon its taking the decision to capitulate, dissatisfaction would originate from diverse sources: the cessation of being able to initiate any aggressive behaviour (the cessation of positive reinforcement creates punishment), the punishment of being dominated and having to adopt submissive posture or to flee, as well as the punishment coming from physical pain (blows and bites) and repeated harassment from the dominant. Thus the winner learns that it is authorized to attack or not to be afraid of that specific rival, whilst the loser learns to avoid or to be afraid of that specific opponent. Such a reinforced acquisition is the basis of social discrimination and recognition.

Subsequent effects of prior victory and of prior defeat can be explained by another process called *generalisation* to a new or “testing” situation. Principles of generalisation are rather simple: the more the testing situation bears resemblance with the learning one, the more there ought to be generalisation from the part of the learner. The more the learning is recent, i.e., fresh to memory, the more it will generalise easily (otherwise memory decays and experience is forgotten). The more learning has been repeated consistently (i.e., with the same ending result), the more experience was consolidated and the more it should generalise integrally to a similar but new situation. Thus when the prior winner and prior losers are subsequently introduced into the test situation where they encounter a new opponent, the generalize to the new situation: the prior winner behaves as a prior winner, and the prior loser as a prior loser unless the new situation (opponent, milieu) bears no resemblance with that in which learning was established.

The present results support the hypothesis that the more intense an encounter was, the more experience it left upon the winner protagonist, and the more effect it had subsequently as measures by scores reached at the mirror post-tests. In the case of winners, this effect was still measurable by mirror tests 24h after cessation of the encounter.

The present evidence in favour of victory only, and not defeat, thus contradicts authors who have suggested that only defeat experience or prior subordination influenced individual propensity to obtain subsequent victory (Frey & Miller, 1972; Rowell, 1974; Francis, 1983).

It also contradicts “hard” explanations based on neuroendocrinal data, especially the one stating that defeat increases corticosteroid levels in *Xiphophorus* (Hannes et al., 1984), the Green anole (Greenberg, 1983), the pig (Bouissou, 1983), and the domestic mouse (Leshner, 1980, 1983). Hannes et al. (1984) have reported that after fierce fights for rank order position amongst swordtail males there was an increase in concentrations of corticosteroids in both the blood and the body extracts of winners at times ranging from 1h to 14 days after the end of the fight if the rivals were kept together. The corticoid levels of both winners and losers rose drastically during the fight, returned to control level within 6h, then increased moderately from 3 to 14 days thereafter. A first problem with a rise of corticoids is that it is a non specific index of stress. An increase in corticosteroids can be induced by any kind of stressor (Toates, 1995). Fights demand energetic action and their consequences can be stressful, so the pituitary-adrenal hormones are likely to play a role in agonistic behaviour (Huntingford & Turner, 1987). A second problem is that corticosteroids are at the same time a cause and a consequence of defeat or submissive behaviour. For instance, they are associated in rats and mice to an increase in subsequent use of submissive or defensive behaviour during social interactions (Leshner, 1980, 1983; Schuurman, 1980), apparently augmenting the punishing effect of defeat (Kahn, 1951; Taylor, 1979). Thirdly, corticosteroids cannot be used to discriminate high ranking from low ranking males coming from already stabilized hierarchies in Xiphophorus: the baseline of corticosteroids in these fish of different ranks were found by Hannes (1984) to be indistinguishable. The results of the corticoids determinations suggest that low-ranking males are not more stressed or aroused than high-ranking males, which is quite incongruent with what can be inferred from the observation of their behavioural interactions (Beaugrand et al., 1984; Beaugrand & Beaugrand, 1991). Moreover, Hannes (1984) found that social deprivation for 4 weeks had the consequence of lowering basal levels in blood androgens and corticoids equally in high- and low-ranking males. Thus, if there is a relationship between corticoids and experience then it is rather intricate.

