

# **Conflict outcome in male green swordtail fish dyads**

## **(*Xiphophorus helleri*): Interaction of body size, prior dominance/subordination experience, and prior residency**

by

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## Summary

The relative contribution of asymmetries in prior experience, size, and prior residency to the determination of dyadic dominance between unacquainted individuals was examined using pairs of green swordtail fish, *Xiphophorus helleri*. Four types of encounters were staged between an intruder and a smaller resident: (1) both had experienced prior victory; (2) both had experienced prior defeat; (3) the intruder had experienced prior victory and the resident prior defeat; and (4) the intruder had experienced prior defeat and the resident prior victory. In a fifth condition in which two intruders met, one was a prior subordinate and the other a prior dominant smaller in size than its opponent. In all these encounters, the superiority in lateral surface of one fish varied between 0 to 30% over that of its opponent. Results showed that (1) when size differences between contestants were within the range of 0-10% and there was an asymmetry in prior social experience, conflicts were essentially resolved according to prior experience with prior winners systematically defeating prior losers; (2) prior residency of 3 hours was an advantage only when both opponents had experienced prior defeat before meeting and when size asymmetries were small (e.g. <20%). It was not an advantage between prior winners or between a prior winner and a prior loser; (3) when large size asymmetries existed (e.g. 20-30%), size uniquely determined dominance outcome and nullified other advantages or disadvantages due to prior social experience and prior residency; and (4) at intermediate levels of size asymmetries (e.g. 10-20%), size partially cancelled any advantage due to a prior victory, and gradually became the most important factor in accounting for victories.

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## Introduction

Body size is most often identified as the best cue for gauging «resource holding potential» (**RHP**, Parker, 1974) in animal conflicts. Size correlates naturally with strength which is presumed to be an important factor in conflict outcome in fish, with the larger individual usually winning (Myrberg, 1971; Jakobsson *et al.*, 1979; Francis, 1983; Turner & Huntingford, 1986; in *Xiphophorus* genus: Noble, 1939; Braddock, 1945, 1949; Beaugrand & Zayan, 1985).

However, size cannot always be a reliable indicator of **RHP** because it remains unaffected by changes in psychological conditions or physiological states that also affect **RHP** (Clutton-Brock & Albon, 1979; Robertson, 1986). Moreover, animals rely on alternate means of settlement when available (Barnard & Burk, 1979). Undeniably, when contestants are closely matched in size, the cost of size/strength assessment must be high.

**RHP** may also be affected by factors related to the history of the contestants. Amongst experiential factors, prior dominance experience and residency are of interest here. Recent prior dominance experience seems to account for an increase in **RHP** while recent subordination experience seems to decrease it (Frey & Miller, 1972; Zayan, 1975a; Francis, 1983; Beaugrand & Zayan, 1985; Beacham & Newman, 1987).

Differences in familiarity with the area in which the contest occurs (Braddock, 1949; Zayan, 1975a; Henderson & Chiszar, 1977) also seems to have a decisive role in conflicts. Prior residency, understood as familiarity with the surroundings in which the meeting takes place, favours dominance in the individual, over one in a place that is unfamiliar to it. Thus, the advantages of a 3-h familiarization period with the future meeting place were clearly demonstrated in the green swordtail (*Xiphophorus helleri*) for individuals of equivalent size that had been put in isolation for 18 hours beforehand (Zayan, 1975a, b, c; Beaugrand & Zayan, 1985; Beaugrand & Beaugrand, 1991). Under these conditions, where dominance is favoured from the outset by a familiarity with the environment, this advantage does not disappear as the intruder in turn gains in familiarity (Beaugrand & Beaugrand, 1991).

Size difference between opponents becomes the most likely determinant of dominance when size cues are great and clearly perceptible. Beaugrand *et al.* (1991) have shown using *X.h.* males that prior social experiences accounted for dominance when the size advantage of a prior subordinate over a prior dominant opponent was smaller than 25 mm<sup>2</sup>. As the size advantage of the prior subordinate individual increased, neither previous social experience nor superiority in size clearly accounted for conflict outcome. Even when the lateral surface for prior losers was between 126 and 150 mm<sup>2</sup> larger than prior winners, size did not strictly explain the outcome. Males, handicapped by prior subordination experience, had to be at least 40% larger than prior dominant

opponents in order to win conflicts more frequently. These results clearly suggest that prior dominance/subordination experience and size can either add or cancel each other out when size differences are not extreme. Similarly, Beacham (1988) has shown that when the asymmetry of weight was small the prior experience effect could negate that of weight in conflicts between *Lepomis gibbosus* fish pairs.

