

The role of individual differences in the formation of triadic dominance orders of male green swordtail fish (*Xiphophorus helleri*)

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Abstract

*Triads of *Xiphophorus helleri* males composed of a large prior winner (A), a small prior winner (α), and a small prior loser (ω) were formed. In one condition, A was used as bystander while in another condition it was the small ω . The bystander could see through a transparent partition and observe conflict settlement between the two other fish without interacting with them. As soon as a dominance relationship clearly emerged, the partition was raised and the fish on standby could establish dominance relationships with them. The most frequent triadic structures obtained were $A > \alpha > \omega$ and $A > \omega > \alpha$ indicating that individual characteristics played a determinant role in hierarchy formation. Patterns of assembly depended on individual differences of the fish. The fact that the same dominance structures were reached through various patterns of assembly suggests that individual differences are more determinant than paths of resolution in *Xiphophorus*.*

*Key words : Dominance hierarchy; Prior experience of victory or defeat; Size; Individual differences; Agonistic behaviour; *Xiphophorus helleri**

Introduction

*The dominance model formulated by Beaugrand and Zayan (1985) and expanded by Beaugrand et al (1991, 1996) indicates that individual differences could be used to predict and account for dominance outcomes in dyads of *Xiphophorus* fish. Among initial attributes though to affect on dyadic outcomes were prior experiences of victory and defeat, which in a polyadic context could correspond to transfer effects from successive encounters during hierarchy formation. Though Beaugrand and Zayan's model has been developed and tested with pairs of fish, the principle of parsimony suggests that similar factors and mechanisms ought to account for the formation of triadic and polyadic dominance structures as well. The objective of this research is thus to test this possible extension to dominance structures composed of three male *Xiphophorus* fish. To achieve this goal, we created*

asymmetries of size combined with that of prior victory or defeat experience amongst three unacquainted fish. The hierarchy formation was then studied under two triadic conditions of step-assembly where the fish predicted by Beaugrand and Zayan's model to occupy either the higher or the lower rank in the hierarchy was left on standby and introduced once the conflict between the two other fish had resolved.

In the present study, recent experiences of victory and defeat will be considered as initial individual differences rather than as consequences of the process of hierarchy formation itself. There are many precedents in such a use (Beaugrand et Zayan, 1985, Beaugrand et al., 1991, 1996; Beacham, 1988) but we admit that it is partly a matter of convention. For Landau (1951a, 1951b) and Chase (1974, 1980, 1982a, 1982b), the term "(initial) individual difference" refers solely to differences existing between individuals before being put together to form a hierarchy. In the present study, the experimenter will impose victory or defeat on the fish before having them encounter to form a hierarchy. Thus methodologically speaking, recent experiences of victory or defeat satisfy the definition of initial individual differences in the present experiment.

Predictions

The results of previous studies on dyadic encounters of fish were used to derive the following postulates upon which are based our predictions:

P₁ Given equivalent sizes (<10%), the fish with dominance experience should defeat a fish that experienced subordination (Beaugrand and Zayan, 1985; Beaugrand et al., 1991, 1996).

P₂ Given an equivalent social experience, the larger individual (>20%) should defeat an individual of smaller size (Beaugrand et al., 1991, 1996).

*P₃ Prior experience of victory and size superiority could combine additively in *X. helleri* (Beaugrand et al., 1991, 1996).*

Prior experience of victory or defeat and size were thus combined here to create three different propensities for winning: a large prior alpha (A) fish, i.e. having previously won an encounter and of a large size; a second fish as a small alpha (α), i.e. having previously won an encounter but a smaller size than an A; a third fish as a small omega (ω), i.e. as being of the same size as an α but having previously experienced defeat. Based on the three postulates presented above, we predicted that the most frequently obtained structure would be of the type $A > \alpha > \omega$; the sign ">" means the agonistic dominance of the first individual over the next one(s) in the chain.

