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**Distinguishing kinds of prior dominance and subordination experiences
in males of Green swordtail fish (*Xiphophorus helleri*)**

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Abstract

In experiments, there are usually two general ways of obtaining dominants and subordinates to test for the effect of recent experience upon ulterior behaviour and dominance. One is to “impose” such an experience on the contestants by a priori deciding which individual of the pair will become the dominant and which will become the subordinate through the use of rigged contests. The second technique is to let contestants “self-select” the winner and loser by waiting for the spontaneous outcome of dyadic encounters between two usually well matched opponents. These two techniques of obtaining dominants and subordinates probably represent extreme cases on a single

continuum of investment made by animals to settle dominance. To test this, we compared dominants and subordinates obtained from these two techniques in *Xiphophorus* fish males. It was found that pairs obtained through rigged contests (R) were much more aggressive in subsequent encounters than pairs in which the dominant and subordinate could self-select (S). They recuperated more rapidly from handling, initiated contact earlier, took more time to assess each other, and fought for a longer period of time. Prior-winners and prior-losers of the R condition more frequently relied on aggressive behaviour during contest than that of the S condition. As a consequence, prior-winners and prior-losers of the R condition won equally the subsequent contest. On the contrary, prior-winners of the S condition defeated their prior-loser opponent in a majority of cases. These results can be tentatively explained by the following principle: winning or losing against a well matched opponent would leave more “experience” than winning over a much weaker opponent, or losing to a much stronger one. This reinforces the hypothesis that prior-experiences are not qualitative states but come in various degrees.

Key-words: Agonistic experience; Self-selection; Dominance; Subordination; Animal conflict; Social learning; Discrimination; Green swordtail fish; *Xiphophorus helleri*

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1.0 Introduction

Dyadic dominance is affected by factors related to the history of two given contestants, factors which we shall refer to as “experiential” ones. Among these experiential factors, recent dominance experience accounts for an increase in the propensity to dominate again in a subsequent encounter, while recent subordination experience would produce the counter effect (Francis, 1983; Beaugrand & Zayan, 1985; Beacham & Newman, 1987, Beaugrand et al., 1991, 1996).

Previous research has treated experiential state related to prior dominance as a categorical variable as in e.g., as being a prior-dominant or a prior-subordinate. However, winning and losing experiences most probably come in various types and possibly degrees. In different contests, a winning individual would receive a given amount of dominance experience, while another would receive a different amount. The same would exist for a losing experience, which could vary according to defeated individuals from different encounters. Indications for the existence of a continuum in prior agonistic experience rather than of qualitative states come essentially 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.

In experiments, there are usually two general ways of obtaining dominants and subordinates to test for the effect of recent experience upon ulterior behaviour and dominance. One is to “impose” such an experience on the contestants by a priori deciding which individual of the pair will become the dominant and which will become the subordinate through the use of rigged contests. For instance, when a small intruder *Xiphophorus* is introduced into the home aquarium of a much larger fish which already resides there, one can be almost certain that the larger resident will

defeat the smaller intruder. The second technique to obtain dominants and subordinates is to let them self-select: one waits for the spontaneous outcome of dyadic encounters between two usually well matched opponents.

Our hypothesis is that these two techniques of obtaining dominants and subordinates represent extreme cases on a single continuum of investment made by the animals to settle dominance. In rigged contests for instance relying on size differences to give advantage to one of them, most opponents easily perceive such conspicuous size differences and most probably use it to settle without much agonistic investment nor with much escalation. On the contrary, when opponents are closely matched in size and other aspects, no conspicuous cues correlated with dominance potential can be used to settle dispute; opponents have to rely more extensively on displays to assess each other, a situation which is prone to give rise to more frequent escalations than in rigged contests.

To test this general hypothesis, the present experiment compared encounters between prior dominants and prior subordinates obtained from these two techniques in male *Xiphophorus* fish.