What happens when an additional factor affects **RHP** to give further conflicting cues ? To gain more insight into the interaction of factors contributing to **RHP**, experiential and prior residency asymmetries were experimentally combined or opposed to varying degrees of size asymmetries. In doing so, their relative capacity to influence dominance could be better understood.

## Methods

### *Subjects and equipment*

A pool of more than 1,200 adult green swordtail fish *X.h.* was constantly available in the laboratory. We bought them all from the same breeder (5D Tropical Inc., Plant City, Florida 33566, USA). We maintained them in mixed groups of 100-150 adult and immature males and females in 9 large communal tanks of 165 litres each (90 x 50 x 40 cm). When needed for the experiment, adult males were netted randomly from these communal tanks. Males from the same tanks were never matched against one another. All 40 pre-experimental and experimental glass aquaria that we used were of identical dimensions (30 x 15 x 15 cm) and contained 13.5 litres of water. Miscellaneous objects such as plastic tubes, charcoal chips, rocks and shells were arranged on the bottom of these tanks in various configurations in order to create patterns favouring discrimination by the fish in different tanks.

### *Size measurement*

We took three measurements of each fish: (1) **total length**, from the snout to the end of the caudal fin; (2) **flank height**, from the base of the dorsal fin to the origin of the gonopodium; and (3) **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 maintained 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  $X.h$ . Size measurements were obtained before pairs were formed.

A given difference in surface area between two opponents can influence outcome in a manner that depends on the absolute value of their respective sizes. To avoid such a scaling effect, we worked out a dimensionless ratio (Gold, 1977) similar to that used by Beaugrand *et al.* (1991) in the same species. The size differential ( $d$ ) between contestants was expressed by a percentage of the smaller fish lateral surface.

## *Design*

Five type of encounters were staged (Table 1), each corresponding to one independent experimental condition and sample. A given fish thus served only once in the present research. Conditions 1 to 4 were obtained by the encounter of an intruder with a smaller resident. Condition 5 involved the pairing of two intruders, one being a prior subordinate (noted  $\omega$ ) and the other being a prior dominant (noted  $\alpha$ ) smaller in size than its opponent. For encounters between an intruder and a resident, we created 4 states of prior experience asymmetry in prior  $\alpha$  or prior  $\omega$  : (1) both the intruder and resident had experienced prior victory (condition noted as  $I\alpha R\alpha$ ,  $I\alpha$  standing for the properties of the «left» fish of the dyad, and  $R\alpha$  standing for those of the «right» fish); (2) both the intruder and resident had experienced prior defeat ( $I\omega R\omega$ ); (3) the intruder had experienced prior victory and the resident prior defeat ( $I\alpha R\omega$ ); and (4) the intruder had experienced prior defeat and the resident prior victory ( $I\omega R\alpha$ ). In all theses encounters, the superiority in size ( $d$ ) of the «left» fish of the dyad varied between 0 to 30% over that of its opponent.

## *Procedure*

The fish were provided with prior experiences of either winning or losing on the first day as the result of «self-selection»: An encounter was staged between two animals, and the experimenter took, *ex post facto*, the winner and the loser. We first measured 2 fish from different communal tanks and isolated them for 2 hours in separate pre-experimental aquaria. Fish had to be unfamiliar with each other and have a size differential smaller than 10%. We carried out the encounter by simultaneously introducing both opponents into a third aquarium where they stayed together for the next 12 hours. During this period, behavioural observations of social interactions were carried out behind blinds. We noted which fish was the dominant ( $\alpha$ ) and subordinate ( $\omega$ ) pair member; otherwise, at the end of the 12 hours, the encounter was considered null and was therefore terminated.

We considered a dominance relationship as being established when one fish (the winner) was successful in chasing its opponent (the loser) on 6 occasions without having been threatened, attacked, or bitten in turn. Beaugrand & Beaugrand (1991) demonstrated the validity of such a criterion.

**Experimental phase.** On day two new pairs of fish were formed by means of recombination of those opponents who had experienced prior victory or prior defeat on day one. Selected fish were unfamiliar with one another and sufficiently different in size so that they could correspond to one of the size differentials acceptable for that day. Depending on the desired test condition, the fish must have had similar or divergent prior dominance experiences. In conditions 1 to 4, the smaller fish of the pair was made resident by being left alone for 3 hours in the aquarium in which the final contest was to take place. During that time, the intruder was left alone in another aquarium. Then the resident and the intruder were netted and simultaneously introduced into the aquarium of the resident. In condition 5, the same procedure was followed but the final contest was staged in an aquarium that was unfamiliar to both fish. The pair was then observed for a maximum of 60 min or until one clearly dominated its opponent. Encounters that had not settled after 60 min were cancelled and the fish returned to communal tanks.