Our second objective was to determine if sequences of conflict resolution would affect the structure of the resulting hierarchy and if their effect outweighs that of initial individual differences. The use of two conditions of introduction enabled us to gauge the importance of the order of interaction between fish and that of initial individual differences in the process of hierarchy formation. Dominance of two individuals by a third insures transitivity in a triad even when the third relation of the triad is not established. However, according to Chase (1982a), transitivity is greatly favoured if the individual to occupy the highest rank has the possibility to interact first and twice in a row to obtain double dominance. Therefore, in order to disrupt the behavioural sequences we created two conditions of assembly. In the first one, the conflict between α and ω was first resolved and then the large A was introduced. In a second one, the conflict between large A and small α was resolved followed by the introduction of the small ω . If individual differences are more important than sequences of assembly then similar triadic structures should be obtained under both conditions of assembly.

METHODS

Subjects and material.

*A pool of more than 1,200 adult Green swordtail fish, *Xiphophorus helleri* (Heckel), was constantly available in the laboratory. We bought all of them from the same breeder (5D Tropical Inc., Plant City, Florida 33566, USA). We sustained them in mixed groups of 100-150 males (adults and immatures) and females in nine large communal tanks of 165 litres each (90x50x40 cm). When needed for the experiment adult males were randomly netted from these communal tanks. All the 20 pre-experimental glass aquaria used were identical (30x15x15 cm) and contained 13.5 litres of water. The formation of triads was studied using 30x30x30 cm tanks separated along their width into two equal parts by a sliding partition made of white tulle fabric mounted on a glass frame. The fish on standby could readily observe social interactions occurring between the two fish meeting in the front compartment. A sash and pulley system allowed the partitions to be slowly raised from behind a hide, thus permitting the fish on standby to move from its compartment to meet the others in the front one.*

Size measurements.

*We took three size measurements on each male: (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 1 mm was maintained throughout. We paired males according to differences in their lateral surface (LS), which was obtained by adding the sword-length to the product of total length and flank height. Calculated in this way, Beaugrand and Zayan (1985) found that LS showed a 5% mean error when compared to lateral surfaces measured using a planimeter. Moreover, these authors have shown that LS had a significantly greater correlation to dyadic dominance outcome than the standard length in *X. helleri*.*

Size measurements were obtained before pair formation. We used a specially designed aquarium to measure the fish. Using a mesh partition that we could freely move about, the fish was gradually cornered and immobilized against the front glass. We then rapidly marked its length, height and sword length on the front glass with a felt pen. We measured distances between markings on the glass using a ruler after having released the fish.

Experimental procedure.

Design. Two independent samples of triads were formed, each corresponding to the nature of the fish left on standby, which was either a large prior winner (condition EA) or a small prior loser (condition E^{ωω}).

Prior experience was obtained by having unfamiliar fish meet in a pre-experimental encounter and by selecting winners and losers. Fish with a size difference less than 10% met until one of them clearly dominated (see below for the dominance criterion). From these we formed 40 triads composed of a large prior winner (A), a small prior winner (α) and a small prior loser (ω). No more than 10% in size difference differentiated the α and ω fish. The large A fish was 30-40% larger than its two smaller opponents. In condition EA, the large A was put on standby while the smaller α and ω opponents settled dominance in the front compartment. Under condition E^{ωω}, the fish among the three having the lowest propensity to win was put on standby while a large A encountered a small α in the front compartment.

As soon as a dominance relationship clearly emerged among the fish put in the front compartment, the partition was raised. Invariably, the fish on standby passed into the front compartment to join the

other two to establish a dominance relationship with them. While the three fish were always unfamiliar to each other, they had independently acquired prior victory or defeat experiences. Familiarity between opponents was further eliminated by selecting fish from different communal tanks.

Phases.

Pre-experimental phase. Prior social experiences of dominance or submission were established on the first day. Two fish from different communal tanks were measured and isolated for two hours in separate pre-experimental aquaria. Both fish had to be unfamiliar with each other and to have a difference in lateral surface between 0 and 10 mm². 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 from behind blinds. We noted which fish was the dominant pair member; otherwise at the end of the 12 hours the encounter was considered null.