2.0 Methods

2.1 Subjects and material

A pool of more than 1,500 adults male Green swordtail fish, *Xiphophorus helleri*, was constantly available in the laboratory. They were acquired from the same breeder (Florida Fish Pounds, Tampa, Florida, USA) and kept in heterosexual groups of 100-150 individuals in 10 large communal tanks of 165 litres (90x50x40 cm). When needed for the experiment, adult males were randomly netted from these communal tanks. Forty identical pre-experimental and experimental glass tanks (30x15x15) of a capacity of 13.5 litres were also used.

2.2 Size measurements

Three size measurements were taken of 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 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 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*.

2.3 Design

Two samples of 20 pairs were formed, each corresponding to one experimental treatment. Treatments were rigorously the same, except for the way winners and losers were obtained. A first sample to be called “Self-selected” (S) was composed of pairs of males which had settled contest in independently staged encounters against opponents of equivalent size ($\pm 5\%$). One opponent, the winner, became spontaneously through self-selection the prior dominant pair member, the other being the prior subordinate. A second sample, to be called “Rigged” (R), was composed of pairs of males which were not acquainted to each other but which had received divergent experiences acquired independently. One fish had received experience of dominance against a much smaller opponent ($<40\%$) in a pre-staged contest. Its opponent had received an experience of subordination in a similar contest against a much larger fish. S fish never met R fish in the present experiment. Each individual fish did not serve more than once in this research.

Pairs met in aquariums which were unfamiliar to both pair members. Pair members were also unfamiliar to each other. In the final contests R and S pairs were

formed of fish showing less than $\pm 5\%$ differences in LS ratio. This range of ratios between lateral surfaces corresponds to a zone for which Beaugrand et al. (1991, 1996) have shown that victory was principally determined by prior experiences rather than by size differences.

2.4 Procedure

The experiment was divided into two phases 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 of a pair of fish. The fish were netted from the various communal tanks, measured, and their morphology described to insure proper recognition by the observer.

The fish were first isolated for 3 hours in separate pre-experimental aquaria. We then carried out encounters of each kind 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 dominant and subordinate individuals of each pair. The encounter was cancelled at the end of these 18 hours when no dominance relationship had been clearly established. Fish from such unsettled encounters did not serve in the next phase.

The experimental phase began by imposing 3 hours of isolation onto the fish. After that, future opponents were netted and simultaneously introduced into a further unfamiliar tank. In the two samples, the fish were unfamiliar to each other and had received independently opposite prior experiences of dominance. Within each kind, new pairs were formed by recombination of opponents having received prior experience of dominance or subordination at the previous phase in the same manner: spontaneous dominants encountered unfamiliar spontaneous subordinates, and rigged dominants met unfamiliar rigged subordinates. Pair members had to show a ratio in lateral surfaces within $\pm 5\%$ difference and to originate from different communal tanks, as well as be unfamiliar to the future test tank. A computer program assisted in randomly pairing potential candidates and in affecting pairs to the various aquariums.

The interaction of two fish was observed until one clearly dominated its opponent, or for 30 minutes, whichever came first. In the latter case, the two fish of the unsettled encounter were discarded from the rest of the research. This happened in 4% of S pairs but never in R ones. Discarded pairs were replaced by new ones until 20 pairs were completed.

2.5 Behavioural observations

Observations were carried out from behind hides by two observers not cognizant of treatments and randomly assigned to the recording of the behaviour of only one of the opponents. They used two OS3 data logger (Observational Systems, Redmond, WA) whose internal oscillators had been synchronized. 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 described by Beaugrand et al. (1991, 1996) were directly encoded. attacking, biting, mouth-fighting (offensive category); tail-beating, lateral-displaying (menacing category); fleeing, adopting a folding posture (defensive category); approaching, fluttering, bottom immobility, rising from the bottom, eating and breaking the surface (skimming and air gulping). From these individual acts, interactive units were constructed such as chasing and offering resistance.