In both phases, the selection of pairs was computer assisted. Using a database manager, we constantly monitored information concerning each fish: communal tank of origin, body measurements, previously visited aquaria and prior dominance experience. A program then applied this information and computed specific directions concerning the pairing of specific opponents that corresponded to acceptable size differentials. It also randomly assigned pairs to the various available aquaria and assumed that the various types of encounters progressed evenly and equally during experimentation.

## Results

Binary categories and frequencies were tested using the Binomial test; when  $N > 25$ , its  $Z$  normal approximation was used (Siegel & Castellan, 1988, pp. 38-44). In the present research, the appropriate null hypothesis concerning victory within pairs was  $p=q=1/2$ . Frequencies with which larger «left» fish defeated their smaller «right» opponents within each condition and for each size sub-range are presented in Table 1, together with binomial/ $Z$  statistical decisions concerning which opponent had significantly won more often. Data were also analyzed using logistic regression (Hosmer & Lemeshow, 1989). The unit of analysis was the dyad. These dyads were equally and randomly coded for asymmetries from the point of view of the winner or the loser. One dyad served only once in the analyses. In the following text, the notation will stand for the asymmetry (or symmetry) existing between the members of each dyad in regards to one status variable. The two letters that follow the  $\blacktriangle$  sign will stand for the respective statuses of the two fish concerned, depending on their point of view. Thus, for instance, condition  $I_{\alpha} R_{\omega}$  generates asymmetries  $\blacktriangle_{ir}$  and  $\blacktriangle_{\alpha\omega}$  from the point of view of the «left» fish (intruder prior-winner), and asymmetries  $\blacktriangle_{ri}$  and  $\blacktriangle_{\omega\alpha}$  from the point of view of the «right» fish (resident prior-loser). Since data suggested the presence of an interaction between prior  $\blacktriangle_{\omega\omega}$  experience and residency, these two factors were replaced in the analyses by their corresponding combination terms (*i.e.*  $\blacktriangle_{\omega\omega ri}$ ,  $\blacktriangle_{\omega\omega ir}$ ). The size asymmetry  $\blacktriangle_{LS}$  was calculated from the point of view of the fish concerned, as a percentage of superiority or inferiority in lateral surface over its opponent. Recall that size differentials  $d$  were calculated from the point of view of the larger «left» fish of the pair, *i.e.*,  $d$  is the absolute value of the corresponding  $\blacktriangle_{LS}$ . In order to compare the relative importance of size with the other asymmetries, in some analyses,  $\blacktriangle_{LS}$  values were binary coded

as categorical variables covering the whole 0-30%  $d$  range by steps of 10%. All other status factors were always represented in the logistic analyses as binary variables coded for their presence (**1**) or absence (**0**).

Several basic regularities were identified and are conveniently synthesized by Figure 1. This figure was obtained by substitution of values in the following logistic equation obtained by regression on all data combined:

$$P(\mathbf{X}) = \frac{\exp(\text{logit } P(\mathbf{X}))}{1 + \exp(\text{logit } P(\mathbf{X}))}, \quad \text{where}$$

$$P(\mathbf{X}) = 0.1024\Delta LS + \begin{bmatrix} +1.2611\Delta\alpha\omega \\ -1.2611\Delta\omega\alpha \end{bmatrix} + \begin{bmatrix} +1.5759\Delta\omega\omega_{ri} \\ -1.5759\Delta\omega\omega_{ir} \end{bmatrix}$$

