AN EXPERIMENTAL MODEL OF AGGRESSIVE DOMINANCE IN

Xiphophorus helleri (*Pisces*, *Poeciliidae*).

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ABSTRACT

   An experimental model was constructed using seven postulates derived from the experimental results of Zayan (1974, 1975a,b,c, 1976). The model specifies the relative importance of several asymmetries in predicting aggressive dominance in *Xiphophorus helleri*. These asymmetries concern differences between opponents with respect to: prior residence in the tested area (*versus* intrusion); immediate social experiences of dominance or submission; social isolation; individual familiarity and recognition. The predictions of the general model were checked experimentally and confirmed; a multiple orthogonal regression accounted for about 97% of the variance in our experimental results. The basic experimental results serving as postulates were confirmed and could be generalized; a new synthetic and predictive model was formulated concerning the determinants of aggressive dominance in *Xiphophorus* males. The following empirical generalisations were either confirmed or disclosed by the present study of opponents showing very small size differences: G_1: The dominance propensity is significantly higher in resident individuals than in intruders. G_2: The dominance propensity is significantly higher in previously dominant individuals than in previously submissive ones. G_2 holds true for dyadic encounters between acquainted as well as between unacquainted pair-members. G_3: The dominance propensity is similar in previously dominant individuals and in previously isolated ones. G_4: The dominance propensity is significantly higher in previously isolated individuals than in previously submissive ones. G_5: G_2 overrides G_1 in both acquainted and unacquainted opponents. In general it was found that recent agonistic experience (victory or defeat) was much more important to explain future issues than familiarity with the meeting place. However, negative effects of recent defeat appeared diminished when the prior loser encountered on familiar ground a prior dominant or isolated but unacquainted opponent.

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INTRODUCTION

Laboratory studies made on *Xiphophorus* suggest that the establishment of a dominance-submission relation between two individuals is under the control of a causal complex, including biophysical factors such as size and strength differences, as well as environmental familiarity, immediate social experiences of dominance or submission, and individual recognition. This latter set of factors may be called sociocognitive.

Size differences. It is well accepted by the ethological literature that differences in size and strength between opponents constitute a decisive factor in the outcome of aggressive duels in animals. In experiments introducing, simultaneously, two or more individuals into an unfamiliar milieu, it can be predicted that the larger individual will occupy a higher hierarchical position than smaller individuals. This was confirmed in several species of Teleosts (Noble & Curtis, 1939; Greenberg, 1947; Braddock & Braddock, 1955; Newman; 1956; Huck & Gunning, 1967; Baird, 1968; Gibson, 1968; Jenkins, 1969; Myrberg, 1971) including *Xiphophorus* spp (Collins et al., 1967; Noble, 1939; Braddock, 1945, 1949; Zayan, 1976).

In natural conditions Poeciliids seem to distribute themselves into size classes (Moore & McKay, 1971; Lowe-McConnell, 1964). Larger individuals tend to live in deep water while smaller ones stay near river banks, in more shallow waters. These different classes of individuals constitute distinct hierarchies which are most probably open at their lower extremity to permit emigration and immigration. It thus seems possible that within a class of fish having very homogeneous sizes, asymmetries introduced by other factors than size differences readily contribute to determine the hierarchical organization. For example, it has been often reported that a size disadvantage was less important than could be expected when possessed by a resident individual against a larger intruder. Hence, aggressive dominance is not simply a matter of size differences. Also, the work of Zayan (1976) on *Xiphophorus* has shown that size is a preponderant factor only when size differences between opponents exceed 5 mm. Similar observations were also reported for 3-5 mm size differences in *Trichogaster trichopterus* by Frey & Miller (1968, 1972). It would, then, appear that when size differences are naturally recorded and/or experimentally controlled, they have a negligible effect in determining aggressive dominance regularities.

Relatively few authors have actually measured size differences between opponents in fish. In the present study, however, two divergent objectives were aimed at when taking these measures. One objective was to manipulate size in order to estimate its effect on aggression. The other was to establish, *a posteriori*, a control for the statistical equivalence of two or more treatments, i.e., to neutralize their

effects while studying the action of other factors (but see Braddock (1945) and Zayan (1976) for *ex post facto* estimates of the effects of size differences on dominance or on hierarchical position). In this study, size differences were neutralized in order to study the interaction of socio-cognitive variables when size asymmetries were minimally operant. Although size differences are one of the basic determinants of dominance, the individual contribution of other factors, as well as their mutual interdependence, have to be weighed before considering size in a more complete model of dominance. Among these factors are the socio-cognitive ones.

Prior residence. An individual's familiarity with the environment in which the agonistic encounter occurs increases its probability of becoming the dominant animal, in fish, rodents and gallinaceous birds. In some fish species, a very short residence period often enables an animal to drive out and chase an intruder even if the latter is much larger (Noble & Curtis, 1939; Greenberg, 1947; Braddock, 1949; Baird, 1968).

   In some cases, familiarity with a given area favours one individual over another in such a way that the newly established dominance relation will not be restricted to the area in which it was established, but will apply in any area against the same conspecific. This relation of absolute dominance, initially favoured by prior residence, is particularly recorded in species not required to hold and actively defend a territory in a reproductive context (i.e., in such non territorial but hierarchical species as *Xiphophorus*). The effects of prior residence are well known in fish of the *Xiphophorus* genus, after the classic work of Braddock (1949) who showed that prior residence in an area ensures an individual a greater probability of aggressively dominating conspecifics than it would otherwise have. However, only intruders were handled in these experiments, and Zayan (1975c, 1976) demonstrated that these effects could disappear when both fish, resident and intruder, were simultaneously handled. When isolation periods of 22 hours were given to both resident and intruder prior to the test, final dominance did not appear to be more probable for the resident than for the intruder (Zayan, 1975c). However, Zayan (1976) could also confirm that dominance was significantly more frequent for residents when they were simultaneously handled with intruders, but, paradoxically, when previous familiarization with the home tank was only of 3-hour duration.

   It would seem that a 3h period of residence is sufficient to increase the probability of dominance of the resident over its intruder, although significant modifications of this trend could be expected if social experience instead of isolation was given prior to test, as will be seen.

Recent social experience. Will familiarity with the testing area still advantage residents if one or both individuals have undergone dominance or submission experiences immediately prior to the test?
It is well accepted that social conditioning, even of very short duration, very efficiently modifies subsequent aggression in several animal species. The mere fact of having had a previous dominance

experience was shown to increase an individual's probability of winning a future contest against a new conspecific, in fish (Braddock, 1945; Gibson, 1968; McDonald et al., 1968; Muckensturm, 1969; Rasa, 1969, 1971; Frey & Miller, 1972; Zayan, 1975a), rodents and gallinaceous birds (Colliers, 1943; Craig et a1.,1969; Ratner, 1961). It was also found that a recent submissive experience reduced this probability (Thinès & Heuts, 1968; Frey & Miller, 1972; Zayan, 1975a, b). However, the few systematic works on this subject have not always eliminated effects due to size differences, individual recognition, prior residence and experimental handling, all factors acting as possible major and uncontrolled asymmetries between opponents. Detailed criticisms can be found in Zayan (1975a), who imposed on *Xiphophorus* intruders a social experience of 3 or 24h before having them encounter a standard resident, itself isolated for 3 or 24h. His results reveal that residents significantly dominate previously subordinate and previously isolated intruders. However, the encounters of residents and previously dominant intruders suggest that in this case, dominance is equiprobable. That residents dominate, much more frequently, isolated intruders than prior α intruders indicates that the advantage of prior residence could be reduced by giving recent victory experience to the intruders, especially after a 3h period of isolation following its social experience and preceding the encounter, as is also suggested by the results. However, it is certain that prior residence favours dominance when the resident is isolated and its intruder-opponent subjected to an immediate submissive experience. Other experiments confirm that in unknown pair-members, i.e., unacquainted with each other, recent victory experience increases the probability of winning in a future contest, while recent defeat experience decreases this probability, especially when one of the opponents is a prior victor and its opponent a prior defeated. Whether or not prior dominant individuals defeat more readily a prior submissive opponent than an isolated one, considered as control (i.e., absence of prior dominant or submissive experience), should also be investigated.

It should be noted that isolation is not a proper control for social experience of either dominance or submission considered singly, since it suppresses not only social experiences but also all types of social contact. Such a radical suppression of prior dominance and or prior submissive experiences seems to produce specific effects on the aggressive state. For instance, a period of social isolation of only few hours contributes to increase aggression in fish (Braddock, 1945; McDonald et al., 1968; Thinès & Heuts, 1968; Frey & Miller, 1972; Goldenbogen, 1977; Wilhelmi, 1975). A short period of isolation is frequently used in experimental studies in order to "prime" agonistic behaviours between conspecifics. It is thought, more or less explicitly, that an isolation period eliminates any immediate social experience of submission, as was suggested by Braddock (1949) and by Frey & Miller (1972). However, the positive correlation that seems to exist between social isolation and aggression cannot be directly generalized to apply to the outcome of an aggressive encounter itself, since it has been shown that the most aggressive individuals are not necessarily the ultimate winners of the contests (Thinès & Heuts, 1968; Zayan, 1975a). On the other hand, a number of researchers have pointed to the similarities between the

behaviour of isolated, and prior victory in male mice (Benton & Brain, 1979). Thus, an individual isolated for 24h should dominate more easily a prior subordinate individual than the reverse.

Individual recognition. When two individuals have had a mutual encounter within 24h before another planned encounter, their behaviour during this second encounter differs both qualitatively and quantitatively from that observed between two individuals which are in all respects equivalent but unknown to each other. In *Xiphophorus*, individuals seem to confirm or maintain the dominance relationship that was established in the first encounter, without manifesting again the high frequency of agonistic behaviour that was associated with the establishment of their initial prior winner-prior loser relationship. Thus individuals which have been previously associated and socially connected possess properties which influence the nature of their subsequent relation. This process will be attributed to individual recognition, provided experimental controls reveal that unacquainted pair-members lack such specific changes in behaviour (see Zayan, 1974 for such behavioural evidence and its methodological prerequisites).

The existence of individual recognition in our fish requires that three distinct capacities be at work. Firstly, it supposes the capacity of the individual (brain) to discriminate one particular conspecific from at least another conspecific of equivalent properties. Secondly, it implies the mnesic capacity to memorize the sensory and perceptual information which makes an animal different from another conspecific to a given observer. Thirdly, the capacity to retrieve these data and to put them in correspondence with the associated prior dominance relation between the observer and a particular conspecific.

In the context of the present study, we chose to use, as an indicator of individual recognition, the stability or lack of inversion of the initial dominance relation between two given known individuals, while inversion was expected in the case of unknown individuals, as evidenced by Zayan (1974). Since the evidence of retrieval of perceptual and relational information is clearly dependent upon testing conditions, which induce differences in aggressive/flight behaviour and dominance stability or inversion, it is recognition, rather than recall, which could be assessed unequivocally. However, our experiment was not designed to demonstrate individual recognition but to show that it could have the status of an intervening variable, liable to explain agonistic events and dominance in our fish. Zayan (1975b) also found that when two individuals have established a dominance relation even for a short period (24h, 3h), the initially established relation remains invariant even if the previously dominant individual meets its previous submissive partner in the latter's home-tank. This stable pattern was statistically most frequent when the initially dominant individual was a resident and the initially subordinate one, an intruder. The initial dominance relationship could be expected to inverse when the prior subordinate fish was placed in its former territory (as resident) before receiving its prior dominant partner as intruder. However, such dominance relationship stability opposes an expected inversion of the

effects of prior residence upon (territorial) aggression and (territorial) dominance of the aggressive type. Thus, individual recognition, associated to immediately precedent divergent dominance and subordinate experiences, overrides the effects of prior residence.

Elaboration of the model. Our model was derived from a number of postulates predicting which type of opponent should dominate its opponent in every sample of paired contests which were experimentally prepared and carried out. The model assumed that the outcome of every duel would be determined by certain asymmetries, with respect to definite properties of the two opponents. Also, the degree of determination or predictability of a duel would differ according to the various types of asymmetries: these could be placed in specific order with respect to their capacity for affecting dominance probability, depending on the type of advantage/disadvantage expressed by each asymmetry. Any advantage, and its corresponding disadvantage, was defined by specific individual properties which were pre-experimentally known. Before the contest, every future opponent was accorded (or deprived of) some of the following properties: previous residence in the testing area or intrusion in it; previous dominance or submission after an agonistic encounter; previous isolation, i.e., deprivation of preceding domination or subordination experiences (as well as of any less specific type of social experience); previous knowledge or ignorance of an opponent whose individual properties were likely to be recognized in the course of the duel. Size differences between opponents were not considered as a (pre)experimental variable and were neutralized as much as possible in order to let the other selected asymmetry determine the outcome of the duel, whether singly or by interaction.

Definitions.

   Duel. A dyadic agonistic encounter between *Xiphophorus* adult male opponents possessing controlled characteristics, and which resolves into the dominance of one opponent over the other.

   Prior residence. A 3h-isolation period of a fish in a tank in which the same individual will encounter (receive), for the duel, an intruder-opponent to which that tank is unfamiliar.

   Immediate social experience. Experience acquired as a victory or as a defeat at the issue of an agonistic encounter planned 18-22h before the duel, as well as experience acquired during the 18-22h period which followed during which the winner could express its continuous dominance (α-experience) over its subordinate (ω-experience). The absence of any prior α or ω-experience corresponds to *social isolation* (Iso).

   Social isolation. A 18-22h period of residence in a tank without any conspecific, immediately before the duel.

   Individual familiarity and recognition. Familiarity: Property of a opponent which was previously known by its opponent during the 24h period immediately preceding the duel. Since social experience

was, by definition, of the dominant or submissive type, the two familiar opponents in the test were always α and ω individuals.

   Recognition. Perceptive/behavioural discrimination of the differences between an individual known (α or ω) just before the duel and one which was unknown (though also α or ω). Recognition is a process involving familiar properties of the opponents; it can be indirectly evidenced by significant differences between the previously known and the unknown pair-members. Very significant differences in aggressive behaviour and social dominance were actually found between these two types of pairs in the duels of the present experiment: shorter latencies before first attack, longer fights, more frequent dominance reversals were recorded for unknown opponents: many other results, to be interpreted as valid indicators of individual recognition associated with previous α and ω-experiences, were also found. In the context of the experiment as it is presently reported, what was actually operating as a pre-experimental variable was individual familiarity with an α or ω conspecific. Individual recognition was unequivocally at stake during the initial stage of the duels, and could be considered as an experimental event which progressively determined the eventual outcome of the contests.

Asymmetries.

An asymmetry denotes the difference between pair-members with respect to one property. A *symmetry* on a given property denotes equivalence of the opponents concerning that property. The four general properties presented above could be combined to form asymmetries (or symmetries) between any two opponents. Properties assessed experimentally in individuals paired for contests consisted, essentially, in three factors:

- Prior residence, with only two logical possibilities considered: a resident (Res) meeting an intruder (Int), or two individual intruders meeting in an unfamiliar tank (symmetry Int-Int); the possibility of pairing two residents by reintroducing them in their own tank was discarded.
- Immediate social experience, with the following possibilities: -both opponents were deprived of social contact, i.e., isolated (Iso); -only one opponent was isolated, the other one having been either dominant (α) or subordinate (ω); - both opponents had social contact and their agonistic experience could have been either convergent (both previously dominant, or both previously subordinate), or divergent (one previous α fish was paired to one previous ω fish).
- (Inter-) individual familiarity, a *symmetry* with two possibilities: -both opponents were unknown (Unk) and the three possibilities of social experience applied; -both opponents were known to each other (K), and in such case they could only have had a divergent social experience (a former α fish paired to a former ω), i.e. individual familiarity implied an α-ω asymmetry because there were no intermediate situations (isolation or further agonistic experience) between social conditioning and test-pairings.

   The (pre-)experimental state of each individual was defined by the possession of a triplet of properties from the cartesian product (Res, Int) X (Iso, α, ω) X (K, Unk). There were only three samples with

pair-members being symmetrical on all properties; this was the case of unacquainted intruders which had been both previously isolated (Iso Iso), or dominant (α-α), or subordinate (ω-ω). In all the other cases, different states resulted from asymmetries concerning each of the three basic properties. In some samples, pair-members possessed asymmetries with respect to only one property; this was the case of: - unknown resident and intruder which had been both previously isolated, or dominant, or subordinate; - unknown intruders of which one had been isolated and was meeting either one dominant or one subordinate individual; or, unknown intruders of divergent social status (α *versus* ω); -and finally, known intruders of divergent social prior experience. In the remaining samples of pairs, opponents possessed asymmetries with respect to two properties of their respective states; in all these cases, one asymmetry concerned the resident *versus* intruder property and the other concerned previous social experience of fish which could be either known or unknown to each other.

In most pairs where opponents possessed different pre-experimental states, it could be easily assumed that one fish was advantaged at the expense of the other. Such a critical advantage was warranted by the previous empirical generalizations founding our basic postulates. However, some pairings of asymmetric properties /states did not correspond to obvious predictions concerning eventual winners of duels. Thus, in known as well as in unknown fish the probable advantage of being a resident was compensated for by the concomitant disadvantage of having been a subordinate before encountering a previously dominant intruder. Of course, equivalent states or total symmetry corresponded to a null theoretical gain; in that case, dominance was expected to be equiprobable.

Basic postulates.