2.5.1 Dominance criterion. We considered that a dominance relationship had been established between two individuals when one fish (the dominant) was successful in chasing its opponent on six occasions without being threatened, attacked or bitten in turn. Such a dominance criterion was validated in dyads of *Xiphophorus* males by Beaugrand & Beaugrand (1991) who showed that subordinates identified following the application of this criterion never reversed relationships within the next 20 days that followed.

2.5.2 Welfare. No detectable injury nor death occurred during the experimentation itself.

At the experimental phase, all contestants were returned to their communal tanks as soon as the dominance criterion had been reached.

2.6 Data reduction and analysis

The two computer files containing the observations recorded for each complete contest, one for each opponent, were collapsed into a single interaction file by synchronizing the recordings on timing events which were common to both complete records. 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 occurrence was not considered to be independent of the preceding intra-subject or inter-subject behaviour. Thus, when the temporal gap exceeded the 3-second lag, a *pause* was inserted between the two behaviours or between the two occurrences of the same behaviour. This criterion was chosen following the 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 the logarithmic curves of their survival values (Beaugrand, 1980; Slater & Lester, 1982).

In the present research, all contest records ended with the occurrence of the first defensive behaviour which was part of the six defining the dominance criterion. Acts occurring after this were thus not considered for analysis, because it was estimated that the decision to concede victory had already been taken by the loser of each pair.

The behavioural acts of contestants were not considered as independent data but as systems influencing each other. All statistical tests comparing, within the same sample, (prior-)winners to (prior-)losers on behavioural frequencies, proportions, or rates were thus always of the matched-pairs, correlated or repeated measurements types.

3.0 Results

3.1 Dominance outcomes

In 15 of the 20 staged encounters of S pairs prior-winners defeated prior-losers. Such superiority proved to be statistically significant in a binomial test assuming equiprobability ($p=0.5$, $n=20$, $x=15$, Binomial $P=.02$). On the contrary, R prior-winners defeated unfamiliar R prior-losers in only 10 of the 20 encounters. Though in S pairs, prior-winners defeated prior-losers significantly more often than in R pairs, the difference between the two distributions was not sufficiently extreme, considering the small sample sizes, to reach statistical significance ($G=2.706$, $df=1$, $P<.10$).

3.2 Comparisons of the behaviour of future winners and future losers

In general, R pairs were more aggressive than S ones: Future R winners menaced and attacked more frequently than S winners (menaces: Anova $F=9.89$, $df=1/17$, $P=.006$; attacks: $F=5.99$, $df=1/17$, $P=.026$). They menaced and attacked earlier in the encounter (menaces: $F=6.31$, $df=1/17$, $P=.022$; attacks: $F=5.39$, $df=1/17$, $P=.033$). Future losers of R pairs menaced and attacked more frequently (menaces: $F=5.56$, $df=1/17$, $P=.031$; attacks: $F=15.58$, $df=1/17$, $P=.001$) and earlier than losers of S pairs did (menaces: $F=5.96$, $df=1/17$, $P=.026$; attacks: $F=5.92$, $df=1/17$, $P=.026$). Both the assessing and offensive phases lasted longer in R pairs (assessing: $F=6.57$, $df=1/17$, $P=.02$; offensive: $F=12.89$, $df=1/17$, $P=.002$) and mutual menaces (I menace, You menace in turn) were more frequent in R pairs than in S pairs ($F=11.34$, $df=1/17$, $P=.004$). Future losers of R pairs also showed often more “resistance” (i.e., not responding) to aggressive behaviour ($F=7.93$, $df=1/17$, $P=.012$). Using stepwise discriminant analysis, 100% of cases could be successfully classified into their proper S or R group using the following variables: time spent on the bottom, which was shorter in R pairs than in S ones, mutual aggression, resistance to menace or attack, and escalation, which were all more frequent in R pairs than in S ones. The classificatory function obtained was highly significant (Eigenvalue=14.693, Canonical Correlation=.968; residual Wilks' Lambda=.064, $\chi^2=23.40$, $df=17$, $P=.137$).