Defeat is known to decrease androgen levels in the swordtail (Hannes et al., 1984), the house mouse (Leshner, 1983), the rat (Schuurman, 1980), and the rhesus monkey (Rose et al., 1972; Bernstein et al., 1983). A rise in testosterone levels either naturally or through injections usually increases aggressiveness in a wide range of species. One possibility is that winning aggressive encounters may facilitate testosterone secretion, and hence increase subsequent aggressiveness. In humans, Mazur & Lamb (1980) have shown that a competitive achievement (either winning a tennis double, or obtaining a doctorate) was correlated with an increase of testosterone levels in men. Hannes (1986) has also reported that blood and whole-body androgen levels of male swordtails correlated with aggression measures in a standard-opponent test.

Thus, one cannot deny that neuroendocrinal factors are implied. However, since changes in hormonal levels cannot be said to be either the cause nor to be caused by agonistic behaviour, it is tempting to put these hard explanations aside for the moment, and to stick to more soft explanations, such as those presented above, based upon learning, discrimination and generalisation.

Acknowledgement
This work was funded by a NSERC from Canada.

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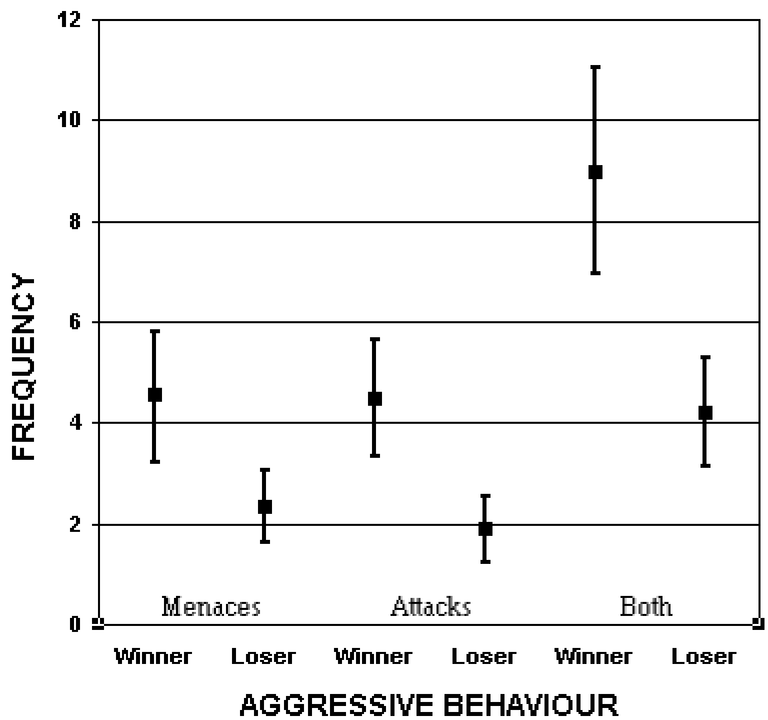

Fig. 1. Mean frequency of menaces, attacks, and their total towards their own mirror image in future winners and losers. 95% confidence intervals are indicated.