Seven propositions can be formulated in order to serve as premises for our model. They are by no means theoretical, let alone formal: these propositions can be considered as experimental generalizations, because they express lawful relations evidenced in specific experiments. In fact, the seven basic propositions correspond to statistically significant results found by Zayan (1974; 1975a,b,c; 1976) with pairs of *Xiphophorus* males. They are not self-evident, and need to be demonstrated in order to be accepted as the building blocks of a predictive model. Despite the methodological correctness of Zayan's experiments, they were not taken for granted but were instead subjected to further testing in the present experiments. A confirmation of these initial findings would support their generalization and would, by the same token, validate the model which they helped to construct. This is why the following seven basic propositions deserved to be termed postulates and, once mapped into probabilities, will become predictions, i.e., specific hypotheses to be tested statistically in the context of a more synthetic experiment.

P1: Dominance propensity is higher in resident individuals than in intruders.

[Res►Int], where ► means a greater propensity to obtain dominance for the pair member possessing the left property over that possessing the right one. The converse applies to the ◄ symbol. Thus, in this case [Res►Int], and also [Int ◄ Res].

P2: Dominance propensity is higher in previously dominant individuals than in previously submissive ones. P2 holds true for duels between known as well as between unknown pair-members.

[α►ω], i.e., [α►ω] and [ω◄α] asymmetries;

more precisely: K U Unk[α►ω]=K[α►ω] v Unk[α►ω].

P3: Dominance propensity is higher in previously dominant individuals than in previously isolated ones. In the present experimental context, P3 holds by definition for pairs of unknown opponents.

Unk[α►Iso], i.e., [α►Iso] and [Iso◄α] asymmetries.

P4: Dominance propensity is higher in previously isolated individuals than in previously submissive ones. As for P3, P4 holds true, by definition, for pairs of unknown opponents.

Unk[Iso►ω], i.e., [Iso►ω] and [ω◄Iso] asymmetries.

P5: P2 is significantly stronger in pairs of known opponents than in pairs of unknown ones. Remark: in the present experimental context, individual familiarity/recognition is inevitably associated to the most divergent asymmetry with reference to previous social experience, i.e., [α►ω]; therefore, effects of the former imply necessarily the effects of the latter (while the converse is false).

K[α►ω]>Unk[α►ω].

P6: P5 imposes a restriction on P1: in pairs of known opponents, the effect of previous social experience (necessarily of dominance or subordination) is a more important determinant of dominance propensity than the effect of prior residence can be. Or, if preferred, individual familiarity/recognition (inevitably coupled to effects of α-ω experiences) inhibits the increase of dominance propensity by prior residence.

K[α►ω]>K[Res►Int].

P7: P6 can be extended to pairs of unknown opponents, i.e.: Unk[α►ω]>Unk[Res►Int].

The combination of P6 and P7 provides a more general postulate:

P6 + P7: P2 imposes a restriction on P1: the most divergent asymmetry with respect to previous social experience is a significantly more important determinant for dominance propensity than is the asymmetry ensuring residence advantage and intrusion disadvantage.

K U Unk[α►ω]>K U Unk[Res►Int].

Prediction of an overall trend

As indicated above, our experimental set-up was designed in order to produce symmetries or asymmetries with reference to discrete properties of two opponents. An asymmetry is a relation of advantage/disadvantage between two fish. Advantage given to an individual with respect to (a) certain property(ies) implies a corresponding disadvantage for the opponent, respecting the formal asymmetry of a (partial) strict order relation; were a certain advantage shared by both opponents (e.g., previous dominance), it should imply symmetry with reference to a given property, defined formally as an equivalence relation. It should be noted that, formally, both the asymmetry and the symmetry relations are transitive because so are the strict order and the equivalence relations. Empirically, any asymmetry should be associated with an obvious prediction concerning the future dominant individual of a pair-contest, according to the fish advantaged by a given property. Accordingly, any symmetry should be associated to equivalent propensity of each opponent to become the dominant individual. Such theoretical equivalence at the level of propensities should be reflected by statistical equivalence in the dominance frequencies of individuals which were mutually assigned advantageous (e.g., α status), disadvantageous (e.g., ω status or intrusion), or neutral (e.g., isolation or social inexperience) properties.

As stated above, asymmetries with respect to residence and/or social experience entail a comprehensive asymmetry holding true for the pre-experimental state of the two opponents. The model assumes that partial asymmetries add up to compose a total asymmetry whose value could be assessed by some means. The model also postulates that a symmetry for any given property either does not interact with an asymmetry for another factor, or does it randomly. Whether this postulate is warranted or not will be verified by *a posteriori* statistical analysis.

Definite predictions regarding the winner of a duel had to rest upon some rule of appreciation of the relative advantage of one fish over its opponent. This was made by attributing some fixed values to all types of asymmetries. Any value expressing the advantage of a fish was considered as an expected gain and thus given a positive sign; of course, the corresponding disadvantage of the other pair-member was expressed by the same value which was preceded by a negative sign, reflecting expected loss of dominance potential or tendency. The value which was presumed to be gained (or lost) due to a given asymmetry was assessed approximately by using weights or degrees of importance. These values, although conventional, were not arbitrary, because the various weights respected the order of importance defined by the basic postulates. They state the various asymmetries which were proven to favour (or disfavour) aggressive dominance in opponents, but they also suggest some ranking of asymmetries according to their relative capacity for determining the probability of dominance. The ordering of the various asymmetries should result from the logical connection among postulates. For instance, the two predictions contained in P3 and P4 should imply P2, which concerns the greatest divergence between previous social status α and ω. Thus, if the order relation ► represents a greater propensity in

dominance tendency and is transitive, it is reasonable to infer that: α►ISO & ISO►ω → α►ω; moreover, these three binary relations suggest the ternary relation: α►ISO►ω. But a more exhaustive ranking should connect this simple prediction to individual familiarity (using P5) on the one hand, and to the advantage of prior residence (using P6 and P7) on the other hand. Such an order was achieved after respecting three additional principles: 1) any positive (advantageous) asymmetry occupies a higher rank than its negative (disadvantageous) counterpart; 2) any positive asymmetry occupies a higher rank than any negative asymmetry; 3) the order of positive and negative asymmetries concerning the same property should be the inverse of each other, since both axe given the same value with opposite signs (we would have, e.g.: +n>+n'>+n">-n">-n'>-n, for n, n' and n" expressing the values of the three asymmetries A, B and C such that A>B>C>-C>-B>-A).

First, a scale was constructed, proceeding from maximal advantage to maximal disadvantage. If previous social experience is considered, P2 states that maximal asymmetry is to be expected in pairs where an α and an ω opponent meet. How, P5 states that individual familiarity introduces the most extreme asymmetry between previously α and ω opponents, whence the following order: K[α►ω]>Unk[α►ω]>Unk[ω◄α]>K[ω◄α].

Next, the effects of previous isolation must be ranked between the two extreme effects of previous α and previous ω-experiences. Zayan's results (1975, plus other unpublished experiments) suggest that: 1) final dominance is more determined by the [Iso►ω] asymmetry than by the [α►Iso] asymmetry: immediately precedent ω-experience lowers more the future dominance propensity than immediately precedent α-experience tends to increase it; 2) previous isolation tends to positively determine future dominance, so that the effect of an immediately precedent isolation experience is closer to that of α-experience than to that of ω-experience. Whence the following ranking: K[α►ω]>Unk[α►ω]>[Iso►ω]>[α►Iso]>[Iso◄α]>[ω◄Iso]>Unk[ω◄α]>K[ω◄α].

Finally, the asymmetry introduced by prior residence may be located in the advantage-disadvantage scale by recalling P6 and P7, according to which the resident-intruder asymmetry is less determinant than both the [α-ω] asymmetry and the individual familiarity. Whence the following order: K[α►ω]>Unk[α►ω]>[Res►Int]>[Int◄Res]>Unk[ω◄α]>K[ω◄α].

There is only one position for which we do not have any solid indication from experimental work, and that is the location of the prior residence asymmetry with respect to [Iso►ω] and [α►Iso] asymmetries, and for their converse asymmetries [ω◄Iso] and [Iso◄α]. One compromise would be to make room for equivalent ranks of dominance determination. But we wanted our general model to consist of a chain of predictions, i.e., in a totally ordered set of asymmetries related by strict (asymmetric) order of importance. This is why the three possible positions for the prior residence asymmetry will be considered, making three alternatives for our general model:

(A1) K[α▶ω]>Unk[α▶ω]>[Iso▶ω]>[α▶Iso]>[Res▶Int]>[Int◀Res]>[Iso◀α]>[ω◀Iso]>Unk[ω◀α]>K[ω◀α]

(A2) K[α▶ω]>Unk[α▶ω]>[Res▶Int]>[Iso▶ω]>[α▶Iso]>[Iso◀α]> [ω◀Iso]> [Int◀Res] >Unk[ω◀α]>K[ω◀α]

(A3) [α▶ω]>Unk[α▶ω]>[Iso▶ω]>[Res▶Int]>[α▶Iso]>[Iso◀α]>[Int◀Res]>[ω◀Iso]>Unk[ω◀α]>K[ω◀α]

Table 1. The asymmetries of the three alternative models were given weights in order to produce predictions. The numbers assigned to asymmetries respect the relative importance of each asymmetry in predicting dominance.

		Alternative models		
		(A1)	**(A2)**	**(A3)**
+1.00		K[α>ω]	K[α>ω]	K[α>ω]
	>			
+0.50		Unk[α>ω]	Unk[α>ω]	Unk[α>ω]
	>			
+0.35		[Iso>ω]	[Res>Int]	[Iso>ω]
	>			
+0.15		[α>Iso]	[Iso>ω]	[Res>Int]
	>			
+0.10		[Res>Int]	[α>Iso]	[α>Iso]
	>			
-0.10		[Int<Res]	[Iso<α]	[Iso<α]
	>			
-0.15		[Iso<α]	[ω<Iso]	[Int<Res]
	>			
-0.35		[ω<Iso]	[Int<Res]	[ω<Iso]
	>			
-0.50		Unk[ω<α]	Unk[ω<α]	Unk[ω<α]
	>			
-1.00		K[ω<α]	K[ω<α]	K[ω<α]

It was assumed that propensities represented in our model (by ►) would be reflected by empirical frequencies and could be represented as probabilities (by >). The asymmetries were given numerical weights in order to produce the predictions of the model which were to be tested experimentally (Table 1). The numbers assigned to asymmetries respect the relative importance of each asymmetry in determining dominance propensity and in predicting dominance frequencies. Values between -1 and +1 were assigned through iteration in such a way that for any type of duel, the sum of the weights corresponding to the asymmetries of prior residence and of previous social experience indicated the tendency of a fish to win or to lose the contest. In the former case, the value is positive and in the latter it is negative: the numerical sum found for both pair-members is identical but of opposite value signs. A total value approaching unity reflects the highest expected tendency to become dominant (+1) or subordinate (-1), and a total value approaching 0 reflects equiprobability for both tendencies (and for both opponents). It is obvious that numerical values assigned to the asymmetries are not truly quantitative, let alone probabilistic. They simply express degrees of the predictability of dominance, and

consist of numerical appreciations at ordinal level. Thus, the sum of two asymmetries could exceed unity, as was the case for the fish advantaged by residence and by α-experience before meeting a known opponent; for example, in the case of alternative A1, their estimated tendency to win the contest amounts to +1.10, while their opponent is expected to lose the duel as unequivocally (-1.10). It could be easily accepted that these extreme tendencies would be adequately expressed by a probability p=1.00 of future dominance and subordination, respectively. As a matter of fact, all the values corresponding to the assumed capacity of asymmetries used for predicting dominance can be translated into theoretical frequencies and compared to the empirical frequencies recorded during the test-contests: these can, in their turn, be given probabilistic values which provide a quantitative evaluation of the predictions and of the model in general. Further predictive models could represent the increasing/decreasing tendency or propensity to dominance by conditional probabilities referring to the (pre-)experimental state of each opponent.

   Since three alternatives were proposed for the relative importance of the prior residence asymmetry, three values can possibly express the total asymmetry (positive or negative) which is expected for each opponent when the contest opposes one resident to an intruder. It should be recalled that the property of intrusion is considered here as implying the property of residence of the opponent (two intruder opponents do not possess an asymmetry with respect to the property of residence, although the fact of being an intruder implies that of not possessing the property of residence). To illustrate the three possible values, we shall consider the duel between a previous dominant resident (Res α) and a previously isolated intruder (Int Iso), isolation implying necessarily that both opponents were unknown to each other. The total positive asymmetry for one fish will combine the values of the [Res>Int] and [α>Iso] asymmetries, and the total negative asymmetry will sum up the values of the [Int<Res] and [Iso<α] asymmetries. In each of the alternatives A1, A2 and A3, the total positive weights are equal, respectively, to 0.25, 0.45 and 0.25: the corresponding values of -0.25, -0.45 and -0.25 are found for the disadvantaged pair-member. The prediction resulting from the A1 solution indicates that previous residents should win 25% more contests than their Iso-intruder opponents. Thus, over, for example, 100 independently planned encounters of the same type, 62.5 duels should be won by the α-residents and only 37.5 by the Iso-intruders. The difference between dominance frequencies predicted for each type of opponent coincides empirically with the expected 0.25 value distance between the dominance propensity of the Res α and the Int Iso opponents. It should be noted that in the fictional case of 100 tests of this type, this 25% difference would correspond to a rejection of dominance equiprobability to the p<0.010 level (for 62 *versus* 38 outcomes; binomial test, one-tailed since asymmetries make it possible to predict explicitly the direction of the difference). Alternative A2, which attributes more weight to the prior residence asymmetry (45%), would predict dominance by the a -resident in 72.5 duels out of 100, the corresponding 27.5 victories by the Iso-intruders being statistically negligible (P<0.0001, binomial test). Of course, other differences in dominance frequencies and probabilities should be found for larger or

smaller samples of the [Res α-Int Iso] duel types. The same remark holds true in adapting the numerical values of asymmetries, in each alternative, to the dominance frequencies predicted for each type of opponent. Since our experiment planned only 20 independent duels of each type, the (difference in) percentage of wins expected for both opponents of each duel type had to be adjusted from a theoretical sample of 100 duels to that of 20 duels.

Table 2 presents the dominance frequencies which could be predicted from the expected values, expressing the total asymmetries between opponents in each of the 18 planned duel types. For each of the alternative models A1, A2 and A3, total asymmetries were made to correspond to a predicted difference in the dominance frequencies of the two opponents in 20 paired contests, independently planned for each duel type. These predicted frequencies were calculated from the percentages of a reference sample of 100 contests of each duel type, and were then applied to the actual samples of 20 pairings. Dominance frequencies predicted for any pair-member of the 20 duels are inevitably complemented by submission frequencies of its opponent, as null outcomes were never recorded. Therefore, expected wins could be presented for only one pair-member instead of referring to the difference with the predicted wins of the opponent. For the sake of clarity, Table 2 conventionally presents the frequency with which the left opponent(s) of each duel type should defeat the right opponent according to the three possible predictions of the model. The dominance frequencies predicted for the left pair-member were compared to frequencies in a binomial distribution for N=20, where they could appear either as equivalent to randomly expected outcomes (i.e., as equiprobable dominance for the two opponents), or as significantly greater (>) than would be expected by chance. Since nearly all asymmetries of the left opponents corresponded to an expected advantage, nearly all of their predicted wins were actually more frequent (>) than equiprobability (the converse would have been found systematically if the right pair-members had been conventionally taken as references in Table 2). The number of victories which could be considered significantly more frequent than expected by chance had to be greater or equal to 13.5, and those which could be considered less frequent had to be smaller or equal to 5.5; these frequencies represent significant trends at the $P<0.05$ level (actually at $P=0.04$, binomial one-tailed test warranted by the specific predictions of asymmetries). This procedure was applied simply to compare the dominance frequencies predicted by A1, A2 and A3 to those actually recorded during the tests otherwise than by impressionistic criteria.

The specific hypotheses of our experiment consisted of the 18 predictions generated by each of the three alternatives A1, A2 and A3 of the model. Each alternative provided 18 specific hypotheses, although many predictions were common to at least two of the alternatives. We hoped the results would indicate if one of the three alternatives made better predictions than its rivals (models should be put in competition in order to avoid ad hoc confirmations given *ex post facto*).

TABLE 2

Predicted and obtained frequencies. Each alternative predicts, for each of the 18 duel-types, the frequency, over 20 independent duels, with which the "left" duellist of the pair (ex: duellist Res Iso of group Unk[Res Iso-Int Iso]) should defeat its "right" opponent. These predictions as well as the observed results were compared to a binomial distribution having the same number of independent trials. The zone between 5.5 and 13.50 was declared equiprobable (=) while values outside this range were considered significantly different at the p<0.05 (one-tailed) level. A comparison plot made between observed (O) and predicted frequencies is also presented. Numbers 1, 2, 3 represent predictions made by each of the corresponding alternatives over 20 duels.