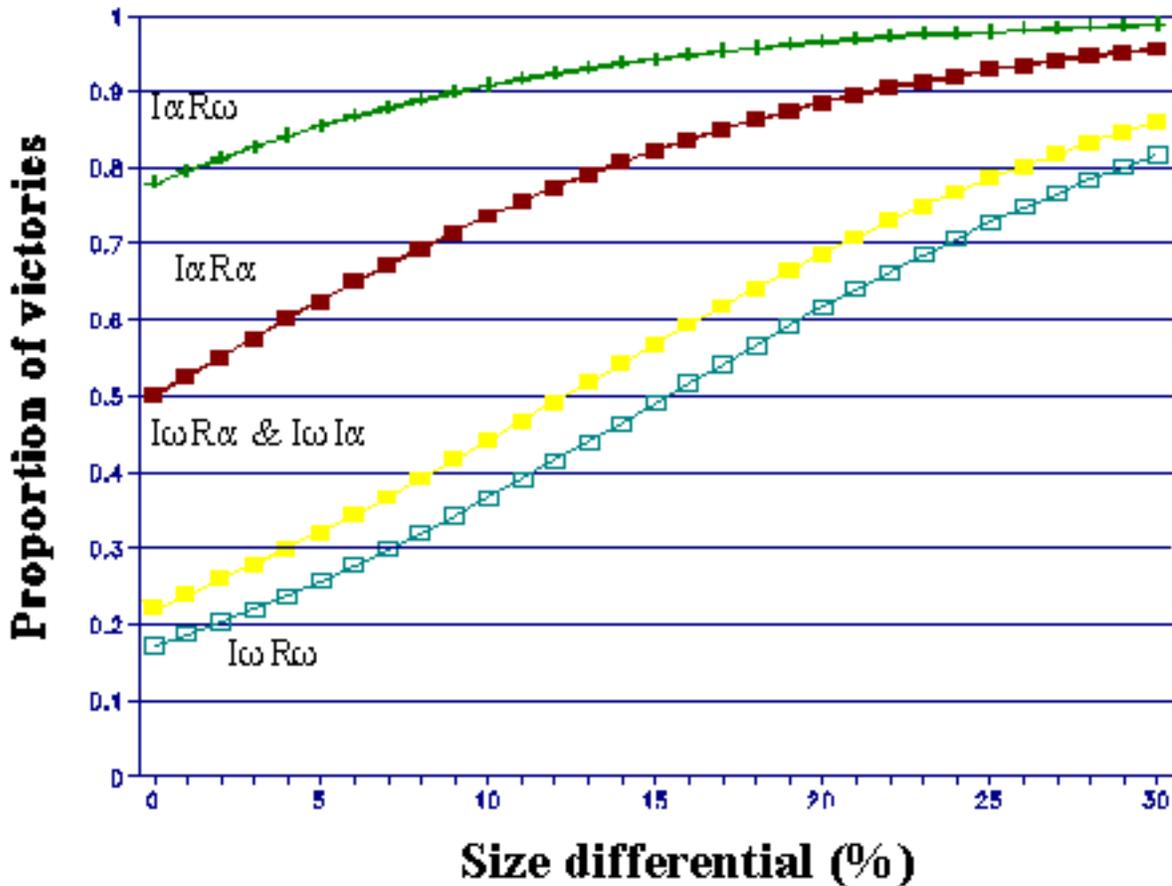


Fig. 1. Proportion of victories of the larger "left" intruders as a function of their size superiority.

The goodness-of-fit test indicated that the obtained logistic model was appropriate for the data ( $\chi^2 = 359.65$ ,  $df = 354$ ,  $P < 0.407$ ). Factors that did not reach significance were not considered by the model. The Wald test for each factor retained by the model reached significance at least at  $P < 0.001$ ; 72% of dyads could be correctly classified applying the obtained function. In this equation,  $\Delta LS$  is a continuous variable and can take values from -30. to +30. depending on the pair member concerned. Other variables in the equation represent binary asymmetries that, when present, are either added, when at the advantage, or subtracted, when at the disadvantage of the concerned pair member. Figure 1 thus presents a synthesis of the effects of the asymmetries that significantly influenced outcome when the 467 dyads covering the 0-30%  $d$  range were considered. Each line was labelled according to the experimental conditions

it corresponds to in terms of the asymmetries that played a statistically significant role on the determination of outcome.

The line labelled « $I_{\alpha}R_{\alpha}$ » represents the "pure" or basal effect of  $\Delta LS$  when all other relevant asymmetries are neutralized and only the size advantage given to the intruder (or to the «left» fish under condition  $I_{\omega}I_{\alpha}$ ) influences outcome. Size was found to influence victory in direct proportion to  $\Delta LS$ . When considered as a continuous variable by regression, each % advantage in  $\Delta LS$  within the whole  $d$  range studied (0-30%) increased chances of victory by almost 11% ( $\exp(\beta)=1.11$ ,  $Wald=84.58$ ,  $df=1$ ,  $P<.0001$ ). However, size influence is best understood by analyzing each experimental  $d$  range separately.

Beginning with the 0-10%  $d$  range,  $\Delta LS$  was found to have no significant effect, outcome being essentially determined by experience and prior-residency asymmetries. This conclusion is supported by the fact that logistic regression did not retain  $\Delta LS$  as a significant factor accounting for outcome within the 0-10%  $d$  range. On the contrary,  $\Delta_{\alpha\omega}$  and  $\Delta_{\omega\omega ri}$  asymmetries reached significance within that range.

In the 10-20%  $d$  range, small increases or decreases in  $\Delta LS$  had important effects on outcome. In general, within that range, odds of victory were 8.73 times higher for the larger opponent than for the smaller one ( $\exp(\beta)=8.733$ ,  $Wald=20.12$ ,  $df=1$ ,  $P<.000$ ). When  $\Delta LS$  was considered as a continuous variable, regression indicated that, above 10% in  $d$ , each additional percent of  $\Delta LS$  advantage increased chances of winning by 9% ( $\exp(\beta)=1.088$ ,  $Wald=23.11$ ,  $df=1$ ,  $P<.0001$ ). However, as we shall later see, experience and prior-residency asymmetries still influenced outcome within this  $d$  range, but when considered with size, they added when in unison, or balanced when in opposition.