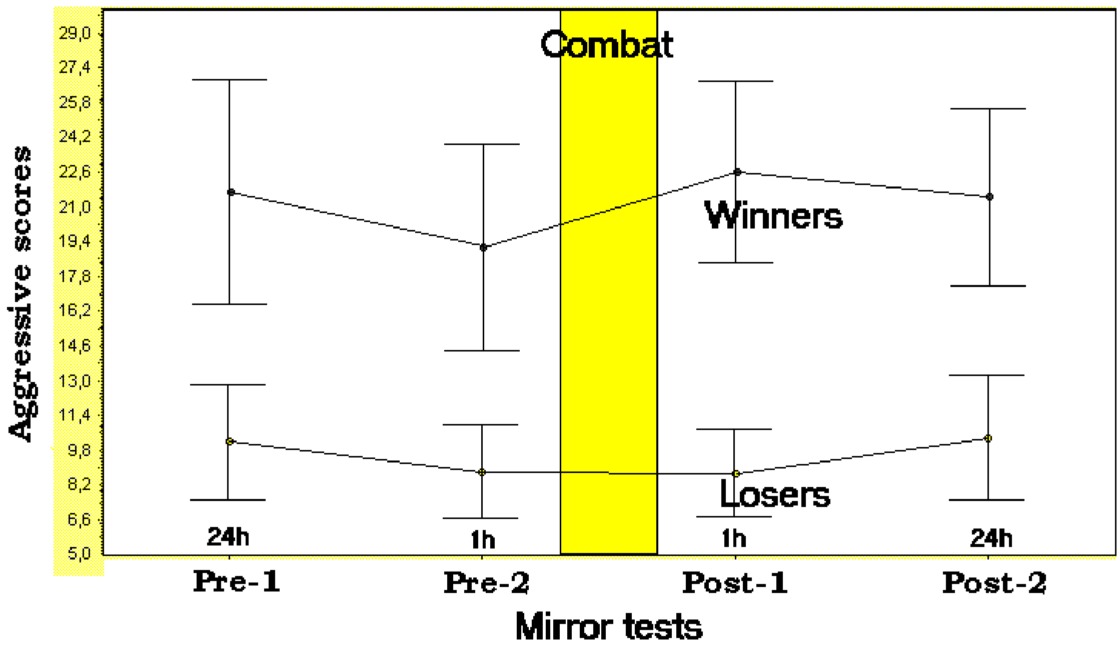

Fig. 2. Aggressive scores at the four successive mirror tests, two as a pre-test before agonistic encounter, and two as a post-test, after agonistic encounter. $CI_{.95}$ are indicated.

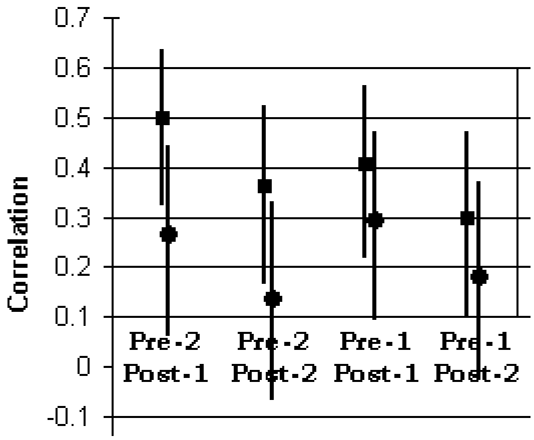

Fig. 3 Correlation between agonistic intensity during encounter and change in aggressive levels as measured by the difference between scores obtained in mirror tests obtained before (pre-) and after (post-) encounter. Squares stands for winners and circles, for losers. $CI_{.95}$ are indicated.