	DUEL TYPE	PREDICTED FREQUENCIES			OBSERVED FREQUENCY	FREQUENCIES (0 5 10 15 20)
		A1	A2	A3		
1	K[Res α-Int ω]	19.90 >	19.90 >	19.90 >	18.00 >	o 1 (at 20)
2	K[Int α-Int ω]	19.90 >	19.90 >	19.90 >	20.00 >	(at 20)
3	Unk[Res α-Int ω]	16.00 >	18.50 >	16.50 >	17.00 >	10 2 (at 15)
4	Unk[Int α-Int ω]	15.00 >	15.00 >	15.00 >	15.00 >	(at 15)
5	Unk[Res Iso-Int ω]	14.50 >	15.00 >	15.00 >	13.00 =	0 1
6	Unk[Int Iso-Int ω]	13.00 =	11.50 =	13.00 =	15.00 >	23 0
7	Unk[Res α-Int Iso]	12.50 =	14.50 >	12.50 =	13.00 =	0 2
8	Unk[Int α-Int Iso]	11.50 =	11.00 =	11.00 =	11.00 =	01
9	Unk[Res α-Int α]	11.00 =	13.50 >	13.00 =	13.00 =	1302
10	Unk[Int α-Int α]	10.00 =	10.00 =	10.00 =	10.00 =	
11	Unk[Res Iso-Int Iso]	11.00 =	13.50 >	11.50 =	16.00 >	13 2 0
12	Unk[Int Iso-Int Iso]	10.00 =	10.00 =	10.00 =	10.00 =	
13	Unk[Res ω-Int ω]	11.00 =	13.50 >	11.50 =	14.00 >	13 0
14	Unk[Int ω-Int ω]	10.00 =	10.00 =	10.00 =	10.00 =	
15	Unk[Res Iso-Int α]	9.50 =	12.50 =	10.50 =	7.00 =	0 13 2
16	Unk[Res ω-Int Iso]	7.50 =	12.00 =	8.00 =	11.00 =	1 02
17	Unk[Res ω-Int α]	6.00 <	8.50 =	6.50 <	4.00 <	0 13 2
18	K[Res ω-Int α]	.10 <	.10 <	.10 <	2.00 <	1 0

(0 5 10 15 20)

Experimental design

This experiment intends to test the general order proposed by our previously formulated general model. It will also compare the three alternative solutions concerning the relative importance of prior residence in the hierarchy of dominance determinants in *Xiphophorus*. The present experiment consists in carrying out all the possible encounters between opponents, amounting to 18 types of combinations of asymmetries (see Table 2). This entails making 18 independent samples, consisting of 20 encounters for each sample of duel types.

METHODS

Subjects.

Seven hundred and twenty adult male *Xiphophorus helleri* Haekel were used in the present experiment. hey were regularly imported from the same breeder (Florida Fish Pounds; Tampa. Florida, USA) and maintained in four heterosexual stocks of 100-150 individuals in 60 litre tanks (60 x 30 x 30 cm) for at least two weeks before the experiment. Fish were fed dry food (Tetramin) in the morning and after each transfer, and received live food once per week.

Aquaria.

Eighteen pre-experimental 15 litre glass tanks (25 x 25 x 25 cm) and 24 additional aquaria (30 x 15 x 30 cm) were used as experimental test-tanks. These tanks were unknown to the fish before the experiment and were chemically and visually isolated from each other. All sides except the one reserved for observations were painted white. Each aquarium was lighted by a 15w fluorescent tube and received natural sunlight from adjacent windows. A 18h photoperiod was used throughout with initiation of the photofraction at 0800h. Water temperature in all tanks ranged from 21° to 24°C during the three months of experimentation. Since all tanks were located in the same room, they were virtually subjected to synchronous and identical daily variations in temperature. Each experimental and pre-experimental aquarium had a 3cm gravel bottom and was aerated by one air-stone. Water in the stock tanks was filtered using several external Dynaflow filters. The pH and salinity of the water was not monitored during the experiment. However, water added daily to tanks was dechlorined and kept for at least 48h before being used. Various objects such as plastic tubes, charcoal chips, rocks and shells were arranged on the bottom of the experimental tanks in order to create patterns favouring discrimination of different tank configurations. Before each transfer, from one aquarium to another or back to the same aquarium, a fish was always isolated for a (maximum) period of two minutes in a small transparent transfer box made of clear plastic (7 x 7 x 5 cm) already containing water from the fish's original tank.

Definitions.

The reader is invited to examine Figure 1 in which a flow chart depicts the operations followed in order to experimentally attribute properties to the individuals in this experiment. This graph can describe 10 types of opponents having particular experiences. When these individuals were paired at the end of Phase 3, 18 different types of encounters were possible.

Recent social experience was defined as the property attributed to an individual (α or ω, Resident or intruder, Known or Unknown) as a consequence of its simultaneous introduction with an unfamiliar conspecific into an aquarium unfamiliar to both of them prior to the test. This encounter at Phase 1

lasted between 18 and 22 consecutive hours and immediately preceded the 3h period of isolation in Phase 2 in order to impose prior residence. Isolation (Iso) was defined as the property attributed to an opponent (Resident or Intruder) which was placed alone in an unfamiliar aquarium for a period lasting between 18 and 22 consecutive hours. This aquarium was not the residence tank nor the eventual test-tank. The isolated individual was deprived of recent social experience (α or ω) and was necessarily unknown to the opponent it encountered for the contest.
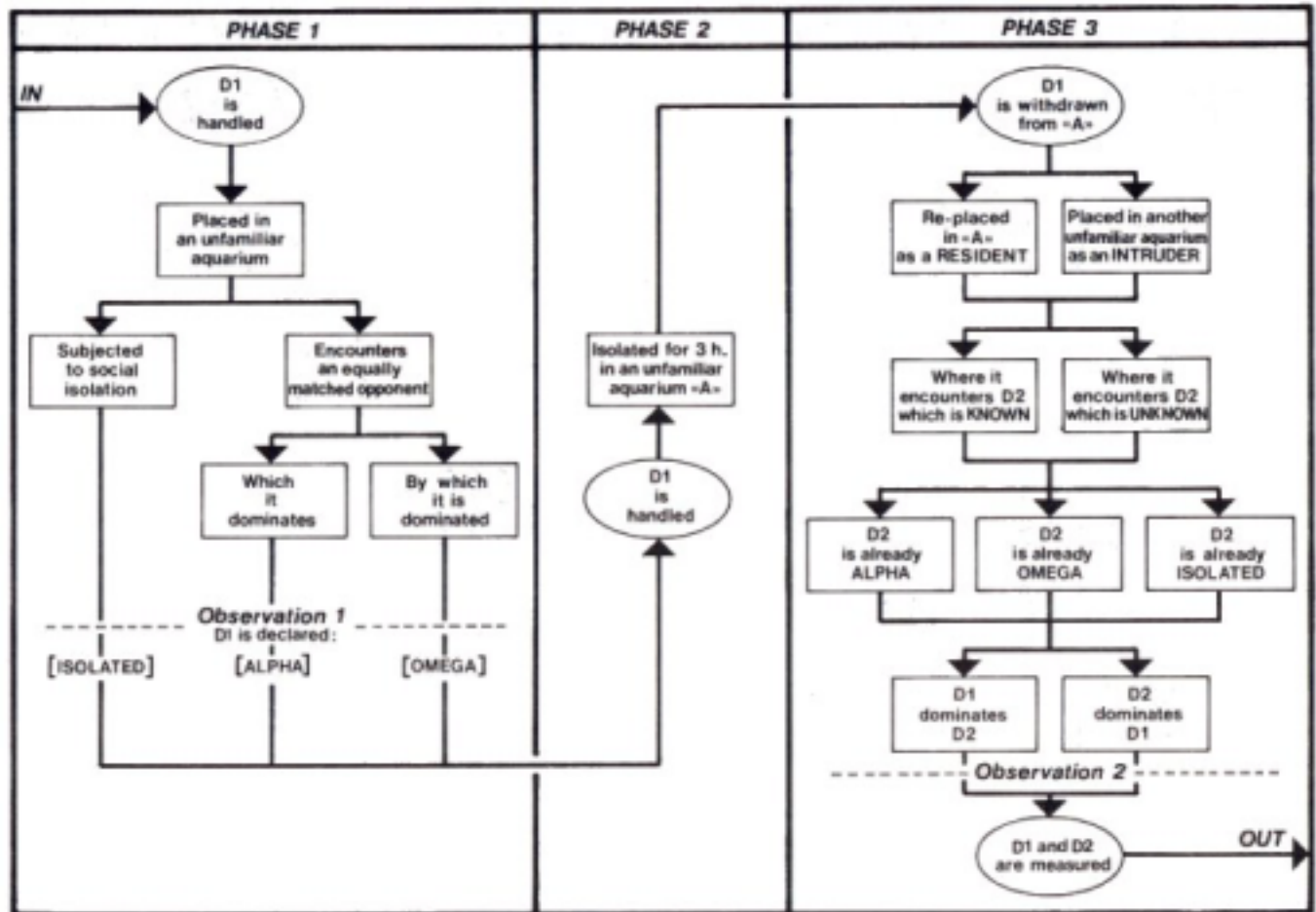
Fig. 1. Flow chart representing the experimental operations necessary to attribute individual properties to the duellists as well as asymmetries to duel-types. Phase 1 lasted between 18-22h and served to attribute social experience or isolation. Phase 2 lasted 3h and allowed attribution of prior residence to resident fish that were to be returned to their familiar aquarium in order to complete the duel-test in Phase 3. Phase 3 lasted 30 min and served to test the hypotheses concerning the outcomes of agonistic duels. D1 = duellist #1; D2 = its opponent.

Alpha (α) was defined as the property of an opponent (Resident or Intruder, Known or Unknown) having had a recent social experience of dominance over an unfamiliar opponent during Phase 1.
Omega (ω) was defined as the property of an opponent (Resident or Intruder, Known or Unknown) having had a recent social experience of submission towards its opponent during Phase 1.
Residence (Res) was defined as the property attributed to an individual (α or ω , Iso, Known or Unknown) having occupied, singly, a residence tank for a 3h period immediately preceding the

duel-test. This fish had prior residence experience, and was re-introduced into its familiar residence tank for the test-contest.

Intrusion (Int) was defined as the property attributed to an opponent (α or ω , Iso, Known or Unknown) having occupied an aquarium which was not the same as the test-tank. The intruder was introduced, for the contest, into an unfamiliar tank where it encountered either a Res or an Int.

Unknown (Unk) was defined as the property attributed to an opponent (Res or Int, α or ω , or Iso) encountering an unfamiliar opponent for the test. Obviously, the two opponents of the test were either unknown or previously known.

Known (K) was defined as the property attributed to an opponent (Res or Int, α or ω , or Iso) by having it encounter, for the test, the same opponent against which it had acquired recent social experience in Phase 1. An α-ω relation always existed between these two individuals before the contest. If one of the individuals concerned was an α , then its known opponent necessarily was an ω.

Dominance referred to the conclusion of a duel. At the end of Phase 3 (test) a fish was either the dominant (α) individual or the submissive (ω) one. The a-individual had satisfied the criterion of aggressive dominance defined below, and an aggressive α-ω relation was said to have been established between these two individuals. When combined, the preceding properties specified 10 different types of fish. The combined encounters of these 10 fish-types constituted 18 samples of duel-types:

1	**Unk [Int Iso - Int Iso]**
2	**Unk [Res Iso - Int Iso]**
3	**Unk [Int α - Res Iso]**
4	**Unk [Res Iso - Int ω]**
5	**Unk [Res α - Int Iso]**
6	**Unk [Int Iso - Res ω]**
7	**Unk [Res α - Int α]**
8	**Unk [Res ω - Int w]**
9	**Unk [Res α - Int ω]**
10	**Unk [Int α - Res ω]**
11	**K [Res α - Int ω]**
12	**K [Int α - Res ω]**
13	**Unk [Int α - Int Iso]**
14	**Unk [Int Iso - Int ω]**
15	**K [Int α - Int ω]**
16	**Unk [Int α - Int α]**
17	**Unk [Int α - Int ω]**
18	**Unk [Int ω - Int ω]**

Experimental manipulations. Experimental manipulations are presented in Figure 2. For all groups, the experiment was divided into three phases which were completed within two consecutive days.

   Phase 1 attributed properties creating social asymmetries between opponents. "Isolation" and "individual recognition" were applied *a priori*. However, a and w-experiences were not pre-experimentally imposed upon particular individuals, but were acquired spontaneously at the conclusion of the agonistic encounter of Phase 1. As illustrated in Figure 2. during Phase 1 a fish was
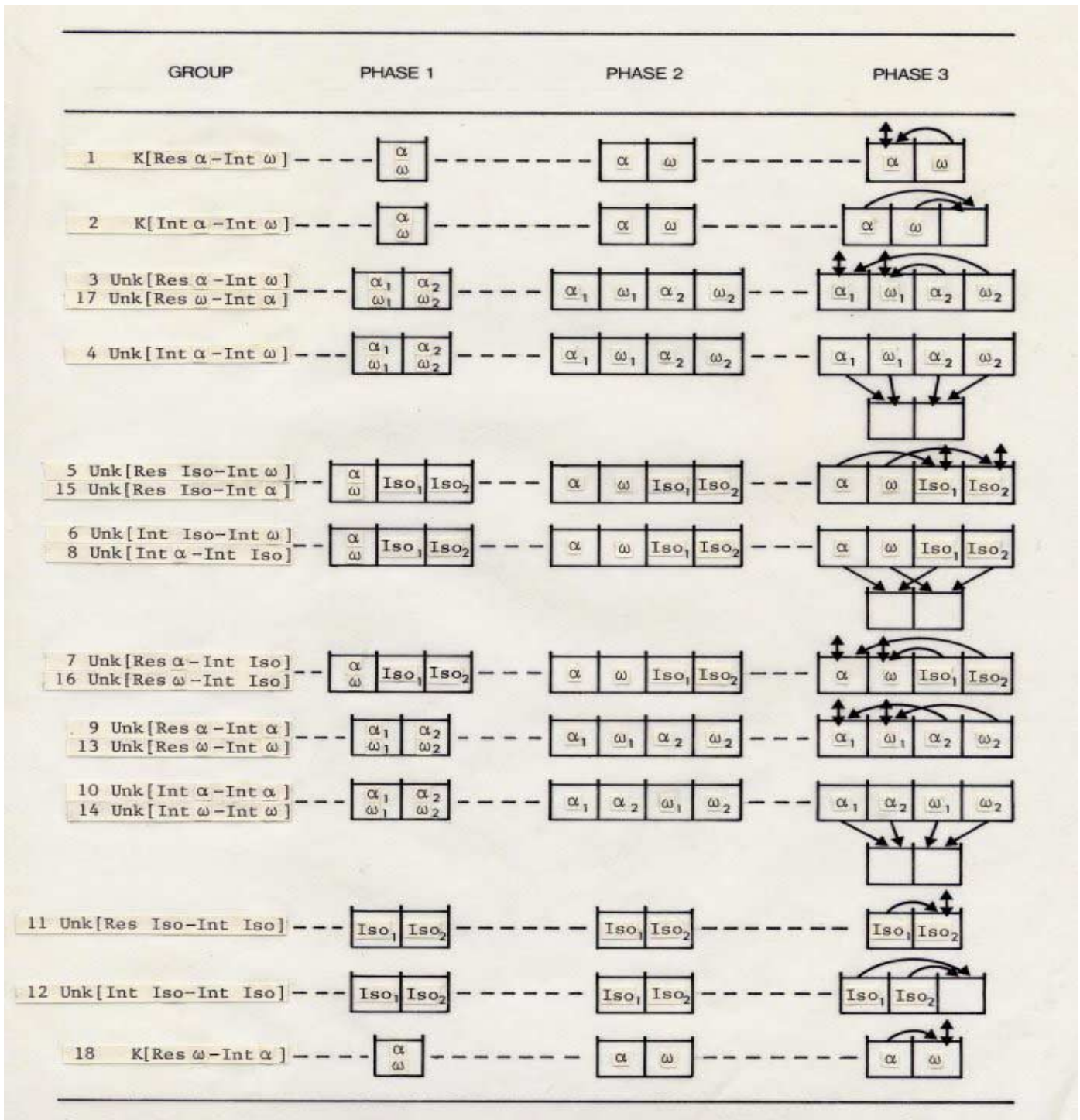
Fig. 2. Experimental manipulations. Phase 1 allowed attribution of social experience or isolation. During Phase 2, all individuals were isolated for 3h in a tank which, for residents, also served as the experimental test tank in Phase 3. In Phase 3, manipulations were performed, in order to create 18 different kinds of duel. Symbols: α = alpha experience, ω = omega experience, Iso = isolation experience, Res = resident, Int = intruder, Unk = unknown, K = known. The same aquaria could serve for Phase 2 and Phase 3. Twenty encounters were planned for each of the 18 duel-types.

either isolated for a period of 18-22h in a pre-experimental. unfamiliar aquarium, or placed with an unknown conspecific of the same size in a milieu that was unfamiliar to both opponents. The fish were netted from the holding tanks immediately before Phase 1. However, special care was taken to not allow the encounter of two fish originating from the same holding tank: the fish were thus unknown to each other at the beginning of Phase 1, which lasted 18-22h. The last 3h of this phase were used to identify the α and ω individuals of each pair.

Phase 2 served to a priori attribute prior residence to some individuals. Future residents were placed alone, for 3h, in the same aquarium as the one that would serve as the test milieu for the same individual and its opponent. However, this aquarium was not the same as the one used during Phase 1 for the attribution of social experience. The fish designated as intruders were treated in the same way as were residents, except that the aquarium in which they had been placed was not the one in which the test occurred. Both of the fish to be pained for the test were thus isolated for 3h, until Phase 3. This short period of isolation made the future resident familiar with the experimental test aquarium.