The effect of size on outcome reached its maximum effect within the 20-30%  $d$  range. Here, size uniquely determined outcome, and other asymmetries played a negligible role. Such a conclusion is supported by the fact that  $\Delta LS$  was the only factor retained by logistic regression to account for victories when size differences were in the 20-30%  $d$  range. Being 20-30% larger/smaller in  $d$  than the opponent significantly increased/decreased odds of winning by 10 ( $\exp(\beta)=10.20$ ,  $Wald=15.34$ ,  $df=1$ ,  $P<.000$ ). Size advantage within that range seemed to nullify all other factors. Moreover, 77% of outcomes were correctly identified

by a logistic model based on  $\Delta LS$  alone (Goodness-of-fit  $\chi^2 = 68.$ ,  $df = 66$ ,  $P < 0.4089$ ). The same conclusions concerning the role of size can be reached by examination of frequencies of victory presented in Table 1.

Table 1 . Respective victories of larger left fish and smaller right fish for various differential size ranges expressed as a percent of the smaller opponent. I: intruder; R: resident;  $\alpha$  : prior-winner;  $\omega$  : prior-loser

Sample	N	Size differential 1 d ranges	Victories by		Binomial/ Z P-value
			Larger	Smaller	
I $\alpha$ R $\alpha$	23	00-10	11 (48%) =	12 (52%)	ns
	29	10-20	23 (79%) >	6 (21%)	<0.0015
	13	20-30	11 (85%) >	2 (15%)	<0.011
I $\omega$ R $\omega$	28	00-10	8 (29%) <	20 (71%)	<0.0192
	16	10-20	5 (31%) $\leq$	11 (69%)	<0.105
	17	20-30	14 (82%) >	3 (18%)	<0.029
I $\alpha$ R $\omega$	28	00-10	22 (79%) >	6 (21%)	<0.0023
	24	10-20	21 (88%) >	3 (12%)	<0.001
	12	20-30	12 (100%) >	0 (0%)	<0.001
I $\omega$ R $\alpha$	27	00-10	4 (15%) <	23 (85%)	<0.0003
	18	10-20	10 (56%) =	8 (44%)	ns
	19	20-30	14 (74%) >	5 (26%)	<0.032
I $\omega$ I $\alpha$	98	00-10	31 (32%) <	67 (68%)	<0.001
	54	10-20	29 (54%) =	25 (46%)	ns
	61	20-30	39 (64%) >	22 (36%)	<0.018

As mentioned earlier,  $\Delta_{\alpha\omega}$  and  $\Delta_{\omega\omega_{ri}}$  were the only significant factors retained by logistic regression carried out on data of the 0-10%  $d$  range. When there existed an  $\Delta_{\alpha\omega}$  asymmetry in prior social experience, conflicts were essentially resolved according to experience, with prior  $\alpha$  s systematically defeating prior  $\omega$  s. Being the  $\alpha$  of a  $\alpha\omega$  pair increased chances of victory by 60% ( $\exp(\beta)=5.97$ , Wald=29.97, df=1,  $P<0.0001$ ). Being the resident of a pair of  $\omega\omega$  also increased chances of victory by 34% ( $\exp(\beta)=3.45$ , Wald=4.78, df=1,  $P<0.0287$ ). These two factors,  $\Delta_{\alpha\omega}$  and  $\Delta_{\omega\omega_{ri}}$  when included in a logistic equation, could alone correctly identify 70% of outcomes (Goodness-of-fit  $\text{Chi}^2 = 203.$ , df=200,  $P<0.4276$ ).

As can be seen from Figure 1, size did play some role below 10% in size differential but its effect was cancelled by  $\Delta_{\alpha\omega}$  and  $\Delta_{\omega\omega_{ri}}$  asymmetries when put in opposition to size. Recent experience and prior residency interplayed with size in a complex manner especially within the 10-20%  $d$  range. The best fitted logistic model obtained for this range included variable  $\Delta_{\alpha\omega}$ ,  $\Delta_{\omega\omega_{ri}}$  and  $\Delta_{LS}$  as significant inclusions (Goodness-of-fit  $\text{Chi}^2 = 359.65$ , df=152,  $P<0.394$ ). The  $\alpha$  member of an  $\alpha\omega$  pair had a 42% more chance of victory than its  $\omega$  rival ( $\exp(\beta)=4.22$ , Wald=8.11, df=1,  $P<0.004$ ). In  $\omega\omega$  pairs, being the resident pair member increased odds of victory by almost 8 ( $\exp(\beta)=7.705$ , Wald=7.65, df=1,  $P<0.006$ ). Still, the larger individual of the pair had 9 more chances of victory than the smaller one ( $\exp(\beta)=9.243$ , Wald=20.401, df=1,  $P<0.000$ ). Such a model in retrospect correctly identified 69.23% of outcomes and all considered factors were significant at least at  $P<0.006$ .