Experimental phase. On day two, dyads were formed by means of recombination of opponents who had independently received a prior dominance or subordination experience at the pre-experimental phase on the previous day. We then introduced the fish on standby into the rear compartment of the aquarium. After 15 min, the two other fish were simultaneously introduced in the front compartment where they met. These two fish were observed for a maximum of one hour or until one clearly dominated its opponent, whichever came first. In the former case, the encounter was cancelled and terminated. As soon as a clear dominance relationship between them was noted, we gently raised the partition to let the fish on standby join the other two. The three fish interacted for an additional hour during which we noted behaviour and dominance issues.

In both phases, the selection of fish 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 were all noted. A program then applied this information and computed specific directions concerning the pairing of specific opponents. The program also randomly assigned pairs to the various available aquaria.

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. This criterion has been validated by Beaugrand and Beaugrand (1991).

RESULTS

We used one-tailed tests when a direction within differences was expected or could be predicted. Otherwise bidirectional tests were applied. When binary categories were tested, we used the binomial test (Bin). In some cases we have specified the nature of the null hypothesis under test, e.g. $H_0: p=1/4$, where $q=1-p$. Otherwise, the null is $p=q=1/2$. The tests used and their conditions of application are described by Siegel and Castellan (1988) and the maximum likelihood G-test by Sokal and Rohlf (1995).

Complete and incomplete triadic dominance structures that we noted at least once in the present research can be found in Table 1.

Insert Table 1 around here

Seventy-two percent (29/40) of all structures were both complete (i.e. all relationships were obtained)

and transitive (i.e. if $X>Y$ and $Y>Z$, then $X>Z$). No intransitive structure was noted. Even the 11 structures for which one relationship remained unsettled would have led to transitive triads if observation could have been pursued for a longer period and reversals had not occurred in the meanwhile. That 100% of triads were potentially perfectly linear is not due to chance since this latter probability of obtaining transitive triads is 75% ($p<0.001$ to Z test for proportions).

As we expected from individual differences, the most frequently obtained hierarchical structure was the $A>\alpha>\omega$ (18/40: 45%), followed by structure $A>\omega>\alpha$ (7/40: 17.5%). Assuming that each of the 6 possible complete triadic patterns has a 16.66% chance to occur, the fact that the structure $A>\alpha>\omega$ occurred in 45% of all cases cannot be accounted for by chance alone ($H_0: p=1/6$, $x=26$, $N=40$, Bin $P<0.001$). Considering the 29 complete structures only, the large A dominated both rivals in 86% of cases, the small α in 14%, and the small ω never. Such a distribution is evidently highly improbable ($H_0: p=$, $x=25$, $N=29$, Bin $P<0.001$) thus confirming the importance of individual differences. Essentially the same conclusions are reached when one combines complete and incomplete structures; large A occupies the top rank more frequently than by chance alone ($H_0: p=$, $x=33$, $N=40$, Bin $P<0.001$). In complete structures, small ω occupies the bottom rank and small α occupies the middle rank more frequently than by chance alone ($H_0: p=$, $x=34$, $N=40$, B $P<0.001$; $H_0: p=$, $x=18$, $N=29$, Bin $P<0.001$).

From these results, the most appropriate conclusion is that resultant triadic structures are determined by initial individual differences.

On patterns of resolution.

The terminology used by Chase is presented in the Appendix. For Chase, triadic structures are the product of sequences of resolution (which he calls patterns). According to his model, more DD and DS patterns should be obtained than any others. Observed patterns of triadic resolution are presented in Table 2 together with those published by Chase (1982a) in simultaneous triads. As can be seen from Table 2, in this experiment

 Insert Table 2 around here

patterns of resolution were never conjointly of the DD and DS types predicted by Chase's model. Our model based on individual differences would have implied different patterns of resolution depending on the nature of the fish on standby. In condition EA, patterns were expected to be of the BDID and DS types. Indeed, the small α should first have defeated the small ω , followed by the defeat of the small α by the large A and/or as well by the defeat of the small ω by the large A. This is exactly what can be noted in Table 2. That these patterns represent 92% of all obtained patterns is highly significant.