Phase 3 was the test phase, in which duels between opponents of determined properties occurred. The test consisted of transferring, simultaneously, both fish from the tank in which they had been kept in isolation for 3h, to the test-tank, which could be either unfamiliar to both opponents ([Int – Int]) or unfamiliar to only one of them ([Res – Int]). These fish could also be the same individuals that had had opportunity to settle a contest against each other in Phase 2 (K[α-ω]) or they could be unknown opponents (Unk pairings), in which case one or both opponents could be α, Iso or ω individuals. *Controls.* Between 10 and 15 duels were planned each day so that in two consecutive days the duels of at least one of the 18 treatments was completed. The fish were randomly assigned to groups as well as to different aquaria, to their place in the order of transference within a given pair, and to their place in the order of testing within a day.

A close examination of Figure 2 will show that some groups were operational complements of each other. For ex., groups Unk[Int α-Res Iso] and Unk[Res Iso-Int ω] formed one manipulated test unit. Single groups, plus complements, formed 12 test units which were used as a basis for randomization. To control cyclic effects which could accumulate over a number of days and could bias the order of application of the treatments, the order was assigned a priori according to a pseudo-random chain which compensated for series of two or more repetitions of the same sequence of test units. This ranking was computer-generated using an algorithm of sampling without replacement. A lag auto-correlation run over the first 4000 test unit numbers thus generated did not reveal any inherent periodicity. Examination of Figure 2 will also reveal that the execution of the test unit corresponding to the group Unk[Int α-Int ω] completed two encounters of this type each time, thus making this group progress twice as rapidly as any other group. After seven weeks, the 20 duels of this group had thus been completed. During the experiment, all aquaria were used an equivalent number of times for all groups.

Procedures. Each day, operations were carried out as follows. Beginning at 0900h, between 10 and 20 male adult *Xiphophorus* were caught from the holding tanks and placed individually into clear plastic transfer boxes. Two or four fish, all coming from different stocks and thus unknown to each other, were paired according to size and general appearance. Differences in morphological characteristics (such as pigmentation and colour of fins and body, body and sword lengths, and flank width) were carefully noted, and pairs or couples of pairs forming test units were, in principle, constituted of individuals whose differences in size and morphology were minimal. When differences in body sizes exceeded 3 mm, one of the fish was replaced by another one coming from the same holding tank. Each paired fish was then introduced into a pre-experimental aquarium, singly (for isolation) or with a conspecific, following strictly the a priori protocol established for Phase 1. Dehydrated food was then distributed to the newly transferred fish. This procedure was repeated at 30min intervals, until all the pairings prescribed for the following day were completed. Starting at 0800h the next morning, pairs were observed in order to identify the dominant individual of each pair. Encounters for which it appeared impossible to clearly declare the dominant individual were cancelled and re-scheduled at the end of the experiment by adding new days of experimentation.

Phase 2 began 3h before the test, i.e., at 1000h. The fish were isolated in the experimental aquaria. Their newly-vacated pre-experimental aquaria were immediately re-used in order to prepare the test units for the next day. The final test occurred after the 3h-period of isolation in Phase 2. Phase 3 began by capturing all the isolated fish and placing them into individual transfer boxes for 2 min. The two opponents of each pair were then introduced, simultaneously, into the same test aquarium, which could be the isolation aquarium of one fish (the resident), or a tank unfamiliar to both of them (both intruders). Each encounter was then systematically observed by two observers until one of the opponents was declared obviously dominant over its opponent, after having clearly satisfied the criterion of dominance defined below. All encounters not clearly settled within one hour were cancelled and re-scheduled.

Behavioural observations. For 200 of the 380 duels, agonistic behaviour was systematically recorded using two Datamyte ethographs (Model 916 Electrogeneral Co., Minnetonka, Minn., USA). The selected method of entry allowed each act to be noted as a behavioural code, prefixed by its relative time of occurrence (100hz precision). Each observer was assigned one opponent. Both sequences of observations recorded for the two opponents were collapsed into one interaction vector by synchronizing the recordings of both sequences. The detailed results of analyses performed on the behavioural data will be published separately. Although a detailed description of the behavioural patterns is not relevant to the present paper, those which were used as indicators of aggressive dominance will be defined.

Attack. Sudden acceleration of an opponent towards its conspecific, the initial distance being at least equal to the length of the initiator. This unit may be followed by a bite or mouth contact (butting)

emitted by the initiator. It can be associated to an avoidance movement, or to clear fleeing on the part of the attacked opponent. This last case defines a chase or its initiation.

Bite and Mouth-contact. Mouth-contact consists of application of mouth-parts, usually against the flank of the opponent (nip): biting is defined as grasping, with the mouth, of the ventral or pectoral fins or gonopodium, or even of the mouth of the opponent (mouth-fight).

Chase. Aggressive acts (Attack, Bite, Lateral-display, Tail-beat) by a given opponent in temporal association (antecedent. simultaneous or subsequent) with clear fleeing on the part of its opponent.

Dominance. The final state of a planned agonistic encounter or duel, in which one individual is declared the winner, dominant or alpha (α) if, and only if, it has succeeded to chase its opponent in 5 consecutive occasions without in the meantime having been chased in turn. The other opponent is in a submissive state, and the loser or defeated opponent is declared the omega (ω) individual.

Fleeing. Associated to an approach, or an attack, a bite, a lateral-display or a tail-beat, this movement produces a rapid avoidance of the opponent (escape) by sudden acceleration. It is sometimes accompanied by a submissive posture. The fleeing unit was always recorded with concomitant initiation of an aggressive act by the opponent.

Submissive posture. The attitude of a fish, which lowers its dorsal and caudal fins, sometimes associated with fear (when the ventral fins spread out). It is sometimes accompanied by tilting on the side when the opponent approaches or charges.

Size measurements. After the encounter, both pair-members were netted and immobilized on a sheet of paper to be measured with precision (l mm). Four measures were independently taken (1) Total length: The distance between the snout and the extremity of the sword. (2) Body length: The distance between the snout and the extremity of the caudal fin. (3) Sword length: The distance between the extremity of the caudal fin and the sword end. (4) Flank width: The distance between the root of the dorsal fin and the origin of the gonopodium.

RESULTS

In this section we will see to what extent the general model adequately predicts the observations, and if it is possible to choose the "best" model between the three alternatives. After having admitted that even minimal size differences between opponents could explain part of the results, it is necessary to establish the relative importance of the asymmetries considered to be relevant, including those introduced by size differences. This will be done with stepwise multiple regression analyses. A new predictive equation will then be proposed for a new possible model. Finally, it will be shown whether the initial basic postulates were confirmed by the data. A confirmation would validate the whole model, since the postulates helped to generate its empirical predictions.

The general model and its alternatives. Table 2 reports the frequencies predicted by each of the three alternatives as well as the observed dominance frequencies for the opponents in each of the 18 groups. The accompanying symbols represent binomial decisions, taken at the 5% error level, specifying whether this dominance frequency is significantly larger than (>), or statistically equivalent to chance frequencies. Figure 3 presents the same observed results in a tridimensional graph. It suggests that the tendency to dominate increases with increasingly advantageous social asymmetries. However, the same increase is not as evident for prior residence asymmetries. Positive effects of prior residence seem to be more restricted to the central zone of the social asymmetry dimension, in which the slope appears more accentuated than at the extreme zones.

Table 2 permits to visualize the predictive accuracy of the general model and of the three alternatives. It can be seen that the three predicted vectors coincide well with the vector composed of observational data. The predictive accuracies of the three alternatives were compared by measuring the correlation between their respective predictions and the corresponding observations. The sum of square differences (SSD) between predictions and observations were also used to give the most closely-conforming index for each alternative. These measures are presented in Table 3. This table indicates that the basic model, common to the three alternatives, is well correlated to the observations (min Rho=0.77, *P*<0.001),and that alternative A2 shows the best correlation (Rho=0.81, *P*<0.001). However, the fact that the sum of square deviations is simultaneously larger for alternative A2 than for the two others (SSD=0.775) is an indication that A2, although showing an overall best coincidence with what was actually observed, makes few but larger errors in prediction than A1 and A3. On the other hand, when the frequencies of predictions confirmed by the binomial test ate respectively compared, it is found that all three alternatives have between 13 or 14 of their predictions supported. Alternative A2, giving more weight to prior residence, still has the best score for supported predictions, since 14 of its 18 predictions are accepted. However, close examination of Figure 4 reveals that although the predictions in three cases

where prior-residence was concerned were improved, A2 predicted much more inaccurately than did the other two alternatives in at least two cases: Unk[Res Iso-Int α] and Unk[Res ω-Int α].

Thus, it would seem arbitrary to retain one of the alternatives on the basis of such precarious advantages. Moreover, visual inspection of Figure 3 will show the existence of interactions between social and residence asymmetries, interactions that none of the present alternatives can account for. The results will be analyzed in mode detail in order to include these interactions in the basic model by retrodiction. However, before proceeding further, it seems imperative to eliminate possible explanation of the results by size asymmetries between opponents, which may arise even if precise measures were made to neutralize size effects.
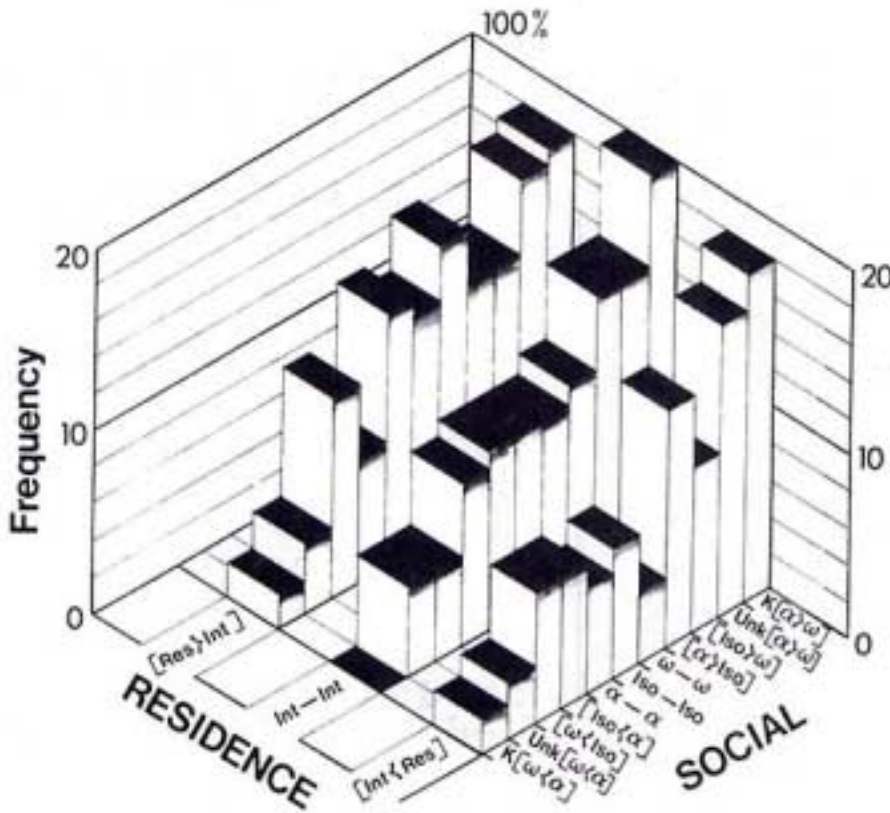

Figure 3. Frequencies of dominance as a function of social and residence asymmetries. Each column is based on 20 duels.

TABLE 3

Correlations and sum of square deviations obtained between the predictions made by each alternative and the observations. The number of realized predictions is the number of predictions made by each alternative and confirmed at the 5% level (binomial test).

Alter-native	Number observ.	Spearman Rho	Kendall Tau	Pearson R	Mean-sq. Deviation	N Realized predictions
A1	18	0.7741*	0.6549*	0.8168*	0.637	13
A2	18	0.8117*	0.6784*	0.8347*	0.775	14
A3	18	0.7803*	0.6502*	0.8309*	0.629	13

* $p < 0.001$

TABLE 4

Size measures for each group and for the 360 pooled individuals. Body measure, the mean of the group, the mean difference between the ultimate winner and loser (M-Dev) and the standard deviation of this difference (S.D.) is presented in mm. The same measures are also presented for the 228 subjects that fought at the pre-experimental phase in order to acquire social experience (228 PRE).

	GROUP NAME	BODY-LENGTH Mean	M-Dev	S.D.	SWORD-LENGTH Mean	M-Dev	S.D.	FLANK-WIDTH Mean	M-Dev	S.D.
1	K[Res α-Int ω]	49.60	0.30	2.69	19.40	2.10	5.01	11.20	-0.10	0.89
2	K[Int α-Int ω]	49.50	2.90	7.14	20.33	-0.65	4.75	11.70	0.70	1.10
3	Unk[Res α-Int ω]	46.78	0.35	3.41	17.38	-0.45	4.27	10.68	0.35	0.79
4	Unk[Int α-Int ω]	46.08	0.95	2.40	17.08	0.55	6.26	10.48	0.55	0.74
5	Unk[Res Iso-Int ω]	48.22	0.25	2.66	18.38	-0.35	5.69	11.00	0.10	0.83
6	Unk[Int Iso-Int ω]	47.40	-0.30	2.47	18.50	-0.40	5.44	10.83	0.35	0.96
7	Unk[Res α-Int Iso]	48.30	-1.10	2.89	18.15	1.00	4.40	11.05	0.10	0.83
8	Unk[Int α-Int Iso]	47.43	0.95	2.54	18.55	1.50	5.85	10.90	0.50	0.87
9	Unk[Res α-Int α]	48.20	0.90	3.46	17.65	0.00	6.24	11.08	0.35	0.79
10	Unk[Int α-Int α]	49.43	-0.55	3.06	18.25	1.60	6.12	11.33	-0.25	0.77
11	Unk[Res Iso-Int Iso]	53.60	0.40	2.62	22.40	1.40	4.89	12.17	0 25	0.89
12	Unk[Int Iso-Int Iso]	54.53	0.65	3.29	21.48	0.35	4.42	12.63	0.25	0.94
13	Unk[Res ω-Int ω]	48.22	1.55	2.69	18.98	0.35	5.59	11.10	0.40	0.73
14	Unk[Int ω-Int ω]	47.20	0.00	2.61	16.70	1.10	5.75	10.85	0.20	0.60
15	Unk[Res Iso-Int α]	50.38	1.05	3.07	19.13	3.55	6.71	11.65	0.40	1.02
16	Unk[Res ω-Int Iso]	47.85	0.80	2.25	17.63	1.45	6.42	10.73	0.15	0.96
17	Unk[Res ω-Int α]	47.22	0.05	3.84	17.75	0.30	7.34	10.50	0.10	0.83
18	K[Res ω-Int α]	49.55	0.90	2.91	17.95	-2.20	5.49	11.40	0.00	0.84
	360 POOLED	49.16	0.58	3.42	18.82	0.56	5.86	11.29*	0.26	0.89
	228 PRE	48.32	0.78	2.72	18.38	0.91	4.90	11.06*	0.25	0.96

* $p < 0.01$

Size differences. Size differences between opponents can, in principle, become a major determinant of dominance when they exceed a certain limit. The present study recognizes the effects of size asymmetries upon *Xiphophorus*, although the experiment itself attempted to establish that aggressive dominance can be determined and even predicted by factors other than size differences between opponents. The fact that the effects of size differences were neutralized in order to study the interaction of other pre-experimental asymmetries implies that size was not at all an underestimated factor of dominance.

Size measures were taken for each opponent, after the experiment. so that it could be seen whether very small differences had systematically influenced the results. Planned comparisons were carried out for each of the following measures: (1) total length (TL), (2) body length (BL), (3)sword length (SL), (4) flank width (FL), (5) estimated lateral surface (ELS), (6) estimated weight (EW). The first four measures were defined previously. An estimate of the lateral surface (ELS) was obtained by taking the product of measures (2) and (4) and adding measure (3). By tracing off the contour of 33 representative individuals spread out and placed on a sheet of paper, and comparing the planimetrically measured surfaces with the estimated ones, an average error of 5% was found and was considered acceptable. The estimated weight (EW) was arrived at by the application of a transfer function from BL, FL and SL. The transfer function was obtained by regression of real weights into body measures for the 33 precisely weighed and measured male *Xiphophorus* representative of those serving in this study. The resulting regression equation was the following: EW=0.091BL + 0.135FL + 0.004SL-1.925

All of the above measures were compared with t tests for independent measures. Whenever it was possible, a one-tailed test was used, following the currently accepted hypothesis that larger individuals have a greater probability to win a contest than their smaller opponents. Due to lack of space, it is not possible to present the results of the 252 comparisons made: Table 4 summarizes statistics of the various group measures.

First, in order to determine whether individuals had systematically defeated their smaller opponents during Phase 1 (when previous α and ω experiences were determined) size measures were compared for the 228 winners and the 228 losers which were retained for use in Phase 2 of the experiment. The results indicated that the 228 winners of the pre-experimental phase had a tendency to be the larger individual of a pair, and this for all measures of size (TL: t(454)=1.69, *P*<0.05, one-tailed; BL: t(454)=1.603, *P*<0.01; FL: t(454)=2.195, *P*<0.01: ELS: t(454)=2.06, *P*<0.01; EW: t(454)=2.115, *P*<0.05) except for sword length (SL: t(454)=1.43, ns).

Second, we hypothesized that larger individuals had systematically won the duel during the experimental test. Size measures were thus compared between winners and losers for each of the 18 experimental groups. None of the 114 comparisons made reached significance (largest: t(38)=1.72, ns). However, when the 360 encounters were combined and winners compared to losers for size measures,

winners showed a larger flank width than their loser opponents, (FL: t(758)=2.5, *P*<0.01, one-tailed), although no significant differences were found for TL, SL. BL, ELS and EW (largest: t(758)=1.63, ns). Finally, it was demonstrated that the visual pairing made by the experimenter for the 20 duels of each group could not have favoured, systematically, one type of opponent over its opponent. For each group, the "left" opponent was compared to its "right" opponent for all size measures, and none of the planned comparisons attained the required level for significance (largest: t(38)=1.98, ns).