Figure 1 allows to visualize how size, recent experience and prior-residency asymmetries combined and interacted to determine outcome especially when  $d>20\%$ . As a rough indication, points of Figure 1 projecting on the ordinate above a value of 0.7 in probability of victory would represent a statistically significant superiority (to a binomial) in victory of larger individuals over their smaller opponents for  $N=25$  pairs. Conversely, points situated below the value of 0.3 in probability of victory would indicate that the larger individuals were significantly defeated by the smaller ones. Victory would be equiprobable within the zone

delimited by these two lines.

It could be noted from Figure 1 that  $\Delta_{\alpha\omega}$  and  $\Delta_{LS}$  asymmetries seem to be additive. The course of line labelled « $I_{\alpha R\omega}$ » remains above the 0.7 in probability of victory. This reflects the fact that under experimental condition  $I_{\alpha R\omega}$ , intruders were doubly advantaged by  $\Delta_{\alpha\omega}$  and  $\Delta_{LS}$  and they systematically defeated their smaller opponents. Table 1 confirms this: under condition  $I_{\alpha R\omega}$ , larger alpha intruders always defeated their smaller omega opponents. The difference on the ordinate of Figure 1 between the « $I_{\alpha R\omega}$ » and « $I_{\alpha R\alpha}$ » lines represents the contribution of the  $\Delta_{\alpha\omega}$  asymmetry when added to size. Effects of  $\Delta_{\alpha\omega}$  and  $\Delta_{LS}$  thus seem to be additive, but the contribution added by factor  $\Delta_{\alpha\omega}$  is not constant over the whole  $d$  range. The line labelled « $I_{\omega R\alpha}$  &  $I_{\omega I\alpha}$ » and situated below that of pure size (labelled « $I_{\alpha R\alpha}$ ») represents the net effect of  $\Delta_{\alpha\omega}$  experience when opposed to size. Here, the  $\Delta_{\alpha\omega}$  asymmetry in favour of the smaller individual puts in balance or partially cancels the advantage of size of the opponent. The advantage introduced by the  $\Delta_{\alpha\omega}$  asymmetry initially diminished the net advantage given by size superiority by almost 30% in terms of probability of victory. In terms of units of  $\Delta_{LS}$ , the  $\Delta_{\alpha\omega}$  asymmetry was found to be more or less equivalent to 11% of  $\Delta_{LS}$ , which it could neutralize when in opposition. Again, this suggests that prior experience and size asymmetries combine in an additive manner.

As seen on Figure 1, prior-residency was sufficiently important to balance the advantage in size given to the intruder when both opponents were prior losers. The line labelled « $I_{\omega R\omega}$ » on Figure 1 indicates that when size superiority given to the opponent was rather small, familiarity with the meeting site was clearly an advantage for the smaller resident (see also Table 1:  $I_{\omega R\omega 0-10\%}$ , 8:20,  $Z=2.0788$ ,  $P<0.0192$ ). However, this advantage due to familiarity was gradually neutralized ( $I_{\omega R\omega 10-20\%}$ , 5:11,  $P<0.105$ , Binomial) and finally overridden by the advantage in size given to the intruder until size became the essential determining factor of victories when size  $d$  was greater than 20% ( $I_{\omega R\omega 20-30\%}$ , 14:3,  $P<0.029$ , Binomial). Familiarity for 3 hours with the meeting site was found to be an advantage only when both opponents had experienced prior defeat before meeting and when size asymmetries were less than 20%. As it can be seen from Table 1, prior residency was never an advantage between prior  $\alpha$ s or between a prior  $\alpha$  and a prior  $\omega$ . Conditions  $I_{\omega R\alpha}$  and  $I_{\omega I\alpha}$  can be compared to assess prior residency