3.3 Comparisons of prior-winners to prior-losers

The results obtained by comparing prior-winners and prior-losers across treatments give similar results to those presented above for future winners and losers. In general, prior-winners and prior-losers were found to be more aggressive in R pairs than in S ones. Prior-winners attacked first more often in R pairs ($F=5.39$, $df=1/17$, $P=.033$) and also used both attacks and lateral displays more often (attacks: $F=5.99$, $df=1/17$, $P=.026$; lateral-displays: $F=9.89$, $df=1/17$, $P=.006$). Prior-losers were also more often the first to use lateral display ($F=8.73$, $df=1/17$, $P=.009$) and tail-beats ($F=5.88$, $df=1/17$, $P=.027$) in R pairs than in S ones. They displayed more often with lateral display ($F=6.24$, $df=1/17$, $P=.001$). Individuals of R pairs showed more frequent mutual menaces ($F=10.15$, $df=1/17$, $P=.005$), as well as unilateral menaces ($F=10.75$, $df=1/17$, $P=.004$), i.e., menaces not responded to within 3 seconds. Mutual menaces initiated by the prior-losers could serve to distinguish R pairs from S ones in 89.5% of cases (Discriminant analysis, Eigenvalue=.63, Canonical Correlation=.62; residual Wilks' Lambda=.61, $\chi^2=8.09$, $df=1$, $P=.004$).

3.4 Comparisons of future winners to future losers within conditions

Only one behaviour pattern was significantly associated with future winners in S pairs: future winners were found to be the ones initiating the first approaches ($t=3.36$, $df=8$, $P<.01$). Otherwise in R pairs, except at the extreme end of the encounter where future winners attacked while future losers fled, no behavioural difference could serve during contest to foretell future winners from future losers.

4.0 Discussion

It is clear from the present results that the spontaneously obtained prior-winners or losers, i.e., those obtained by letting fish self-select, are not equivalent in terms of experiences to that of ones in which experiences were imposed through rigged contests. In general, R pairs were found to be much more aggressive than S pairs. They

recuperated more rapidly from handling, initiated contact earlier, took more time to assess each other and fought for a longer period of time. Prior-winners and prior-losers of the R condition more frequently relied on aggressive behaviour during contest than that of the S condition. As a consequence, prior-winners and prior-losers of R pairs won equally the second contest. On the contrary, prior-winners of S pairs defeated their prior-loser opponent in a majority of cases.

In the present research we did not systematically tally behaviours of the fish interacting while obtaining their prior experiences. Nonetheless, it was noted that in rigged pairs there rarely occurred any mutual aggression: victory was systematically and rapidly reached by the much larger fish which unilaterally charged, without any contest from the part of the much smaller fish. On the contrary, encounters of S pairs were planned between opponents which were well matched for size and these encounters were much more protracted, implied more frequent aggressive acts and also lasted longer.

One could reasonably expect that winners of S fights would have profited from their experience and would have been more combative in the encounter which followed because they just had won. This does not seem however to be the case. Prior-winners of S pairs were less aggressive in the encounter which followed than prior winners of R pairs. On the other hand, one could expect that prior-losers of S pairs would be less combative in the encounter following their initial defeat because they had just been defeated and this does not seem to be the case. Prior-losers which self-selected were found to be much less aggressive than prior-losers obtained through rigged contests, as if they had been more affected by their previous defeat.

In this research, the fish which obtained victory “easily”, i.e., without much agonistic expenditure, were not as affected by their victory or by their defeat as the ones which had to invest more in fight. Conversely, fish which were put in a situation in which they had to give up easily against a much larger opponent were not much affected by their defeat. In the subsequent encounter they behaved as if they had received similar experiences as the prior-winners of rigged contests. On the contrary,

fish which had to assess each other and to escalate in order to settle dominance were more affected by their respective victory or defeat experiences. As a result, in the subsequent encounter, they more readily behaved according to their respective prior experiences, settling dispute more rapidly and in favour of the individual advantaged by prior victory experience.