These results show that size differences could explain part of the experimental results. Future analyses in this research would be better to include a term representing size asymmetries and let it "compete" for explanation with other candidate factors. Our results indicate that a difference in flank width is the best predictor of dominance among size measures (R=0.27), immediately followed by differences in the estimated lateral surface (R=0.26). Estimates of the lateral surface will be used and included in the next analysis as a synthetic measure of size.

Relative importance of asymmetries. Data were analysed using stepwise multiple regression analysis. This general technique could properly analyse the relation between a criterion or predicted variable (e.g., number of wins) and a set of predictors, here the experimentally manipulated independent variables and the selected size factor, all suspected to influence agonistic duel outcomes. The stepwise procedure is used here as a descriptive tool in order to isolate the specific contribution of each factor or set of factors to dominance, then to extract the best predictive equation and evaluate its predictive accuracy. A step-forward procedure introduces the predicting variables hierarchically into the analysis, provided they satisfy a precise statistical criterion, namely, the proper contribution of a given factor to the explainable variance of the observations. Variables are introduced one at a time, starting with the variable which explains the largest proportion of the totally explainable variance. The next variable introduced is the one which, in conjunction with the first one, but independently of it, explains the next largest proportion of variance, and so on. At each step the next best variable is included in the regression, until either a stop criterion is reached or all the variables are included. Stated otherwise, the variable that explains the greatest proportion of variance not yet explained by other variables enters at the next step of the analysis. In the present research, the hierarchy disclosed by the stepwise procedure was considered to represent the relative importance of the factors concerned, in their capacity to determine aggressive dominance in *Xiphophorus*.

The major difficulty with multiple regression analysis is that the order in which the predictors are successively added by the regression is essential. If one wishes to explain the maximum total variance in the criterion (or dependent) variable, one should look for predictors that are relatively unrelated to each other, but which have at least moderately high correlations with the dependent variable. Thus, if we have two highly interrelated predictors, the second will explain essentially the same variation as the first, since there will be considerable overlap between them. If the predictors are uncorrelated, they will each

explain a different portion of the total variation, and the interpretation of their supposed effects will be clearer. In those cases in which variables do not have a high degree of multicolinearity (intercorrelation), regression coefficients are directly interpretable. When the intercorrelation between the predictive variables is zero (i.e., they are orthogonal), the interpretation is greatly simplified, since the square of the multiple correlation, R, becomes the sum of the squared partial correlations between each predictive variable and the criterion (or predicted) variable. Moreover, the proportion of observed variance explainable by one predictive variable becomes equal to the square of its correlation with the criterion variable. In this case also, beta regression coefficients are equal to the simple correlation between one variable and the criterion variable.

Our variables were partly orthogonal due to the experimental design itself. However, they were further rendered orthogonal by special coding. All correlations between the coded vectors had to be zero. The following variables were included in the analysis presented in Table 5: prior residence asymmetries [Res – Int], social asymmetries [α-ω],   [Iso-ω], [α-Iso], and individual recognition K[α-ω]. The possible interaction between the absence of social asymmetry ([Soc=Soc], i.e. [α-α], [Iso-Iso], [ω-ω]) and the presence of an asymmetry of residence [Res – Int] was also included ([Soc=Soc] X [Res – Int]). The various factors were coded using dummy variables; the coding respected the polarity imposed by the basic postulates. For example, the case of the opponent advantaged by the [Res>Int] asymmetry was coded "1" while the case disadvantaged by the [Int<Res] asymmetry was noted "-1". The absence of the asymmetry concerned (e.g. [Int – Int], or any component of [Soc=Soc]), was noted "0" . It will have been noticed also that all the asymmetric duel types could be represented by two distinct acronyms corresponding to the interchange of the two opponents' designations. For example, group Unk[Res α-Int ω] is the same as group Unk[Int ω-Res α]. Since asymmetries of one encounter were always represented by the advantages or disadvantages of the "left" opponent of the pair, this swapping actually transformed the original [Res>Int] + [α>ω] asymmetries into [Int<Res] + [ω<α]. Half of the encounters of each group were thus always coded according to one scheme, and the other half according to the other. In addition, variable [Soc=Soc] X [Res – Int] was coded "19" when the left opponentof a pair was simultaneously advantaged by the [Res>Int] asymmetry, while its social asymmetry neutralized ([Soc=Soc]). When the left opponent was disadvantaged by the [Int<Res] asymmetry, while its social asymmetry was neutralized, the (Soc=Soc] X [Res – Int] variable was coded "-3"; otherwise this variable was coded "0". Unless otherwise stated, in all our analyses the criterion, or dependent, variable of this experiment was the proportion of duels won by the "left" opponent-type over the "right" opponent-type for the corresponding encounter-type. Differences in estimated lateral surfaces between the opponent (D), obtained in square mm, were included in the first two analyses. [Note: Logistic regression was not available at the time of the writing of this paper]

The first analysis makes D compete with other variables representing determinant asymmetries, as well as some of their multiple interactions. The results are presented in Table 5, where both parts A and

B form, together, the total regression table. One can immediately see that the terms corresponding to residence and social asymmetries, and to their mutual interactions, are all entered first in the analysis, and that their order of inclusion strictly follows their partial correlation with the dependent variable. This was to be expected, since these variables were orthogonal. One can also see that the first interactional terms between D and other asymmetries were introduced only later in the analysis (step no 11) . This suggests that D and its interactions are relatively less important than residence and social asymmetries. Moreover, beta   regression coefficients related to D and to its interactions do not reach significance (largest t=1.22, P= 0.222).

   As mentioned earlier, the order of introduction of the variables by the stepwise regression is important, and may have led to an underestimation of the real contribution made by D. For this reason, D variables and their interactions were forced with priority into the first steps of a second analysis. The variables were coded exactly as in the previous analysis. Only the order of the entry of variables was changed. The results of this second regression are presented in Table 6. It was found that no regression beta coefficient related to D reached significance (largest: F=2.53, P =0.112).

TABLE 5

Summary table for main stepwise regression analysis. The upper (A) part can be considered orthogonal, while the lower (B) part includes differences in estimated lateral surface (abbreviated: D) and their interactions with the main factors. N=360 duela.

	STEP	VARIABLE ENTERED	F TO ENTER	MULTIPLE R	R SQUARE	R*R CHANGE	SIMPLE R	OVERALL F	BETA	B	STD ERROR B
A	1	K(a - u)	534.9664*	0.7415	0.5498	0.5498	0.7415	534.9600	0.7416	0.4500	0.0039
	2	Unk(a - u)	434.4615*	0.8799	0.7743	0.2244	0.4737	749.4200	0.4743	0.2878	0.0038
	3	(Soc-Soc)x(Res-Int)	207.6997*	0.9204	0.8471	0.0728	0.2699	805.1600	0.2455	0.0084	0.0002
	4	(Iso-u)	289.4593*	0.9530	0.9082	0.0611	0.2472	1075.7600	0.2469	0.1498	0.0038
	5	(a-Iso)	182.2530*	0.9671	0.9353	0.0271	0.1648	1255.6500	0.1644	0.0998	0.0038
	6	(Res-Int)x(Iso-u)	313.4717*	0.9811	0.9625	0.0271	-0.1648	1852.0000	-0.1644	-0.0998	0.0038
	7	(Res-Int)xK(a -u)	95.4650*	0.9845	0.9693	0.0068	-0.0824	1947.3800	-0.0822	-0.0499	0.0039
	8	(Res-Int)x(a -Iso)	122.2619*	0.9880	0.9761	0.0068	0.0824	2197.5500	0.0820	0.0498	0.0038
	9	(Res-Int)xUnk(a-w)	81.6395*	0.9899	0.9799	0.0038	0.0618	2327.9200	0.0623	0.0378	0.0038
	10	(Res-Int)	77.2931*	0.9914	0.9830	0.0031	0.1581	2474.5900	0.0617	0.0159	0.0018
B	11	Dx(Res-Int)x(a -Iso)	1.6906	0.9915	0.9830	0.0001	-0.0269	2253.4000	-0.0085	0.0000	0.0000
	12	Dx(a -Iso)	1.6744	0.9915	0.9831	0.0001	-0.0194	2069.0100	-0.0085	0.0000	0.0000
	13	Dx(Soc-Soc)x(Res-Int)	1.0681	0.9915	0.9831	0.0000	-0.0800	1910.2400	-0.0045	0.0000	0.0000
	14	D	0.6511	0.9915	0.9832	0.0000	0.2562	1772.3900	-0.0060	0.0000	0.0000
	15	Dx(Res-Int)	0.2852	0.9915	0.9832	0.0000	-0.1125	1651.4700	-0.0042	0.0000	0.0000
	16	Dx(Iso- u)	0.1878	0.9915	0.9832	0.0000	-0.0076	1545.2900	-0.0027	0.0000	0.0000
	17	DxUnk(a - u)	0.1801	0.9916	0.9832	0.0000	-0.0387	1451.5900	-0.0027	0.0000	0.0000
	18	DxK(a - u)	0.0229	0.9916	0.9832	0.0000	-0.0021	1367.7700	-0.0009	0.0000	0.0000
		CONSTANT								0.5414	0.0016

* p<0.001

STEP	VARIABLE ENTERED	F TO ENTER	MULTIPLE R	R SQUARE	R*R CHANGE	SIMPLE R	OVERALL F	BETA	B	STD ERROR B
1	D	30.7593*	0.2561	0.0656	0.0656	0.2561	30.7593	-0.0028	0.0000	0.0000
2	Dx(Res-Int)	2.4427	0.2661	0.0708	0.0051	-0.1124	16.6517	0.0143	0.0000	0.0000
3	Dx(Soc=Soc)	7.5827*	0.2944	0.0867	0.0158	-0.1502	13.7963	0.0072	0.0000	0.0000
4	Dx(Soc=Soc)x(Res-Int)	1.4640	0.2996	0.0897	0.0030	0.0952	10.7242	0.0056	0.0000	0.0000
5	DxUnk(α-ω)	0.5608	0.3015	0.0909	0.0011	-0.0387	8.6829	-0.0073	0.0000	0.0000
6	Dx(α-Iso)	0.0409	0.3017	0.0910	0.0000	-0.0193	7.2266	-0.0167	-0.0001	0.0000
7	DxK(α-ω)	0.0146	0.3017	0.0910	0.0000	-0.0020	6.1822	0.0128	0.0000	0.0000
8	Dx(Res-Int)x(α-Iso)	0.1399	0.3022	0.0913	0.0000	-0.0269	5.4161	-0.0118	0.0000	0.0000
9	(Res-Int)	13.1688*	0.3440	0.1183	0.0270	0.1580	6.4135	0.1615	0.0479	0.0027
10	(α-Iso)	12.6093*	0.3788	0.1435	0.0251	0.1647	7.1889	0.1623	0.0984	0.0063
11	(Iso-ω)	32.2021*	0.4510	0.2034	0.0599	0.2671	9.9381	0.2473	0.1501	0.0063
12	Dx(Iso-ω)	0.0515	0.4511	0.2035	0.0001	0.0075	9.0941	-0.0002	0.0000	0.0000
13	Unk(α-ω)	137.0266*	0.6303	0.3973	0.1938	0.4737	21.6092	0.4729	0.2870	0.0064
14	K(α-ω)	1915.8902*	0.9437	0.8905	0.4932	0.7415	247.1115	0.7425	0.4507	0.0062
15	(Res-Int)x(Iso-ω)	138.2170*	0.9578	0.9174	0.0269	0.1647	314.3163	0.1647	-0.0999	0.0063
16	(Soc=Soc)	177.5810*	0.9705	0.9418	0.0244	0.1595	428.4907	0.1597	0.0042	0.0027
17	(Res-Int)xK(α-ω)	52.2624*	0.9738	0.9482	0.0064	0.0823	455.2330	-0.0847	-0.0514	0.0066
18	(Res-Int)x(α-Iso)	58.6421*	0.9770	0.9546	0.0063	0.0823	491.9271	0.0803	0.0487	0.0063
19	CONSTANT								0.5413	0.0027

* p<0.001

However, D and one of its interactions (term [Soc=Soc] X D) contributed significantly to the multiple R (F=30.75, P<0.001: F=7.58, P<0.006). These results confirm our previous ones concerning size. In general, size effects are not negligible since they explain approximately 7% of the total observed variance (R*R=0.065), and since their multiple interactions probably explain an additional percentage of 2-3% of a total 10% of variance explainable by size. However, these effects are less important than other factors considered in the present study. Besides, it should be remembered that more than 15% of the duels included in our analyses were neutral with respect to both residence and social asymmetries (namely: Unk[Int Iso-Int Iso], Unk[Int α-Int α] and Unk[Int ω-Int ω] encounters), so that dominance in these duels could be determined by size asymmetries, even though these were minimal. The same conclusion is also suggested by the fact that the interaction [Soc=Soc] X D reaches significance, since in this case social asymmetry is absent. The relative importance of other asymmetries can now be examined.

A third analysis was done using the same coding method as for the two previous analyses, but dropping D and all terms having D as an interactive component. All factors were orthogonal, except multiple interactions with their respective "main" factors. Since the results of this third analysis were essentially redundant with those of the first one, the results presented in part A (upper) of Table 5 can be considered, practically, as those of this third stepwise regression on orthogonal variables, which constitutes a saturated additive model for all the factors of interest here.

Table 5-A shows that all the asymmetries considered to be determinant factors in the present research contribute significantly to the multiple correlation. The multiple regression coefficient increases at each of the 10 inclusive steps to attain a value of 0.9914. This means that the conjunction of the six variables

concerned, and their interactions, can explain more than 98% of the total variance observed in the results. Retrospective predictions made by the regression equation obtained are presented in Fig 4. As can be seen, there is a very close conformation, even if the level of measurement is not very sophisticated.

The order in which the variables were sequentially introduced by the stepwise procedure confirms the order initially proposed for the positive social asymmetries: since these variables had been coded in order to contrast their "advantage-disadvantage" poles, we can be sure ($p<0.001$) that the order of the disadvantages is symmetrical to that of the advantages, such that:

K[α>ω]>Unk[α>ω]>[Iso>ω]>[α>Iso]>[Iso<α]>[ω<Iso]>Unk[ω<α]>K[ω<α]

This confirms the first expression of the general model. Moreover, the fact that some terms, including effects of prior residence and their interactions with other factors, are included only in the last steps of the analysis, confirms the second expression of the general model

K[α>ω]>Unk[α>ω]>[Res>Int]>[Int<Res]>Unk[ω<α]>K[ω<α]

On the other hand, it must be noted that our incapacity to neatly seriate prior residence asymmetries *a priori* finds a parallel in the present analysis, since the several interactions between prior residence and social asymmetries appear to have greater explicative value than the prior residence factor *per se*. In particular, the interaction between prior residence and the absence of social asymmetry ([Soc=Soc] X [Res – Int]) is noteworthy, since it contributes as much to the explained variance as do the social asymmetries [ISO-ω] and [α-ISO]. Although included later than [Soc=Soc] X [Res –Int], the [ISO-ω] condition seems to explain as much variance (6%). On the other hand, the [α-ISO] condition contributes to only 2% of the variance. The same applies to the interactions [Res – Int] X [ISO-ω]: although it does not explain much variance when entered after its colinear [ISO – ω], it suggests the presence of a significant interaction ($P<0.001$) between the [Res>Int] and [ISO>ω] asymmetries. The correlation of [Res – Int] X [ISO–ω] with the dependent variable is negative (r=-0.1648). This negative result indicates that an opponent cannot be conjointly advantaged by both asymmetries without losing some "advantage". This might reflect the small decrease of advantage on the part of the ISO opponent when it is in addition resident (Unk[Int ISO]>Unk[Int ω]: 15/20, $P<0.01$, compared to Unk[Res ISO]>Unk[Int ω]: 13/10, $P<0.14$); this paradoxical effect is best interpreted as "noise". On the other hand, it might also reflect the reduced advantage that is observed in one ISO opponent when its opponent is the resident (Unk[Int ISO]>Unk[Int ω]: 15/20 , $P<0.01$, compared to Unk[Int ISO]>Unk[Res ω]: 9/20 , ns). This last effect is consistent with a "fear" hypothesis, according to which the ω individual (having the [ω<ISO] asymmetry) would be much less disadvantaged when introduced into a familiar environment than when introduced as an intruder. This hypothesis could be explored in the future.

Finally, the results presented in Table 5 also indicate that several interactions were at work between prior residence asymmetries and other types social asymmetries (ex: K[α>ω], [α>ISO], [α>ω]). Although these interactions are statistically significant, the paradoxical effects they suggest, and the fact that their beta coefficients are smaller than the [Res – Int] X [ISO-ω] interaction, incites us to consider them as spurious or chance effects. They will not be explored systematically or interpreted in this research.

Re-examination of the basic postulates

Postulate 1: [Res►Int]
P1 states that dominance propensity will be greater forr residents than for intruder-opponents. P1 should not, a priori, hold true for previously known opponents, since the pairing of familiar individuals implies at these had necessarily a previous α or ω experience together. If it were assumed for known pair-members, P1 could conflict with P6, assuming that the advantage of residence in known pairs should tend to be made less distinct by an advantage with respect to previous α experience on the part of intruders. Of course, P1 should hold true for extremely divergent asymmetries between familiar opponents, i.e., when fish advantaged by residence are also advantaged by α experience. This is what was actually found, in both known and unknown pairs of the same type:

K[Res α>Int ω], 18/20, $P<0.001$,

and Unk[Res α>Int ω], 17/20, $P<0.002$.