advantage and it indicates that familiarity, when given to the smaller  $\alpha$  fish, did not significantly balance the effect of size (largest  $\text{Chi}^2 = 1.09$ ,  $\text{df} = 1$ , ns). Conditions  $\text{I}\alpha\text{R}\alpha$  and  $\text{I}\omega\text{R}\omega$  were symmetrical on prior dominance experience (both rivals were  $\alpha$  or  $\omega$ ), and their comparison indicates that  $\alpha$  pairs did not react in the same way as  $\omega$  s when the smaller pair member was familiar with the meeting site. When size differences were small (*i.e.* in the 0-10%  $d$  range), prior-residency was not an advantage to  $\alpha$  pair members ( $\text{I}\alpha\text{R}\alpha_{0-10\%}$ , 11:12, ns to a  $Z$ ). On the contrary for  $\omega$  pairs within the same size  $d$ , it was a significant advantage ( $\text{I}\omega\text{R}\omega_{0-10\%}$ , 8:20,  $Z = 2.0788$ ,  $P < 0.0192$ ). When the intruder's size was larger than that of the resident in the 10-20%  $d$  range, the advantage of prior-residency diminished ( $\text{I}\omega\text{R}\omega_{10-20\%}$ , 5:11,  $P < 0.105$ , Binomial). In the 20-30%  $d$  range, the larger intruder significantly defeated the smaller resident, indicating that size definitively took over residency within that size range ( $\text{I}\omega\text{R}\omega_{20-30\%}$ , 14:3,  $P < 0.029$ , Binomial).

## Discussion

The question asked here was how three factors, potentially contributing to individual differences in **RHP**, interacted. The picture that emerges from the present data confirms basic empirical generalizations that were already well established concerning prior experience and size. However, it reveals intricate interactions among these factors and with familiarity with the meeting place.

When an asymmetry of the type  $\blacktriangle_{\alpha\omega}$  exists and the advantage due to size of the  $\omega$  rival is small, prior  $\alpha$  s systematically defeat prior  $\omega$  s, confirming a now well established empirical generalisation (Beaugrand & Zayan, 1985; Beacham & Newman, 1987; Beacham, 1988; Beaugrand *et al.*, 1991). However, when size differences are large, asymmetries in prior experience and prior residency do not significantly determine conflict issues. Size in  $X.h.$  is thus especially impressive in determining conflict issues when size differences between opponents are large. However, the nullifying effect of size upon prior experience  $\alpha$   $\omega$  advantage is gradual, thus confirming the findings of Beacham (1988) and Beaugrand *et al.* (1991). In general one can affirm that as the superiority of size of one opponent increases, size becomes the essential determining factor accounting for victory in spite of other differences between opponents in prior experience or residency. This is clearly evident from Figure 1 by examination of proportions of victories

obtained by successively larger fish, and it is amply supported by the statistical analyses presented herein.

While prior residency was expected to favour dominance (Zayan, 1975a, b, c; Beaugrand & Zayan, 1985; Beaugrand & Beaugrand, 1991), it was not generally confirmed by the present data. Prior residency was found to bring some advantage to the resident only when both fish were prior losers. It is a clear advantage in  $X.h.$  to be a resident when both rivals have experienced defeat ( $\omega\omega$ ) but it is not when both are prior winners ( $\alpha\alpha$ ), or when one has experienced victory and the other defeat. Such a result is not accidental as it replicates in essence what Beaugrand & Zayan (1985) had obtained in similar conditions with  $X.h.$  These authors had interpreted this effect as a support for a «fear» hypothesis: A fish is less disadvantaged by a prior defeat experience when introduced into a familiar environment than when introduced as an intruder into a strange one. Frey & Miller (1972) came to similar conclusions in their study of blue gouramis (*Trichogaster trichopterus*) that were residents of the meeting place for 24 hours. In general, residents did not defeat intruders significantly more often than the reverse, and residents (isolates or having received prior  $\omega$  experience) were systematically defeated by  $\alpha$  intruders. However, many of the behaviours occurring during conflicts appeared to be affected by prior residency, while not affecting dominance outcome itself. Their data led these authors to a «fright-residency» hypothesis that may be restated as follows: When a prior loser is introduced into an unfamiliar environment it triggers additional fright input that may inhibit normal fighting behaviour. For Frey & Miller (1972), the residency factor did not seem to act as a positive effect due to environmental familiarity but rather as a negative factor associated with unfamiliarity. Barlow (1961) implied that «new surroundings» produce a lowering of a «fright threshold» in *Badis badis*. Frey & Miller's (1972) hypothesis was that both intrusion and subordination could affect fright level independently. The present research finds that the combination of intrusion and subordination in the same fish has even more detrimental effects.

The present results also suggest that the effect of being in a familiar environment after having experienced defeat would be sufficiently important to even neutralize a relative disadvantage in size. This is supported by the fact that in  $I\alpha R\alpha$  pairs of the 10-20  $d$  range a significant majority of conflicts (79%) were resolved to the advantage of the larger intruder, while in  $I\omega R\omega$  pairs showing comparable size

differences smaller residents still won significantly more conflicts (69%). Such a result is also reflected on Figure 1 by an important difference on the ordinate between the «I $\alpha$ R $\alpha$  » and «I $\omega$  R $\omega$  » lines.