Similarly our model would have predicted that condition E^{ω} would be characterized by the pattern ISDB and DD. Indeed, the large A should have first defeated the small α , followed by the defeat of the small ω by the large A, and/or as well the defeat of the small ω by the small α . Again, examination of Table 2 confirms this expectation since DD and ISDB patterns together form 90% of obtained ones under the E^{ω} condition. This distribution is extreme when compared to the null hypothesis of a random uniform distribution of $1/4$ ($P<0.001$ to a Kolmogorov-Smirnov).

If we compare the frequency distributions obtained under each condition with that obtained by Chase (1982a), it is found that the former distributions differ from the latter (for EA, maximum-likelihood

$G=33.65$, $df=3$, $P<0.001$; for E^{ω} , $G=9.89$, $df=3$, $p<0.02$). Observed patterns of resolution differ when the fish on standby is a large A or a small ω (EA vs E^{ω} : $G=45.94$, $df=3$, $P<0.001$). This suggests that different mechanisms are at play when triads are assembled in steps, as in this experiment, rather than simultaneously as Chase did. Also, the process seems to be controlled by individual characteristics rather than by sequences of resolution per se as proposed by Chase (1982a).

Other regularities found.

The design of the present research was based on three postulates concerning the roles of prior experiences and size differences. These can be tested again using the present data.

Dyadic dominance structures are summarized in Table 3. A first regularity borrowed from Beaugrand and Zayan (1985) was that prior (small) dominants would defeat prior subordinates ($\alpha > \omega$) more frequently than the reverse ($\omega > \alpha$). This is confirmed under both conditions of standby A and ω ($H_0: p=1/2$, EA: 15:5, Bin $P<0.021$; E^{ω} : 10:2, Bin $P<0.019$).

A second postulate was that the A fish which was 30-40% larger than the smaller α would more frequently and significantly defeat it, experience being equal. Examination of Table 3 allows us to confirm this regularity borrowed from Beaugrand et al. (1991, 1996). Indeed, under both experimental conditions the larger individual significantly dominated the smaller α ($H_0: p=$, $x=33$, $N=40$, Bin $P<0.001$).

A third postulate concerned additivity of size and prior victory experience. This would be supported by the fact that the large A, which is simultaneously advantaged by size and prior victory experience, would more frequently dominate both its rivals than would the small α , which was advantaged only by prior dominance experience. In effect, Table 3 shows that the large A dominated both rivals in 33 out of 40 cases while the small α did only in 7 cases, and the small ω , never. These frequencies are evidently highly improbable when contrasted to an equiprobable distribution of 33% chance of each obtaining the first rank ($H_0: p=$, $x=33$, $N=40$, Bin $P<0.001$).

The three principles based on prior experience and size superiority that guided the design of this experiment on individual differences are thus supported.

DISCUSSION

The present results show that individual differences determine resultant triadic structures. The importance of individual differences is revealed by our ability to use them to predict triadic hierarchies in swordtails. Prediction was made possible by using individual differences that had been found to be determinants of dominance encounters in pairs of fish. Thus asymmetries in prior experience of dominance or submission and in size were experimentally combined to create fish having various propensities to dominate others in triads. Such results question Chase's issue of generality of the assembly model on two fundamental grounds. First, by showing that individual differences determine resultant triadic structures, it invalidates Chase's model that ignores their possible role in hierarchy formation. Secondly, we show that the same end structure can be reached by following resolution paths that are not principally of the DD and DS types. This casts doubt on the role of patterns of conflict resolution in insuring transitivity in a hierarchy, or at least it limits their role to cases where initial differences are small. The demonstration is particularly clear since Chase's model based on DD and DS patterns logically implies that bystanders should invariably end up in the middle of the hierarchy due to the necessity to satisfy these DD and DS patterns. Such a prescription is implicit in Chase's assembly model but did not materialize in the present data.