An adequate testing of P1 should be provided only by the results of the pairings whose opponents were unknown to each other and had their social asymmetry eliminated. These results tend to confirm P1, as seen in the regression analysis in Table 5 ($P<0.001$ for [Soc=Soc] X [Res – Int]):

Unk[Res ISO >Int ISO]: 16/20, $P= 0.006$

Unk[Res ω >Int ω]: 14/20, $P<0.06$

Unk[Res α ≥Int α]: 13/20, $P>0.05$

Total Unk[Soc=Soc & Res>Int]: 43/60, $P<0.001$

These results confirm the findings of Zayan (1975c and 1976). They make possible to infer that if paired encounters were randomly drawn from a normal population of residents and intruders, residents would have a much eater probability of dominance. Such inference would not necessarily require that asymmetries with respect to previous social experience of the opponents be discarded (i.e., neutralized), whether naturally or by experimental control. It could also be admitted that, provided previous α and ω opponents are as frequently selected, and that random selection assigns them equivalently to residence and to intrusion conditions, dominance will be equiprobable. In these cases, the total number of advantages due to residence and of disadvantages due to intrusion should be compensated by the number of α advantages and by the number of ω disadvantages, given as frequently to residents as to

intruders. It is interesting, however, to have a closer look at the performance of residents which were disadvantaged by a social asymmetry, and this for two reasons: first, to check the extent to which prior residence is efficient in increasing dominance potential: second, to examine the results of three types of duels for which no specific prediction could be made on the basis of logical inference, although some empirical support could be gathered from Zayan (1975a, b). The results show very clearly that prior residence does not increase chances of dominance when social experience is at the advantage of the intruder: Unk[Res $\omega \geq$ Int ISO], 11/20, $P > 05$; Unk[Int $\alpha \geq$ Res ISO], 13/20, $P > 0.05$. As could be expected, the most conclusive result in this respect concerns the duels with most divergent social asymmetry, i.e., where a previously dominant intruder encounters a previously defeated resident: Unk[Int $\alpha >$ Res ω], 16/20, $P = 0.012$ (two-tailed test). We are now intruding into the testing of Postulate 2.

Postulate 2: K U Unk[$\alpha \blacktriangleright \omega$]

P2 states that dominance propensity will be significantly higher for previously dominant individuals than for previously subordinate ones in all contests where opponents possess this most widely divergent asymmetry with respect to social experience. As will be seen, P2 receives overall confirmation for duels of all types: between known and unknown opponents, between opponents with prior residence asymmetry, and between intruder pair-members:

Unk[Int $\alpha >$ Int ω]: 15/20, $P = 0.02$

K[Int $\alpha >$ Int ω]: 20/20, $P < 0.0001$

Unk[Int $\alpha >$ Res ω]: 16/20, $P = 0.006$

K[Int $\alpha >$ Res ω]: 18/20, $P < 0.001$

Unk[Res $\alpha >$ Int ω]: 17/20, $P < 0.002$

K[Res $\alpha >$ Int ω]: 18/20, $P < 0.001$

These results are in agreement with Zayan's (1974, 1975a, b). As a general rule, P2 is supported by our multiple orthogonal regression. First, the K[α-ω] asymmetry is highly correlated to the outcome of the duel ($r = 0.74$), and is the first asymmetry to be picked up by the regression analysis, explaining more than 55% of the total variance. Secondly, the Unk[α-ω] asymmetry is also positively correlated ($r = 0.47$) to duel outcome and holds second rank in explaining total variance ($R*R = 22\%$).

Postulate 3: Unk[$\alpha \blacktriangleright$ Iso]

P3 states that dominance frequencies should be greater for previously dominant individuals than for previously isolated ones. In the context of the present experiment, it can only apply to unknown opponents. P3 appears to have been refuted, since no significant differences could be found, although previous α individuals did show a tendency to win duels more frequently than their Iso opponents.

Unk[Int $\alpha \geq$ Int Iso]: 11/20, $P > 0.05$

Unk[Int α ≥ Res Iso]: 13/20, $P>0.05$

Unk[Res α ≥ Int Iso]: 13/20, $P>0.05$

Pool: Unk[α > Iso]: 37/60, $P=0.046$

   This result confirms, however, that previously isolated individuals have a dominance potential close to that of previous α individuals, as was assumed in our procedure of placing the various asymmetries in the general model in order. It might be that a larger number of experimental pairings would have led to reject the statistical equivalence between dominance probability of α and Iso opponents, especially in duels involving [Res – Int] asymmetry. Indeed, the pooling of the three results presented above indicates that a individuals have a significant tendency to dominate more frequently than their isolated opponents (37/60, and $P=0.046$). Another finding suggests that P3 might be considered as poorly confirmed, this being the late inclusion of the [α-Iso] asymmetry in the orthogonal regression, and the fact that it explained only 2.7% of the total variance. But methodological aspects could very well account for such divergence.

Postulate P4: Unk[Iso►ω]

P4 states that dominance frequencies should be significantly greater for previously isolated opponents than for previously subordinate ones ; as with P3, P4 can only apply to unknown pair members. As will be seen, it was confirmed, though only in duels where the prior residence asymmetry was eliminated:

Unk[Int Iso>Int ω]: 15/20, $P= 0.02$

Unk[Res Iso ≥ Int ω]: 13/20, $P>0.05$

Unk[Int Iso<= Res ω]: 9/20, $P>0.05$

Pool: Unk[Iso >ω]: 37/60, $P= 0.046$

   When these results are pooled, it is found that, as a general rule, previously isolated individuals dominate more frequently than their ω opponent (37/60, and $P= 0.046$). Contrary to P3, which was found to be basically confirmed in the context of [Res – Int], P4 would tend to be basically refuted in the same context. However, the results of our orthogonal regression support the conclusion that P4 received an overall confirmation, since the corresponding [Iso – ω] asymmetry was included at step 4 and explained 6% of the observed variance, enough to reach statistical significance ($P<0.001$).

Postulate 5: K[α>ω]>Unk[α>ω]

   P5 states that determination of dominance frequencies, resulting from [α-ω] asymmetry, should be increased when opponents are previously known to each other. This difference between this and dominance frequencies between unfamiliar opponents can be checked in experimental pairings involving or not involving the prior residence asymmetry.

When the prior residence asymmetry is eliminated by the pairing of intruders, it is true that dominance frequency by the previous a individuals is maximized:

K[Int α>Int ω]: 20/20, $P<0.0001$.

Significantly more frequent dominance is also recorded for a unknown individuals, as stated by P2 Unk[Int α>Int ω]: 15/20, $P= 0.02$.

However, this equivalent tendency is indeed significantly more accentuated in familiar opponents ($X^2=3.67$ and $P<0.05$, one-tailed). This confirmation of P5 corroborates Zayan's (1974, and other unpublished data) findings, and parallels the conclusion that recognition of individual properties was responsible for such widespread determination of dominance in familiar opponents.

When the prior-residence asymmetry interacts with the [α-ω] one, P5 is not significantly validated. In these pairings, dominance of the previous α opponents is also much more frequently recorded than dominance of the previous ω individuals, but this tendency is found, in equivalent measure, in familiar and in unknown pair-members: K[Res α>Int ω], 18/20, $P<0.001$ and Unk[Res α>Int ω], 17/20, $P<0.002$; K[Int α>Res ω], 18/20, $P<0.001$ and Unk[Int α>Res ω], 16/20, $P= 0.006$.
It will also be remembered that the effects of individual familiarity or recognition appeared as the most regular effect to be selected by our regression analysis.

Postulate 6: K[α►ω]>K[Res►Int]
P6 states that the effects of individual familiarity or recognition upon dominance should override corresponding effects of prior residence asymmetry. Remark: in the context of the present experiment, effects of individual cognition imply necessarily effects of the [α-ω] asymmetry, since only previously α or ω individuals were paired as familiar opponents. Therefore, P6 means that in pair-members which were previously acquainted to each other before the encounter, advantage or disadvantage with respect to previous α or ω experience is more determinant for future dominance than is advantage or disadvantage with respect to previous residence or tank unfamiliarity (intrusion). An evaluation of this statement should be indicated by the dominance frequencies recorded when an incompatibility between the two types of advantages or disadvantages existed. A confirmation of P6 should be evidenced by the following result: dominance will be significantly more frequently recorded for opponents which were advantaged by α experience (and disadvantaged by intrusion) than it will be for opponents advantaged by prior residence (and disadvantaged by ω experience). A confirmation is actually found:

K[Int α>Res ω]: 18/20, $P<0.001$

It should be noted that P6, resulting from experimental findings (Zayan, 1975b) confirms this, and at the same time refers to a type of duel for which specific prediction concerning the most frequently

dominant opponent could made without this postulate. Moreover, other duel types in our experimental context provide specific explanations for such a result. They are as follows:

First, the effects of individual familiarity and recognition increase dominance probability in the previous α fish and decrease it in the ω previous fish. These effects are exemplified by two results, confirming P5 for duel types in which the residence asymmetry is eliminated by the pairing of intruders:
K[Int a>Int ω]: 20/20, $P<0.0001$, and
Unk[Int a>Int ω]: 15/20, $P= 0.02$

The significant difference between these results certifies that individual cognition is specifically involved in the process of achieving higher dominance frequencies for the opponents.

Second, effects of [α-ω] asymmetry increase dominance probability in the previous α fish and decrease it in the previous ω fish. These effects are exemplified by the results of pairings between unknown opponents which were previously α intruders and previously ω residents:

Unk[Int α>Res ω]: 16/20, $P= 0.006$

The fact that this result does not differ at all from the one found for equivalent types of opponents which were previously known to each other (specific test pairings of P6), confirms that an advantage gained by residence very markedly overridden by an advantage with respect to α status.

Finally, the results of our regression analysis confirm that P6 was incontestably supported: while the K[α-ω] asymmetry explained more than 55% of total variance, only less than 1% of it was accounted for by the interaction [Res – Int] X [α-ω].

Postulate 7: K U Unk[α►ω]>K U Unk[Res►Int]

P7 states that the effects of [α-ω] asymmetries should override corresponding effects of [Res – Int] asymmetries. In its most general form, P7 holds for both known and unknown pairs. However, P6, which was confirmed, can be considered as the version of P7 applying to known pair-members. Therefore, P7 must be specifically tested for its application to unknown opponents. A confirmation would be indicated by dominance recorded more frequently for opponents advantaged by α experience (and disadvantaged by intrusion) than for opponents advantaged by prior residence (and disadvantaged by ω experience). Such a result was actually found:

Unk[Int α>Res ω]: 16/20, *P*= 0.006

   The results of other experimental pairings demonstrate that it is the asymmetry with respect to previous social experience which determines this confirmation of P7. On the one hand, dominance by an a intruder shows a non-significant tendency to be more frequent than dominance by a resident which has been isolated instead of disadvantaged by an ω experience: Unk[Int α ≥ Res Iso], 13/20, *P*>0.051. On the other hand, a previous ω fish advantaged by residence does not appear to be more frequently dominated by an intruder which does not benefit from an α experience but has been simply isolated: Unk[Res ω ≥ Int Iso], 11/20, *P*>0.05. It is important to note that the dominance frequency of the Iso-intruders is significantly smaller than that which was found for the α intruders of P7 (X^2= 3.84 and *P*<0.05, two-tailed). Finally, the fact that the advantage of residence could be neglected is indicated by the pairing of α and ω intruders, thus eliminating the residence asymmetry while conserving the asymmetry with respect to previous social experience: Unk[Int α>Int ω], 15/20, *P*= 0.02. As in the case of the pairs used to test P7, the a intruders had a significant tendency to dominate more frequently than their ω opponents; although the tendency is slightly less accentuated in this case than it is in the case of ω opponents advantaged by residence, the two results are far from differing significantly, and can thus be considered statistically equivalent.

   Finally, a general validation of P7 can be seen in the fact that in our regression analysis, the Unk[α-ω] asymmetry explained more than 22% of the total variance, while the Unk[α-ω] X [Res – Int] interaction explained less than 1% of it.

Effects of isolation. In the present experimental context, effects of isolation can only be assessed in the case of unknown opponents. A conclusion can be drawn unequivocally: the effects of previous isolation upon dominance probability are much closer to the effects of α experience than to those of ω experience. This was demonstrated by the statistical equivalence between the dominance frequencies of α and Iso intruders (P3), whereas ω intruders were significantly more often defeated by Iso intruders (P4). Moreover, ω intruders appear to be exactly as frequently defeated by α intruders as they are by Iso intruders (15/20, p=0.02). It is likely that isolation progressively increases a potential aggressive state and thus increases the probability of subsequent (aggressive) dominance. Finally, it should be admitted that specific effects of isolation can hardly be evidenced in pairings involving the [Res – Int] asymmetry. In such cases an interaction should be suspected between isolation and residence effects, because prior residence and pre-experimental isolation could be inevitably associated, even if much care was taken in the present research to accord these properties in different tanks and in a sequential order

Effect of neutralizing social asymmetries. Some results have to be mentioned and discussed in order to complete the evaluation of our predictions. These results concern the dominance frequencies which were

recorded in all pairings where α symmetry existed with respect to previous experience, and where the prior residence asymmetry was eliminated. Contrarily to the four types of pairings for which no specific predictions could be made (due to a compensation between advantage with respect to prior residence and advantage with respect to social experience), these duel types imposed to expect a definite tendency in dominance frequencies: equiprobability. Whether this was achieved empirically had to be checked. As will be seen, the predictions were perfectly confirmed:

Unk[Int Iso=Int Iso]: 10/20, *P*= 0.50

Unk[Int α=Int α]: 10/20, *P*= 0.50

Unk[Int ω=Int ω]: 10/20, *P*= 0.50

Although there is no reason to overemphasize numerical coincidences which happen to express perfectly statistical equivalence between frequencies, these results suggest the following conclusions: 1) Previous isolation seems to determine dominance (equi)probability the same as α and ω experiences do. 2) Pre-experimentally neutralized asymmetries with respect to both prior residence and social experience really constitute symmetric states of potential dominance. 3) These symmetric pairings should thus be considered as y adequate control conditions, to which other pairings with corresponding asymmetries could be very specifically compared.

Evaluation of the general predictions. The model predicted the relative contribution of each of the pre-experimental factors in the determination of successive dominance. The following general order was proposed for social asymmetries:

$$K[\alpha>\omega]>Unk[\alpha>\omega]>[Iso>\omega]>[\alpha>Iso]>[Iso<\alpha]>[\omega<Iso]>Unk[\omega<\alpha]>K[\omega<\alpha]$$

The results presented here agree, in general, with the predicted order. It was also postulated that prior residence asymmetries were much less important in the species studied than those introduced by individual recognition (P6) or by the encounter of an α opponent with an unknown ω opponent (P7). These two additional postulates were also confirmed by the data. However, none of the three proposed alternatives concerning the relative importance of prior residence asymmetries compared to [α>Iso] or [Iso>ω] asymmetries clearly predicts better than any of the two other orders. It can be concluded that prior residence asymmetries only very moderately favour dominance when added to social asymmetries (excluding individual recognition), and that they trigger a much greater effect when social asymmetry is neutralized and when the resident individual is already favoured by ω experience.

The present study demonstrates that the outcomes of agonistic duels can analysed successfully in terms of differences or asymmetries between opponents rather than in terms of the possession of particular properties by individuals. The determinants of dominance which were selected for the experiments can also be considered to perform efficiently in this respect. Possession of a positive factor

can, as a general rule, be viewed as an advantage, while its absence constitutes a significant disadvantage for the opponent. However, the actual effect of an asymmetry can be emphasized or inhibited according to the other properties which characterize a given opponent, especially when two incompatible advantages exist (e.g., either residence and ω experience or intrusion and α experience).

Relative importance of the various asymmetries. The existence of an [α-ω] asymmetry between two known individuals, i.e., between which a binary α-ω relation already exists, is the most important factor determining the agonistic outcome of a duel between two individuals. In such a case, the individual with previous α experience very rapidly dominates its former ω opponent, with a probability higher than 0.90. The previously established α-ω relation is immediately re-established even if the second encounter occurs in the tank which is familiar only to the former ω individual (i.e., if the former a fish is an intruder in the previous residence area of its former subordinate). These results confirm those of Zayan (1975b) on the nearly absolute preponderance of individual recognition over the advantage of prior residence in the same species.

   When individuals are unknown to each other, the effects of social experience appear to be algebraically additive between the opponents. For a opponent, the advantage of having had an α experience adds to the opponent's disadvantage of having had an ω experience, and both effects produce an [α-ω] asymmetry which is much more important than the [α-ISO] and [ISO-ω] asymmetries. Generally speaking, one can say that the individual having had a recent α experience is advantaged, compared to an individual having received an ω experience or even an experience of social isolation (P2 or P3). Similarly, an individual having had an ω experience is disadvantaged when compared to a previous α conspecific (P2) and, to a lesser degree, to a previously isolated one (P4). On the other hand, the individual isolated for a 18-22h period is advantaged over an ω opponent (P4), but less clearly disadvantaged over an α opponent (P3).