These results can be tentatively explained by the following principle: winning or losing against a well matched opponent would leave more “experience” than winning over a much weaker opponent, or losing to a much stronger one.

This general idea was already well contained in the renowned verses published in 1637 by the French dramatic author Pierre Corneille: “À vaincre sans péril, on triomphe sans gloire;” (Act II, scene II, verse 436, page 69), which can be translated as “By defeating without peril, one’s triumph is without glory”.

4.1 Mechanisms underlying experiential effects

The precise nature of the process underlying the relationship between agonistic behaviour and recorded experience remains undetermined. A “soft” explanation is workable within the framework of associative learning (Scott & Frederickson, 1951; McDonald et al., 1968; Scott, 1971).

Flanely & Blanchard (1981) and Beaugrand (1984) have suggested that the formation of a hierarchy was simply the establishment of inter-individual discrimination learned by the individuals composing the group. When the group remains composed of the same individuals for a certain period of time, each group member becomes able to discriminate each other individual from any other, i.e., to individually recognise other members, and when all members have such recognition, a stable hierarchy is said to be in place. But discrimination is a form of learning, and learning is only possible if victory or defeat or the process leading to dominance over a rival or submission to a rival present reinforcing properties. The process leading to victory or defeat is composed of aggressive behaviours which appear to have intrinsic

reinforcing properties. Animals will perform an operant response to obtain the opportunity to menace or attack an opponent, suggesting that it is a positive reinforcer (Hinde, 1970; Rasa, 1976) and that attacking has appetitive properties. For instance, *Betta splendens* and *Macropodus opercularis* males can be operantly trained to obtain as the reinforcer their own mirror image, at which they can subsequently display (Hogan, 1967; Bols, 1977; Hogan & Roper, 1978; Gerlai & Hogan, 1992). Moreover, experiments by Tellegen et al. (1969), Legrand (1970) and Tellegen & Horn (1972) have shown in mice that the reinforcing properties of attacking a strange mouse were dependent of the subject's level of prior aggressive motivation.

The problem with the reinforcing quality of displays and attacks is that during a fight, both the future winner and future loser equally attack, keeping up in steps in terms of behaviour until one of them suddenly capitulates. Indeed, many studies have shown the difficulty of distinguishing between the future winner and loser using their behaviour during encounter, except near the end of a contest (Simpson, 1968; Dow et al., 1976; Jakobsson et al., 1979; Beaugrand, 1997). Thus both the winner and loser would be equally positively reinforced during the encounter itself.

This suggests that the decision taken by the loser to concede victory might imply important divergent consequences for the winner and the loser, so much as it could change the nature of the reinforcing properties of the situation. Data supporting such a hypothesis can be found in Franck & Ribowski (1987). These authors have investigated the problem whether escalated fighting activities can change an animal's aggressiveness and its chance of winning a subsequent aggressive encounter. In one experiment, *Xiphophorus* males were first subjected to a mirror test. Then 72h later they were imposed 9 escalated fights of 10 min duration distributed over a period of 3 days. In none of the encounters did the fish have the final experience of winning or losing the fight, the fight being interrupted before decision. Each experimental male was then confronted with one "control" male, which had been mirror tested but had not experienced any fighting activity, and the winning and losing individuals were determined. Franck & Ribowski (1987) found that biting rate significantly increased

from one mirror test to the other in both experimental and control fish. However, the biting rate of the experimental sample was significantly higher than in the controls. These authors concluded that repeated fighting activities increased the aggressive motivation of males. In the subsequent fight between experimental and control fish, 10 out of 13 control fish defeated experimental fish, which is an apparent contradiction considering that the fish which had shown lower levels of biting rates to the prior mirror test were the ones which won most fights (Binomial test: $n=13$, $x=10$, $p=.5$, $P<.05$).