The discrepancy between the present results and those obtained by Chase concerning patterns of resolutions can be due to methodological differences between the two studies. The present research assembled triads in steps rather than simultaneously as Chase (1982a, b) did. We did not form a control group in which the three individuals were introduced simultaneously and could choose among themselves the order in which to settle successive conflicts. Such a «simultaneous» group would have been required to properly compare the assembly of triads in steps to that of assembling them at once as Chase (1982a, b) did. However, such a control condition is available from the work of Cloutier et al. (1996) in domestic hens. In their experiment they compared the simultaneous meeting of a large

A hen, a small α , and a small ω to that of a meeting in steps where the large A could attend the encounter between the other two and was introduced only once they had established dominance. The obtained dominance structures were essentially the same when the triads were formed

simultaneously or in steps (i.e. $A > \alpha > \omega$). The simultaneous condition of introduction produced patterns predominantly of the DD (90%) type as that obtained by Chase (1982a). However, when triads were assembled in steps, patterns of assembly were a mixture of BDID (38%), DS (38%), and DD (24%) types; that is very similar to that obtained by the present research for large A as bystanders. Thus similar triadic social structures could be reached through alternative paths of conflict resolutions while the resultant dominance structure remained invariant. This is clearly an indication of the preponderant role of initial individual differences over resolution paths, at least when individual differences are relevant and under experimental control.

A second difference between the present results and those of Chase (1982a, 1982b) may come from different preconceptions guiding the research of Chase and that of the present authors. Being convinced for theoretical and empirical reasons that individual differences could not account for hierarchy formation in animals (e.g. Chase, 1974), Chase (1982a, b) did not systematically vary initial individual differences. On the contrary, much care was taken to neutralize nuisance variables such as those due to previous encounters and to equalize individual differences. These rigorous controls contributed to maintain homogeneity in individual differences within the sample of hens. Even the residual individual variations that remained were not put into correlation with obtained dominance statuses. Thus it is no surprise that in the studies of Chase (1982a, 1982b) patterns of conflict resolutions remained the only salient factor to which observed transitivity could be attributed.

*This research assumed on the contrary that individual differences played a determining role during hierarchy formation and this preconception guided the experiment we did by varying relevant individual characteristics. Individual characteristics such as size and prior experience playing a determining role in *Xiphophorus* was already contained in research data obtained from dyads (e.g. Beaugrand and Zayan, 1985; Beaugrand et al., 1991, 1996). Moreover, since in our system of explanation prior experiences of dominance or submission were included and defined as initial individual characteristics, there was no reason to think that in groups composed of more than two individuals new mechanisms would be required to account for social structuring. The results obtained clearly show that individual differences effectively played the expected role and this role seems more preponderant than sequences of resolution per se.*

However, the present results can be reconciled with the Chase's approach by assuming that DD and DS sequences of resolution attest for the existence of a more profound explanatory mechanism, that is successive experiential effects of victory and defeat. Such effects are known to be very powerful since Beacham (1988) and Beaugrand et al., (1991, 1996) have shown that an advantage of 30-40% in weight/size in fish was required in a prior loser to defeat a prior winner. Victory would have the consequence to greatly increase momentarily the winning potential of the victorious animal A, and defeat, to greatly decrease that of the animal B. During that time bystander C is not affected by victory nor by defeat; therefore when it joins, its winning potential is located between that of A to which it most probably readily submits, and that of B, which it most probably submits. In such a case, proportions prescribed by Chase (1982a, 1982b) are realized: a majority of DD (animal A will also dominate C), and DS (B is also defeated by C).

Basically, intrinsic properties would determine the victory potential of the individual. However, as soon as encounters begin there is a carry-over effect from previous encounters to following ones.