   Taking into account the capacity of a given social asymmetry to increase the probability of the advantaged individual's winning of a contest, the following expression summarizes the relations confirmed above:

$$1.00 > [α>ω] > [Iso>ω] > [α>Iso] > 0.50 > [Iso<α] > [ω<ISO] > [ω<α] > 0.00$$

   Our results thus confirm the empirical generalizations according to which previous social experience of dominance increases the probability of dominance in future contests among fish, while a recent submissive experience reduces this probability (Zayan,1975a). On the other hand, immediate social isolation would have an effect of intermediate magnitude, with respect to α and ω experiences, in favouring dominance, but of a magnitude closer to that of α experience than that of ω experience. However, the effects of isolation do not appear to be as clear-cut as they are for α and ω experiences.

The picture becomes more complicated when prior residence interacts with social experience. Generally speaking, one can say that prior residence (and familiarity with the tank in which the encounter occurs) procures a slight but significant advantage. However, in our experiment prior residence exhibited more complex effects than expected. First, familiarity with a tank greatly advantaged the resident when no social asymmetry interfered with it, as shown in our results by the significance of the [Soc=Soc] X [Res – Int] interaction. Prior residence effects were particularly noteworthy when both conspecifics had been isolated for a 18-22h period before the test. These findings agree with those of Zayan (1976). To a lesser degree, these effects still appeared when both individuals had similar α or ω experiences. Second, the effect of prior residence seemed to reduce the disadvantage introduced by ω experience, especially when the opponent had been isolated. This is supported by the significance of the [Res – Int] X [ISO-ω] interaction in the orthogonal regression. However, when one social [ω<α], [Iso<α] or [Iso>ω] asymmetry was concurrently advantaging or disadvantaging the resident individual, prior residence brought only a very slight gain to the resident, as was only seen when the data were pooled. This effect was so small that only interactions between prior residence and either [α-ω] or [Soc=Soc] social experiences could be retained in the final model without loss of any (synthetic) retrodictive power.

These results contrast with those of Frey & Miller (1972). In their study, residents were never removed and then re-introduced into their home tank, while their intruders were inevitably handled. In spite of this systematic advantage given to the resident over the intruder (Zayan, 1976), these authors, working with Gouramis, found no effects exerted by prior residence on aggressive dominance, although residents were more often first to manifest offensive behaviour during a contest. On the other hand, these authors reported a significant interaction in their analyses which suggested a tendency for residents to win more often than intruders, after having occupied their home tank for 24h without a dominant or subordinate partner. Our results for the [Soc=Soc] X [Res – Int] interaction confirm this trend.

Our results also suggest that the effects of a 18-22h isolation period interact with prior residence. As mentioned above, the importance of prior residence is increased when the two individuals have been isolated for a period of 18-22h. This effect can be explained by the absence of social asymmetry between the two opponents, thus allowing for amplification of the modest advantage given normally by prior residence. Similar effects, of lesser importance, are noted for opponents presenting similar experiences of dominance([α-α]) or subordination ([ω-ω]). There are good reasons to believe that the effects of depriving fish of social contacts for short periods of time are not unequivocal, and concern simultaneously social, agonistic, epigamic and sexual activities (Morris, 1956; Clark et al., 1954; Franck, 1970; Hinde, 1970). The effects of even very short periods of isolation cannot be understood simply in terms of occupation of an intermediate social status in between the possibilities of α and ω status. First, strictly speaking it was inappropriate in the present research to contrast (through control) social isolation with social α and ω experiences. However, our research intended to integrate these three

factors into various complexes of asymmetries, the experiment being designed so as to neutralize the uncontrolled specific effects of isolation. In general, isolation appeared to be advantageous when compared to a recent ω experience. However, this advantage disappeared when, in addition, the ω opponent was a resident. Second, the effects of isolation do not seem to consist, essentially, in dampening previous social ω experience, since [Iso-ω] and [α-ω] asymmetries were not equally important. Third, the fact that unknown isolated residents defeated isolated intruders suggest that residents are less susceptible to fear reactions than intruders are.

Extending the model's structure. It is obvious that our experimental model would not exist without the seven postulates from which it was derived. The only specific feature of the model was that it formulated a complete ordered set of asymmetric properties of the opponents, and that it provided predictions for this overall trend, instead of a set of partial hypotheses. Although the model implied integration of the various postulates, partial connections were already existing between some of the seven basic propositions. For instance, P6 and its application to P7 generalized a definite hypothesis relating P2 to P1. Since all postulates resulted from experiments and were to be tested again experimentally, the predictive aspect of the model was already contained in each of the initial propositions P1 to P7. In sum, the model served only to synthesize the results of various independent experiments. A simple re-examination of all of these results allowed them to be compressed into a single transitive prediction which placed in order the various pre-experimental asymmetries with respect to their degree of dominance determination. The complex experiment designed to test the model would necessarily either confirm or refute some of the basic postulates. Specific and independent verification of each postulate was guaranteed by adequate statistical comparisons between the dominance frequencies of any type of opponent, and either those of an asymmetric opponent (intra-duel comparisons) or those of a same type of opponent encountering another type of opponent, symmetric or asymmetric (inter-duel comparisons).

Let us suppose that all postulates could be mutually connected, with respect to both their distinctive effects upon dominance and their relative importance in determining it. Such interdependence could very well be realized in the future, precisely as a result of further elaboration of models and empirical testing which would provide experimental information where it has previously been lacking. For instance, additional information would help to establish the importance of the prior residence asymmetry, and to place it in order within the predictive chain of dominance determinants, particularly with respect to its relation to isolation effects. Then, the model would be no more than the initial network of connections (perhaps logical, i.e., deductive) between postulates and between the predictions they express only, in this case, it might formulate them synthetically (also perhaps by logical formalism, e.g., axiomatically). As far as the content of the predictive network is concerned, there would be, in such an instance, a logical equivalence or reciprocal implication between a confirmation (or a refutation) of

the model, and a confirmation (or a refutation) of the set of basic postulates. This is what we are seeking, considering that the model was only temporarily elaborated for purposes of replication and evaluation of basic postulates. To the extent that these were validated -which was actually the case- it was expected that a more complete model would eventually emerge. Again, such an improvement implies that fresh and factual information may be gained at the level of initial propositions. Since these provide both the content and the structure of any further model, insightful predictions should result from a closer examination of the relations between the seven postulates. The fact that these definitely proved to be empirical generalizations (or, better, experimental laws) will not be of much help in generating more specific hypotheses. Discovery calls for some other testable conjectures and more integration or systemicity within the model's structure.

Figure 5 represents the set of relations between the seven basic postulates P1 to P7, as they were stated. As can be seen, the logical structure is rather poor, since there is only one postulate deduced, namely P2", from the conjunction of P3 and P4. However, postulates P6, P5 and P7 formed a sequence of predictive relations between the components of postulates P1 and P2, i.e.: P1'<P2'>P2">P1". This sequence includes a ternary relation which might be transitive, i.e. P2'>P2">P1", with possibly P2'>P1" resulting from the conjunction of P5 and P7. But it also indicates the lack of a connection between P1' and P1", the two components of P1 for previously known and unknown opponents. This is because our model did not possess any particular postulate comparing (predicting) the effects of prior residence in K and Unk pairs, as did P5, which predicted a greater effect of [$\alpha > \omega$] asymmetry in pairs of known individuals. We shall now attempt to specify this relation because it will certainly increase the integration between the various postulates.
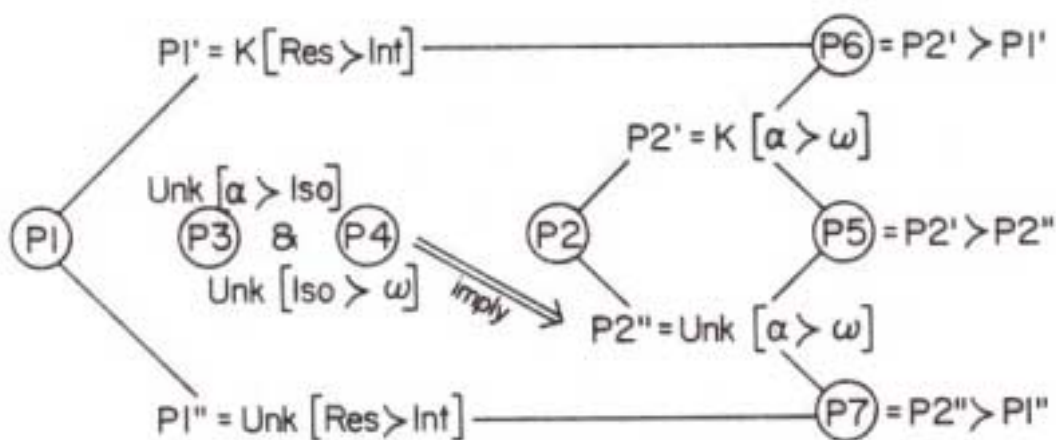

Fig. 5. Set of relations between the seven basic postulates.

In the context of our experiment, an additional postulate, serving to place in the order of the predictive chain the effect of [Res>Int] asymmetry in K and in Unk pairs, would impose a restriction upon P1 in general. This is because the pairings of known individuals imply, necessarily, the most divergent asymmetry with respect to social experience, i.e., [α>ω], which P6 assumed would override the effects of prior residence in these known pairs. Therefore, none of our experimental results had any chance to test whether or not dominance probability was significantly higher for residents than for intruders in pairs of known opponents. For this reason, P1 could not really apply to K pairs, hence to the generalization: K U Unk[Res>Int]. It was only in pairs of unknown opponents that social experience was equivalent for both opponents (i.e., α-α , ω-ω and Iso-Iso, and that a significant advantage of residents over intruders could be demonstrated independently of social asymmetries. Conversely, it was reasonable to expect that dominance could be equiprobable for residents and for intruders which were alternately advantaged by α experience and disadvantaged by ω experience. A confirmation of this hypothesis was found after adding the dominance frequencies of the [Res α-Int ω] and [Res ω-Int a] duel types. It is noteworthy that such equiprobability was found, equivalently, in the pairs of known opponents (wins by 21 residents and 19 intruders: P= 0.44), and in those of known opponents (wins by 20 residents and 20 intruders: P= 0.56). Thus, the [α>ω] asymmetry appeared to compensate for the effects of the [Res>Int] asymmetry in duels which opposed familiar as well as unfamiliar opponents. We know, however, that social asymmetry is actually more determinant than is prior residence in the K pairs (P6) as well as in the Unk pairs (P7). Knowing also that the [α>ω] asymmetry was more determinant in the K pairs than in the Unk pairs (P5), it seems reasonable to suggest that in the context of the present experiment, advantage by prior residence was more important in duels between unknown opponents than in duels between previously own ones. As mentioned above, prior residence increased dominance probability in the Unk duels whenever social asymmetries were neutralized (wins by 43 residents and 17 intruders, $P<0.001$), whereas it did not (and could not) in the K pairs, where [α>ω] asymmetry always existed, and equiprobability was maintained (wins by 20 residents and 20 intruders). As a matter of fact, this different trend, imposed by the present experiment, was significant (X^2=3.95 and $P<0.05$) and we feel confident in proposing: P8=Unk[Res>Int]>K[Res>Int], corresponding to a previously missing connection P1">P1' and suggesting the quaternary prediction: P2'>P2"> P1">P1'.

K ∪ Unk [Res > Int]

(P1) ——————————— (P8) Unk [Res > Int] > K [Res > Int]

(P7) & (P8) $\xrightarrow[\text{imply}]{}$ P = Unk [α > ω] > K [Res > Int]

(P6 + P7) = K ∪ Unk [[α > ω] > [Res > Int]]

(P5) & (P7) $\xrightarrow[\text{imply}]{}$ P' = K [α > ω] > Unk [Res > Int]

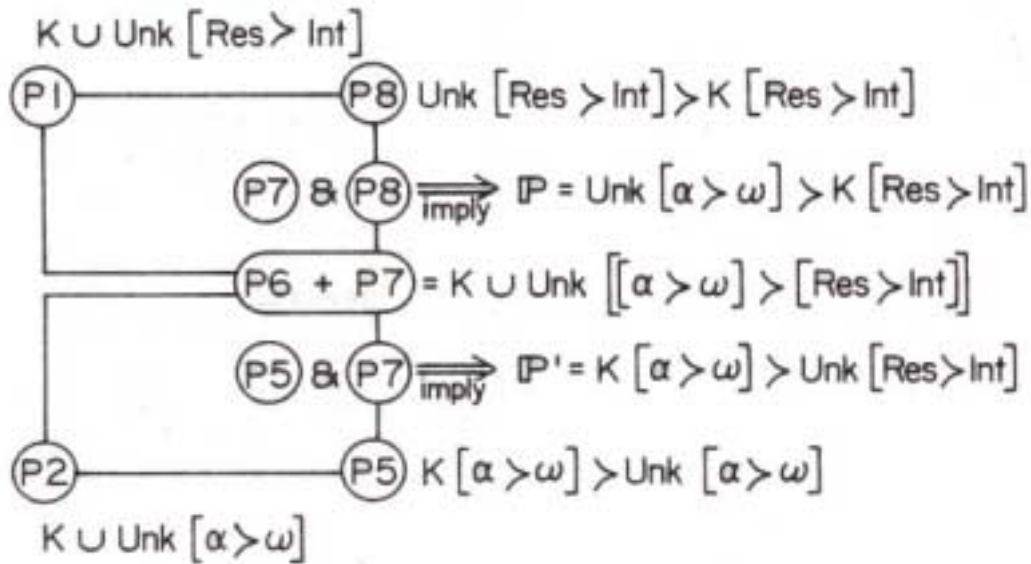(P2) ——————————— (P5) K [α > ω] > Unk [α > ω]

K ∪ Unk [α > ω]

Fig. 6.   Final predictive structure.

The question whether this postulate can be generalized to other experimental contexts cannot be answered presently; it will, however, be discussed later, in connection with a validation of P1 in known pairs, i.e., with a possible confirmation of K[Res>Int] in future research. What matters now is to show that the introduction of P8 increases both the internal consistency and the predictive value of the model's structure, thus improving the model's completeness.

First, the conjunction of P7 and of the additional P8 makes it possible to deduce a new postulate P:

P7 & P8 → P= Unk[α>ω]>K[Res>Int].

P corresponds to a missing connection in the initial structure:

(P2">P1") & (P1">P1') → P= P2">P1'

We have now the ternary relation: P2">P1">P1', which could be preceded the confirmed P5: P2'>P2", to produce

P2' > P2" > P1" > P1', i.e., also P2'>P1'
   P5   P7   P8   P6

Provided the prediction relation is transitive, it is confirmed that P5 & P → P6. This chain includes an interesting prediction: P2'>P1", already suggested by the ternary relation between the predictions of P5 and P7. Indeed, the structure of the seven initial postulates already contained a possible deduction P':

P5 & P7 → P'=K[α>ω]>Unk[Res>Int],

in which P' corresponds to: P2'>P1". Just as P6 could be deduced from the conjunction of P5 & P, our last P8 could be associated to P' to form P6 again:

P' & P8=P2'>P1">P1' → P6=P2'>P1'

There is little doubt that P8 increases the relational consistency between the most specific postulates P5, P6 and P7. However, the validity of the predictions it suggested had to be tested, and not simply accepted on the assumption that the relation between predictions should be transitive. Of course, the order of importance of the various postulates (or postulate components) in predicting dominance frequencies was supported by experimental findings, both past and present. But the predictions which were derived from them, namely P and P', require some confirmation other than a formal one. Only an empirical validation of these derived formulas could decide if they also express experimental laws. The greater consistency of the model's structure could possibly evidence only some new specific relations between initial postulates. It is true that P and P' were produced by elementary deduction (i.e., by *modus ponens* or syllogism), and that they are postulates of higher logical status (i.e., theorems). However, logical implication on the grounds of formal properties such as assumed transitivity is not sufficient: proper entailment of P (and of P') by P7 & P8 (and by P5 & P7) also requires that the implication be factually true. This will be tested by a final look at the results.

- Theorem P', which did not involve the new postulate P8, was strongly confirmed. The effect of social asymmetry [α>ω] in known pair-members was most determinant when the [Res>Int] asymmetry was neutralized in duels between intruder opponents which were previously known, dominance by the previous α individual was recorded in all the 20 duels with ω opponents. The effect of the prior residence [Res>Int] asymmetry in unknown pair-members was also significant when the [α>ω] asymmetry was neutralized: dominance by residents was recorded in 43 out of the 60 duels between [α-α], [ω-ω] and [Iso – Iso] opponents. However, the difference between the two samples was statistically significant; K[α>ω]>Unk[Res>Int]: X^2= 5.60 and $P \leq 0.01$.

This result reinforces the general confirmation of the initial seven postulates.

- Theorem P involved the new postulate P8. A significant effect of social asymmetry [α>ω] was found in unknown pairs when the [Res>Int] asymmetry was neutralized: in duels between intruder opponents not previously known, dominance was more frequently recorded for the previous a individuals (15 pairs) than for the previous ω ones (5 pairs: P= 0.020). In the pairs of known opponents, the effect of the prior residence [Res>Int] asymmetry was totally compensated for by the inevitable α advantage and ω disadvantage which were alternately given to residents (and to intruders). The fact that dominance was equiprobable in these pairs of known residents and intruders (20 wins for each type of fish, P= 0.56) supports the prediction of P, although not strongly because the difference between the two samples is not significant (X^2=2.48).

Unk[α>ω]>K[Res>Int]

P=0.02   *P*>0.5

   The introduction of P8 in the set of basic postulates proved to increase the heuristic value of the model by providing a more complete order of predictions: P2'>P2">P1">P1'. This transitive trend corresponded to a more consistent set of connections between the relational postulates of the model, i.e., P5, P6, P7 and P8. Figure 6 represents the final predictive structure.