In another experiment, the same authors investigated the effect of victory or defeat upon measures to mirror tests passed 90 min before agonistic encounter, immediately after encounter, and 24 hours later. Some of the winners had two fights in succession against prior unfamiliar losers from parallel pairs. Each fight was flanked by mirror tests. They 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 were much nearer to the pre-experimental level but a significant difference was still present 24 hours after the fight. They also confirmed that a winning or a losing experience on a first fight increased the probability of winning or losing a second fight 24 hours later.

The results of these two experiments taken together strongly suggest that the decision taken by one pair member to suddenly capitulate subsequently introduces divergent reinforcing effects upon winner and loser.

We propose that satisfaction would come to the winner primarily from the initiation of aggressive acts which are successful in inducing its rival to flee or at least to signal appeasement. In contrast, dissatisfaction would come to the loser from having to submit. Thus, the future winner 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 capitulation. Each subsequent attack would be greatly reinforcing for the winner which is seeing the loser fleeing or submitting. As for the loser, it would be positively reinforced during

encounter by the initiation of aggressive acts, just like the future winner. However, upon its taking the decision to capitulate, dissatisfaction would be generated from diverse sources. First, the cessation of being able to initiate any aggressive behaviour which acted as a positive reinforcement would now create punishment. Second, being dominated and having to adopt a submissive posture or to flee from attacks, would also create punishment. Third, punishment would come from physical pain inflicted by blows and bites, and from repeated harassment from the now dominant opponent. This state of affairs would create in the winner a positive association between the perceived configuration of its now subordinate rival and the authorisation to attack, and not to be afraid of that specific rival. In the loser, a negative association would on the contrary be established between the winner's perceptive configuration and fear, or avoidance. Such divergently reinforced acquisition processes would form the basis of social discrimination and subsequent individual recognition.

How can we explain that in R pairs the subsequent effects of experience were not as asymmetrical as in S ones? Two possible explanations can be proposed, one concerning the acquisition process, which went differently in R and S pairs, and one concerning the possibilities of generalisation in the subsequent testing situation.

In the present research, differences between treatments could be explained by the fact that winning or losing did not have the same reinforcing capacity under each of these situations. For instance, prior encounters between well matched opponents in S pairs generated more mutual aggressive behaviour and lasted longer than encounters between a large and a small opponent in R pairs. In contrast, R pairs settled much more rapidly and were characterized by unilateral aggression initiated by the larger fish toward its smaller opponent. Thus, one can assume that under the R condition, giving up was less a negative reinforcement than in S pairs which had probably invested much more. It is also reasonable to think that the decision had greater reinforcing properties for S rather than R pairs. Another essential factor which could distinguish R from S pairs is the ratio of reinforcement or degree of certainty of reinforcement during encounter. In R pairs, the ratio was high. Each time the larger individual charged, each

time the smaller had to avoid it. Thus certainty of reinforcement was extremely high from the beginning of the encounter to its end when the fish were separated. In S pairs, on the contrary, certainty of the reinforcement over the same period of time was on the average much lower. It was null in the first period before the loser took its decision to capitulate, high after decision, but nonetheless of an overall lower certainty than in R pairs.

The second explanation is not necessarily independent from the first one just presented. It is based upon the similitude between learning and testing. Effects of prior victory and of prior defeat can be assimilated as an instance of *generalisation* to a new situation. Subsequently encountering a strange opponent can be viewed as a situation in which the previous acquisition is tested and eventually *generalises* more or less. Principles of generalisation are rather simple. First, the more the testing situation bears resemblance with the one in which the learning was acquired, the more there ought to be generalisation on the part of the learner to the new situation. This resemblance concerns morphological and perceived characteristics of the opponent, and of the context in which the acquisition took place. One extreme case would be to meet the same initial opponent in the same environment: there ought to be perfect generalisation. The second principle concerns the force of the habit: the more the learning has been sanctioned by reinforcement, i.e., well memorized, the more it should readily generalise to the new situation. Thus, after their initial victory or defeat, prior winners and prior losers encountered a new opponent in a new environment. They were prone to generalise to the new situation what they had learned in the previous one: the prior winner behaved as a winner towards the new opponent, and the loser behaved as a prior loser, to the extent that the novel opponent and novel context bore some resemblance with the prior learning situation.