This «social» factor was cleverly identified by Landau (1951b) in his «second model». This, in turn, may explain the low correlations between predicted hierarchies based on individual characteristics and observed hierarchies (Jackson and Winnegrad, 1988). When initial individual differences are significant as in the present experiment, they may affect the resultant hierarchy in two possible manners. First, individual differences may essentially determine which animals will obtain the first victory or defeat, which in turn will affect their propensity to obtain further victory or defeat. Cloutier et al. (1996) found that initial individual differences when they are important, influence the order in which hen opponents resolve conflict. The two hens that possess the greatest advantage due to initial individual differences choose each other to settle conflict in the first place. In most cases, the winner of this first settlement later encounters the bystander. Such a mechanism of opponent selection probably promotes the acquisition of a higher rank in the hierarchy. Slater (1986) had correctly foreseen such a mechanism. The second mechanism is that when individual differences are important but fish or hens do not meet simultaneously or are prevented to do so as in the present experiment, individual differences still influence the resultant hierarchies because their effects are not sufficiently perturbed or cancelled by successive victories and defeats. A fortiori, when initial individual differences are extremely small as in Chase's experiments, successive victories and defeats essentially shape the resultant structures due to their carry-over effects. Chase's developmental model of hierarchy formation based on DD and DS would thus be a special case applying when initial individual differences are small and opponents can freely interact. But it remains that DD and DS cannot per se account for transitivity.

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Appendix

Chase (1982a) has proposed a developmental process where preceding dominance interactions influence succeeding ones. This view was characterized as the jigsaw puzzle model of hierarchy formation. There are four and only four possible conflict resolution sequences for the first two dominance relationships formed by three animals in triad formation. By convention, the animal who becomes dominant in the first relationship is named A, the initial subordinate B, and the bystander C. After the initial dominance relationship of A over B (denoted by A>B), there are four possibilities: (1) A>C, the initial dominant dominates the bystander (Double Dominance or DD); (2) C>B, the bystander dominates the initial subordinate (Double Subordination or DS); (3) C>A, the Bystander Dominates the Initial Dominant (BDID); and (4) B>C, the Initial Subordinate Dominates the Bystander (ISDB). Though in principle each sequence is equally probable, Chase (1980, 1982a, b) has found that linear hierarchies commonly observed in small flocks of chickens result from a predominance of DD and DS patterns in component triads of larger groups. According to Chase (1980), DD and DS sequences would insure the formation of triads with transitive dominance relationships; the other two possible sequences could result in triads with intransitive relationships.

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TABLE 1. Obtained triadic dominance structures. The sign > signifies dominance; the sign ? indicates that the corresponding relation remains unsettled. -- represents a structural zero due to the nature of the experiment which renders the corresponding case impossible to realize.

CONDITIONS	COMPLETE STRUCTURES			INCOMPLETE STRUCTURES		Total
	A>α>ω	A>ω>α	α>A>ω	A>(α?ω)	α>(A?ω)	
EA	10	5	3	--	2	20
Eω	8	2	1	8	1	20

TABLE 2. Relative frequency of obtained triadic assembly patterns DD: Double dominance; DS: Double submission; BDID: Bystander dominates initial dominant; ISDB: Initial subordinate dominates bystander.

CONDITIONS	DD	DS	BDID	ISDB
EA	8.33%	50%	41.66%	0%
	(3)	(18)	(15)	(0)
E ω	50%	10%	0%	40%
	(10)	(2)	(0)	(8)
Chase	74%	17%	4%	4%
(1982a)	(17)	(4)	(1)	(1)

TABLE 3. Obtained dyadic relations (legend, same as Table 1).

CONDITIONS	A>D	D>A	A> ω	D> ω	ω >D	A? ω	D? ω
EA	15	5	18	15	5	2	--
E ω	18	2	19	10	2	1	8
Total	33	7	37	25	7	3	8