In the studies of Beacham (1988) and Beaugrand *et al.* (1991), size/weight relative to the opponent was found to be a good predictor of contest outcome only when size/weight difference was very important, not to say extreme. In *X.h.*, prior  $\omega$  s had to be at least 20-30% larger than their  $\alpha$  opponents for size to become the main explanatory factor of dominance outcome. This suggests that size assessment is rather imprecise in *X.h.* However, there are precedents in other species. For instance, Enquist *et al.* (1987) have reported that though *Nannacara anomala* were able to estimate relative fighting ability by visual assessment alone, their precision was quite low. It is only when the smaller fish weighed less than 40% of the larger that it gave up without any fight. Turner & Huntingford (1986) working with *Oreochromis*, also have confirmed that fish with higher standard lengths systematically defeated smaller opponents. However while they reported no relationship between the degree of size discrepancy and contest length, a weak negative correlation was found between the size discrepancy and contest intensity as measured by act/min and by the proportion of all acts that made contact. Such a weak correlation is difficult to interpret considering the round-robin design of their experiment and the systematic re-use of the same 11 opponents.

One can ask about the ecological relevancy of the size differentials selected and studied by the present research. *X.h.* is a tropical *Poeciliidae* fish found in Central America from Veracruz (Mexico) to the Honduras. The first author has made some observations on the populations of *X.h.* of the Atoyac River (Province of Veracruz, Mexico) just before the peak of the dry season (January) and at the beginning of the wet one (June). During the dry season, *X.h.* naturally distribute themselves in classes according to their size (age). Large fish shoal in large schools in the centre of what is left of the river, while small and immature fish form small bands near the banks and in bays of the mainstream. The same stratification has been reported in other species of *poeciliidae* (Baird, 1968; Moore & McKay, 1971). During the period in which the water level rapidly falls toward its dry season level, pools of varying sizes and depths are formed alongside the main stream and small groups of fish of similar sizes remain captive in these pools, which in some cases are no larger than the tanks we use in our

experiments. Within small groups of fish of the same size class, individual differences other than those of size can play a determining role in hierarchy formation.

Our results, together with those of Beacham (1988) and Beaugrand *et al.* (1991), reveal that the effects of recent prior dominance and subordination experience, far from being negligible when compared to size, play an important role in the determination of future dominance relationships. As for prior residency, it only plays a more restrictive role when both opponents are prior losers and when size differences are not extreme. These factors appear, in *X.h.*, to contribute to total **RHP** in a manner that appears additive over a wide range of size differences. They counter a size advantage when opposed to it or combine to size when at the advantage of the same opponent.

There is no contradiction between the present results and those of other studies that showed that even minimal size differences in fish can account for dominance outcome. Weight differences of less than 5% can predict winners in contests between male *Nannacara anomala* (Enquist & Jakobsson, 1986). Barlow *et al.* (1986) found that size differences of 2% were sufficient to predict winners in fights between midas cichlids (*Cichlasoma citrinellum*). Turner & Huntingford (1986) showed that in contests between male Mozambique mouthbrooders (*Oreochromis mossambicus*), the larger fish won more often, even when standard lengths differed as little as 1 mm. In *X.h.*, Ribowski & Franck (1993) found a highly significant relationship between weight and fighting success even in closely matched dyads with weight differences of no more than 10%. In all these studies (Ribowski & Franck, 1993; Barlow *et al.*, 1986; Enquist & Jakobsson, 1986; Turner & Huntingford, 1986), size or weight was the only factor that was varied by selection or *ex post facto*, since it was measured after dominance outcome. Those studies focused on size/weight as the only possible determinant of **RHP**. Other possible asymmetries were considered as nuisances and neutralized as much as possible instead of being systematically contrasted with size. Therefore, it is not surprising that a majority of fish settled according to even very minimal size differences, the only salient cue available, or the only factor coherently operating within such a research design. Thus, more multifactorial experiments opposing several factors are required to understand how they interact to affect **RHP**, and how **RHP** could be overridden by resource value expectation, as did *e.g.* Dugatkin & Biederman (1991).

In the present research, prior experience, familiarity with the meeting site, and size asymmetries could not be used to account for more than approximately 75% of outcomes when size differences of the fish were 20%. It remains to identify other factors that could account for the remaining 25%. Prior latent aggressive motivation as measured by mirror tests conducted before dyadic encounter seems to be a determinant of **RHP** in *X.h.* (Franck & Ribowski, 1987). Using this technique to measure prior motivation, this laboratory (Goulet & Beaugrand, in prep.) was successful in predicting victory in 70% of *X.h.* dyads when other determining factors were neutralized. Future research may show that latent aggressive motivation can be added to already studied factors in order to account for dyadic outcome in green swordtails.

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