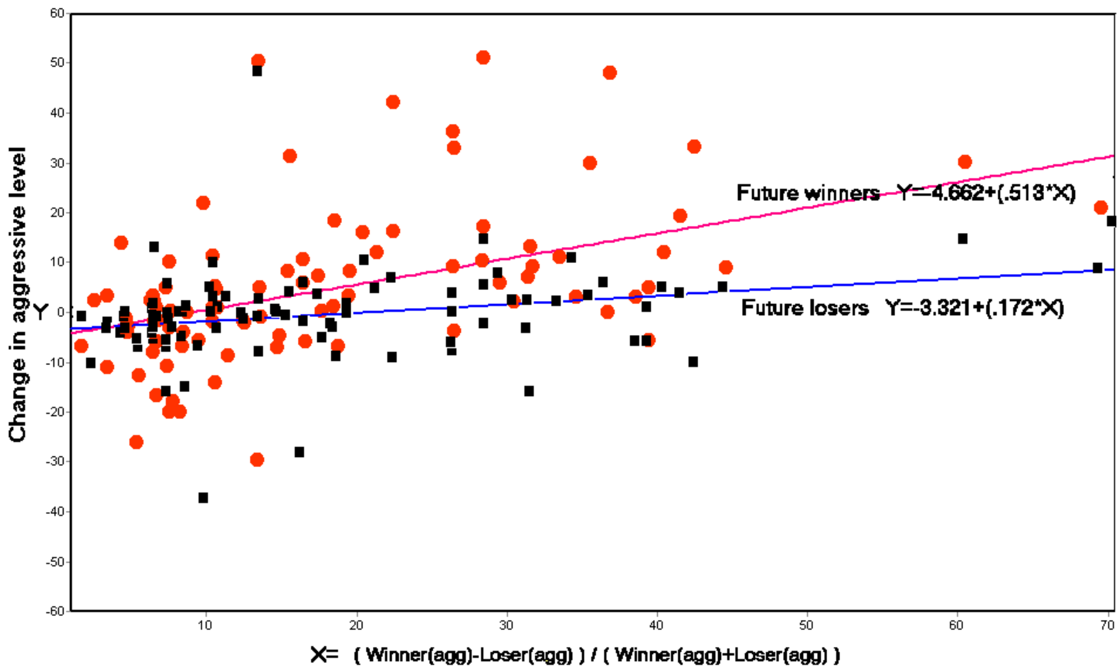

Fig. 4. Regression lines for future winners and losers. Linear regression of agonistic intensity during encounter and subsequent change in aggressive scores to mirror image 1h before and 1h after encounter. Circles are for winners and squares for losers.

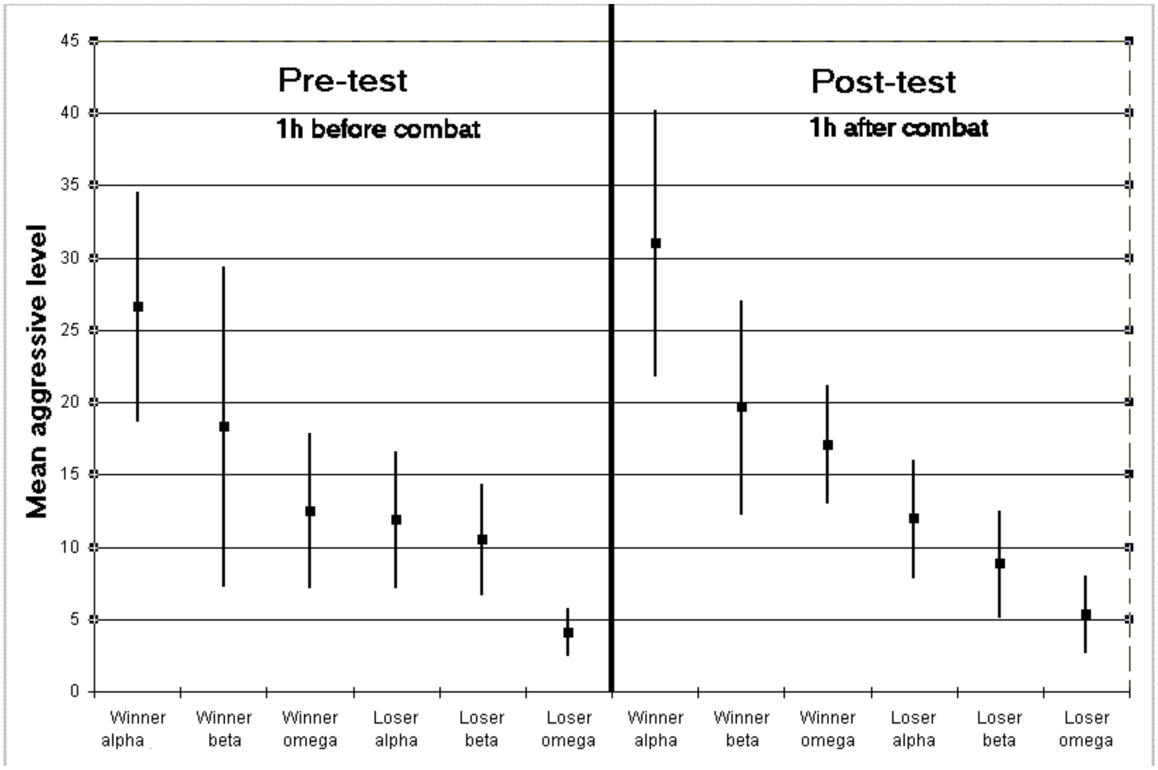

Fig. 5. Mean aggressive levels at the mirror tests performed 1h before and 1h after agonistic encounter. Winners and losers were partitioned into the status they occupied in their respective home hierarchies, to show the relationship existing between prior status and aggressive levels at Pre-1 and Post-1. $CI_{.95}$ are indicated.