In the present experiment generalising capabilities of individuals were facilitated in S pair members as compared to R ones. First, the behaviour of S pairs was more resistant to extinction than in R pairs because dominant and submissive behaviour had been acquired under low entropy and could be immediately tested and

extinguished rapidly. Second, the conditions of the subsequent encounter were much more similar to learning ones in S pairs than in R ones. On the test condition, S pairs met another unfamiliar, but well matched opponent. As for R pair members, they had met a much larger/smaller opponent on their first encounter, but met a well matched opponent on their second one. They had learned to avoid a much larger fish or to approach a much smaller fish, not a fish of similar size. The resemblance between conditions of the first and of the second encounter was thus greater in S pairs than in R ones. Therefore prior S dominants were in general more prone to generalise their dominant behaviour to the subsequent encounter and prior losers more prone to generalise their subordinate behaviour. Moreover, since habit had been acquired under different reinforcing conditions, it was also less inclined to extinguish in the subsequent testing situation. Thus, prior S winners acted more like prior winners, with the consequence that they dominated again more frequently, and prior S subordinates acted more as prior subordinates with the consequence that they repeated more frequently defeat, while showing in general more suppression of aggressive behaviour.

Such an interpretation is coherent with what is known of conditioned defensive responses or conditioned fear, which has been amply studied in animals. For instance, Williams (1991) has exposed rats to a defeat session by a large “alpha” rat of the same species, with odours associated with this conspecific representing part of the context. He found that fear and analgesia existed 24h after a single 15-min defeat session. However, these reactions were observed only when tested in the presence of alpha-colony odours, as opposed to control odours.

Explanations in terms of learning and generalisation processes are not incompatible with harder ones described in terms of neuroendocrinal processes. Defeat is known to increase 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.

Immediately after a fight, the losers showed 4 times higher cortisol levels than winners.

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 it increases in both winners and losers. A third 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). Fourthly, 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 than it is extremely 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 involved and that explanations of experience will have to be translated into neural processes. However, since changes in hormonal levels cannot be said for the moment to be either the cause nor to be caused by agonistic behaviour, one is authorized to put these hard explanations aside temporarily, and to stick to more soft explanations, such as those presented above, based upon learning, discrimination, and generalisation.

4.2 Limitations of the present research

The present research is not without limitations. For instance, encounters of prior-winners obtained in R contests were not planned against S ones, nor against a “standard” opponent. The same applies to prior losers of each kind; they were not pitted against the alternate kind. Thus, the present research cannot establish whether the obtained effects are symmetrical for prior-winners and prior-losers within kinds, or due to only one of them. For instance, only S prior-losers could have been affected by their defeat, and the present result could still be accounted for.

Another important limitation, to be corrected in future research, is the lack of systematic observation during pre-staged encounters. It is essential to know the relationship between what happens during prior-encounters where prior-dominants and prior-subordinates are obtained, and the effects produced on subsequent encounters. One hypothesis is that the more prior-encounters imply behavioural investment in the part of the opponents, the more each of them receive experience of dominance or subordination, and the more each experience influences behaviour and

dominance outcome in a subsequent encounter.

Although the present research generates more questions than answers, it nonetheless reinforces the hypothesis that prior-experiences are not qualitative states but come in various degrees and can be treated as continuous variables. As a corollary, it suggests that research results relying on a single technique to obtain prior-winners and prior-losers (e.g. all obtained through self-selection, or all using a “standard” winner/loser to impose experience on them as did Hsu & Wolf, 1999) might suffer from a lack of generality. Strictly speaking, results obtained through the application of these alternate techniques might be comparable, but difficult to conciliate unless one understands that they cover distinct segments of the continuum of experience.

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