   One last improvement could be made upon the model; it concerned the generality of some basic postulates in the case of both the K and the Unk types of duels. It was already asked if P8 could be generalized to all or most types of experimental models of dominance determinants in *Xiphophorus*. The answer depends itself on whether P1 could ever be assumed in the case of known opponents, as it is assumed (and confirmed) as a general rule for pairs of unknown opponents not possessing asymmetries with respect to social experience. Certain types of experimental duels could result in significantly larger frequencies of dominance for residents than for intruders when previously known individuals are of equivalent social status. This could be possible if the two opponents do not engage in agonistic behaviour during the pre-experimental period; in such a case none of the pair-members would have α or ω experience before being paired again as resident and as intruder. Another adequate situation would be to provide additional α or ω experiences before the duel. Thus, a previously ω fish would encounter its former dominant opponent after an intermediate period of α experience towards a third fish; conversely, an a individual would receive an intermediate ω experience before encountering again its former ω opponent as resident or as intruder. Should P1 apply to the K opponents having symmetric social experience ([α-α], [ω-ω]) or having been equally deprived of it ([Iso-Iso]), the model would gain in concision and P1 could be generalized from

 P1'=K[Res>Int] and P1"=Unk[Res>Int]:

P1=P1' U P1"=K U Unk[Res>Int],

i.e., K U Unk[Res>Int] and K U Unk[Int<Res].

   It will be remembered that the initial model already contained two general postulates: P2, and the association of P6 + P7. A generalization of other initial postulates could be confidently assumed. Thus, P3 and P4 could also be formulated to apply to the case of previously known opponents; for that purpose, an intermediate period of isolation could be given to an α fish before it would encounter its previous ω partner, or to the ω fish before the duel with its previous α partner. The two following postulates would very probably be supported by experimental results:

P3'=K[α>Iso]

P4'=K[Iso>ω]

which would logically imply P2'=K[α>ω].

The former P3 and P4 should be changed to P3" and P4" following the conventional sign adopted for Unk-pairs. They would still entail P2". The general postulate P2 would then be logically implied by the conjunction of the general:

P3=K U Unk[α>Iso]

P4=K U Unk[Iso>ω]

and P3 & P4 → P2=K U Unk[α>ω].

It will be noticed that *P3* and P4 would be consistent with (though not logically deducible from) P5=K[α>ω]>Unk[α>ω], which was confirmed by the present results. This suggests that two additional postulates could be conjectured:

P9=K[α>Iso]>Unk[α>Iso]

P10=K[Iso>ω]>Unk[Iso>ω]

which would logically imply P5:

P9 & P10 → P5= K[α>ω]>Unk[α>ω].

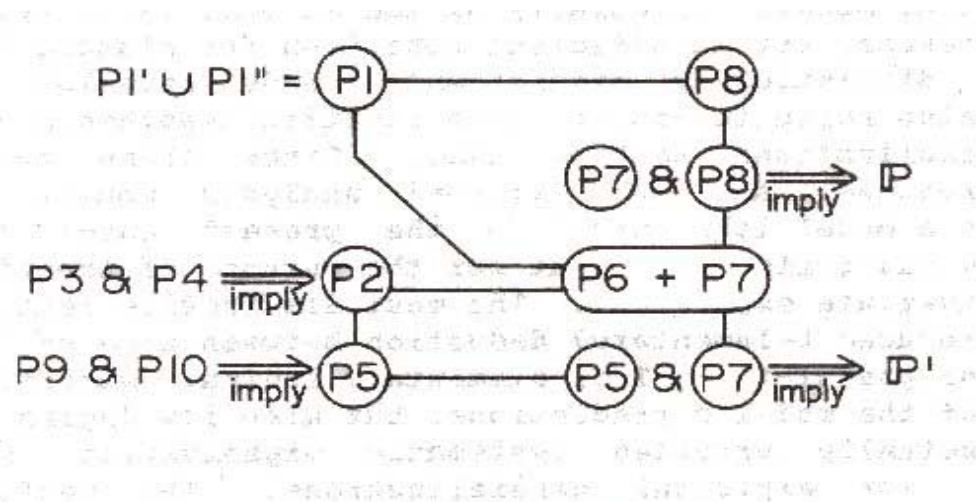Finally, the model's structure is presented in Figure 7.

Fig. 7.   Model's structure.

DISCUSSION

The characteristics of the model need to be outlined, as these characteristics suggest that a particular methodological strategy was associated to the models's evaluation.

Because it conveyed and organized basically factual information, the model deserved to be called empirical. More precisely, the model was of the experimental type: It was based upon previous experimental results, the synthesis of which produced a general prediction also to be tested experimentally. The elaboration of the model will be described in order to emphasize the model's specificity.

The properties which were selected as relevant to dominance determination were known to specifically control aggressive dominance in *Xiphophorus*. They had been applied as independent variables in highly reliable experimental paradigms such as the prior residence condition, initiated by Braddock and generalized by Zayan. In principle, they were more reliable than any bulk of naturalistic observations, at least as far as internal validity was concerned. The fact that prior residence situations could well be present, or even be the general rule, in the natural habitat during the dry season is another story: if ecological variables are not specifically relevant to an ethological problem, experimental observations should always be preferred to naturalistic ones, whenever a choice between the two is possible.

The model, then, integrated the various experimental results initially present into a more specific system of hypotheses. The various relations between the independent variables and the dependent one (dominance) were (pre)-experimentally retested. Since they were confirmed, these predictive relations, contained in the basic postulates, could be generalized and treated as experimental laws, among which connections could be found which accounted for and explained dominance determination. The new predictions, having been derived from a comprehensive confirmation of the model's structure, could be immediately explained by the ancestors of the model, i.e., the set of predictive postulates. Moreover, a partial explanation of dominance was supported by the overall determination of the outcomes of duels by (pre)-experimental variables, as was indicated by the large portion of explained variance. Explanation was possible due to the deterministic character of the model and to causal interpretation of experimentally produced relations. In this respect, experimental models like ours are closely associated to the capacity to reveal and test highly specific predictions: they contrast with correlational models, especially of the *ex post facto* type. Prediction, however, is a necessary but insufficient condition for elaboration of an experimental model. Statistically significant trends revealed by correlational methods could also serve to confirm some specific hypotheses and thus to induce empirical generalizations, perhaps laws. Since these could also be experimentally produced, any correlational analysis would, in principle, be compatible with a model like ours. In the present case, the multiple regression analysis was quite convenient for the purpose of treating some of the data in our multivariate experiment. The most distinctive feature of our model was that it introduced (elementary) deduction between some of the

predictive propositions of the postulates. This elementary logical structure increased the specificity of the model's predictions, but also its degree of confirmation, because it actually provided systematic organization for confirmed hypotheses, i.e., for empirical generalizations. The factual content of the experimental laws thus received a truly theoretical form, even if it was rather modest. Further experimental findings should be able to generate new hypotheses contributing to (derived from and/or deriving) more extended deductions. The specific features of experimental models like ours must be discussed in more detail.

Both the origin (in this case, Zayan's experiments) and the future development of models like the present one suggest that successive systems of experiments may be carried out, instead of isolated tests. These programs should consist of samples of experiments which would each test specific hypotheses mutually relevant to one problem, such as the dynamics of aggressive dominance. Each experiment would test one element of a more synthetic model, independently of the other experiments, and the model would retest some of its basic elements for purposes of generalization. It is clear that such a strategy would increase both the internal and external validity of the experimental relations (laws) chosen for dominance determination. It goes without saying that any experiment carried out in isolation and/or for prospective purposes alone would be quite useless at the stage of the present experimental model. This conclusion holds true even for a multivariate experiment, searching for comprehensive kinds of significant statistical associations between various independent variables and dominance frequencies in *Xiphophorus*. A higher predictive and explanatory level has already been achieved in this respect. This point establishes one of the basic differences between our model and Murchison's (1935a to f) experimental law of dominance hierarchy in the domestic fowl, although his attempt can be considered as the very first one at constructing experimental models like ours. The author programmed a system of interrelated experiments on a group of animals whose ranks in a linear hierarchy were assessed with respect to a number of dominance criteria. The most basic criterion was actually represented by the number of victories and/or defeats recorded for each animal after a series of agonistic encounters planned between all possible pairs of group-members. Other indirect measures of dominance were conceived and experimentally recorded: locomotor activity and average distance covered: degree of attraction or of repulsion, as indicated by an individual being approached or avoided by all other group-members: sexual selection and sexual activity; body weight; morphological/anatomical traits, and physiological (e.g., endocrinological) variables. All these variables appeared to be functionally related to each other. A linear correlation (either positive or negative) was often found between these individual performances/properties and individual rank on the scale of aggressive dominance, so that the former could be considered as dependent variables or indirect indicators of the latter. Murchison (1935f) eventually expressed the sets of functional relations between all the variables by a general mathematical model involving differentiation and integration, and the social hierarchy was represented as a dynamic system akin to physical systems. However, Murchison's work resulted in a formal expression of various

statistical relations, without his "social law" suggesting anything new. His mathematical model boiled down to a set of multiple correlations made *ex post facto*. It must be recognized that Murchison's experimental system represents step towards experimental models like ours. His model was the first to look for interdependence among various variables contributing to dominance and hierarchical status in general. This pioneer multivariate experiment could provide a synthesis of experimentally introduced (and controlled) relations between individual performances/properties and individual aggressiveness/dominance. Since Murchison was actually dealing with a stable and linear hierarchy, individual differences between all group-members tested in pairs reflected asymmetries, particularly with respect to rank in the aggressive dominance scale. Murchison did the groundwork for further models by predicting that the relations he found could be generalized into experimental laws, and explaining the interdependence between variables in terms of pre-experimental properties and asymmetries of individuals, but these models were never concluded.

Experimental models such as ours contrast with statistical models or techniques. Only the testing of the model makes use of statistical techniques, e.g., the multivariate analysis of orthogonal regression. Models for statistical computation are not models of ethological determination; only the latter possess conceptual components interpretable in terms of ethological behavioural/cognitive) variables and relations between variables (e.g., laws). Moreover, the efficiency of a multivariate statistical model/technique will be greater if applied in the context of an experimental research than for the sake of discovering unexpected trends among correlational data. It will be remembered that the combination of our controlled asymmetries accounted for about 97% of the total variance. Such a negligible portion of unexplained variance should be attributed to the experimental character of our model. More precisely, it should be attributed to the deterministic character of the model which was experimentally tested instead of being naturalistic. Only 56% of the variance was accounted for by Collias (1943), who applied multiple correlation analysis (akin to factor analysis) to experimentally produced dominance outcomes in the domestic fowl. According to the present authors, this rather disappointing result could be due to poor pre-experimental control of the variables selected as determinants of aggressive dominance. These factors were more or less naturally selected, instead of being specifically induced: particularly, previous dominance or subordination experience was quite intuitively assessed (as seen, at least, by the method of selection of individuals, as reported in the paper) among group-members of various hierarchies. But we submit that the main difference between our results and Collias' lies in the fact that our model originated from experimental results instead of simply plausible hypotheses. Accordingly, further models on the domestic fowl be better to depart from basic postulates supported by Murchison's results and/or by their previous confirmation, which would generalize them into experimental laws. Randomness of dominance as the issue of an encounter should also be strongly reduced by careful (pre-) experimental induction and control of the properties which are selected to define the state of potential dominance of every individual. As in the present experiment, every individual state (pre-)

experimentally "prepared" could be considered to determine each animal's propensity for aggressive dominance. The classical notions of dominance vector (or ability, or tendency) designate such dominance potentialities, which are adequately quantified by conditional probabilities.

Conceptually speaking, our model implied more stochastic than purely causal determination of dominance. In regard to empirical testing, the model was highly deterministic, since: -all encounters were systematically planned, i.e., duels paired, *a priori*, opponents in either equivalent (symmetric) or differing (asymmetric) states;   -all duels were experimentally planned, i.e., were favouring dominance events which were more induced than spontaneous; -any duel would inevitably result in a dichotomous outcome either victory (actual dominance) or defeat (subordination), with no undifferentiated state(us). Under these conditions, it is likely that many statistical techniques of the multivariate type (e.g., factor analysis, discriminant analysis, multidimensional scaling) would provide a very satisfactory synthesis of the data, as was the case for our multiple regression analysis. It also seems fair to point to inevitable factors to account for dominance determination when such a small portion of unexplained variance remains. Among these factors which interact with the controlled asymmetries, can be mentioned: differences in fighting abilities resulting from genetic or early experimental variables, health conditions, minimal errors in size measurements, sensitivity of some fish to handling preceding any duel, etc.

Although it was basically designed to predict short-term events, our model was not purely predictive, let alone descriptive. It involved intervening variables of the cognitive type, as well as the observable effects of (pre-) experimental inputs upon dominance outputs. The model of *Xiphophorus* was actually built like a black-box, endowed with internal states involved in cognitive mediation of dominance determination. Experiential processes, like previous α or ω status or recognition of a former opponent or of a previous residence area, were postulated in order to explain the dominance frequencies which were predicted. Cognitive properties and processes associated to environmental experience were assumed to be partial mechanisms of dominance establishment. These processes were inferred and could only be supported by indirect evidence on descriptive behavioural grounds. They could have referred to definite internal processes (mechanisms) such as those conditioning neural plasticity; in that case, they would have been treated more like hypothetical constructs, testable by e.g., in neurophysiological experiments. In the present model, it was simply assumed that our species possessed the neural capacities (pre-programmed and/or plastic) controlling elementary cognitive processes such as the ones involved in the experiment: perception, memorization and retrieval, recognition (not necessarily recall), brain representation of immediate past events, as well as short-term anticipation of social interactions, conditioned through agonistic experience, e.g., by fear associated to fights, in strange environments and against strange aggressive conspecifics, etc. These capacities can be found at the behavioural/perceptive level of cognition (Piaget's sensor/-motor developmental stage, responsible for e.g., object permanence). They require only a rudimentary plastic neural system (Bunge, 1980), and *Xiphophorus* seems to fulfil the requirements. It can be conjectured that experiential processes determine dominance establishment

before individuals become involved in agonistic interactions. By some kind of rudimentary awareness, individual properties and potential asymmetries perceived as relevant to aggression or to fear would then be attributed to (and not simply possessed by) conspecifics. Opponents may be very quickly identified by some of their general properties: resident or intruder, aggressive or fearful, previously dominant or subordinate, etc. It is obvious that the prior residence and intrusion situations are immediately perceived by the two opponents: part of the resident's advantage is due to the intruder's inhibited aggression as soon as it detects the presence of a resident, and part of the intruder's disadvantage is due to the resident's aggressive reaction to an intrusion (Zayan, 1975c, 1976). The same holds true for an encounter between opponents which are extremely divergent with respect to agonistic experience, especially if it opposes long-term α and ω individuals. There are indications that animals recognize previously dominant or subordinate conspecifics on the basis of morphological and motor patterns immediately perceptible; in that case, it is very likely that aggression would be inhibited in some individuals, and facilitated in others. If the asymmetries are not very pronounced or if the opponents are not (well) informed of them, the opponents would have to be more aggressive, and could more probably be injured. More determinant would be the role of individual recognition between dominant and subordinate pair-members (and group-members, in general). Individual recognition permits the use of information from previous conflicts between the same potential opponents. The resultant occasional contests would be settled rapidly, suppressing dangerous exchanges of offensive blows. Individual recognition could, as a "convention" (Maynard Smith & Parker, 1976), incite subordinate individuals to respect already established dominance. Such a conservative attitude might serve to postpone costly rebellions until the odds of reversing an α-ω relation should be so greatly increased as to eliminate all undue risks of physical damage. This would also serve to eliminate that the despot confirmed obviously its rank again. It is indeed true that attempts at dominance reversals are extremely rare in pairs of *Xiphophorus*; they are more frequently recorded in small groups, in which individual recognition can be in operation, but an actual change in dominance structure still remains very far from statistically representative. Although such stability is generally recorded between unknown α and ω opponents, reciprocal aggression and dominance reversals are significantly more frequent than in previously known α and ω individuals. Individual recognition, associated to agonistic experiences, might have been selected for its adaptive value of reducing costly conflicts between individuals, especially when a decision to challenge steady dominants would have been either unprofitable or detrimental. It seems rather obvious that individual recognition makes agonistic bluff useless, if not dangerous (Van Rhijn, 1980). Any model applying a game or conflict theory to aggressive dominance which would disregard individual recognition would also be useless. Individual recognition actually (pre-) determines duel outcomes in the direction of dominance stability and of rigid (despotic or linear) hierarchies in small groups or in subsets of a large group. This is why it would be unrealistic for a model to assume that conflict encounters are random events occurring independently of the individual properties and

inter-individual (a)symmetries of the opponents. Equiprobable dominance outcomes should represent a small part of a random sample of natural duels, particularly in gregarious species forming stable groups of few individuals. In such a case, the location of the duel would also determine dominance probabilities. The most dramatic determination will be found for the most extreme asymmetries. In our experiment, this was seen in the case of fish advantaged by prior residence and by immediate dominance experience which encountered previously known subordinates which were also disadvantaged by intrusion, i.e., by fear due to immediate handling as well as by unfamiliarity with the test aquarium. It is noteworthy that the effects of individual recognition are not limited to one test like the duels in the present experiment. Associated to α-ω experiences, it can systematically neutralize the advantage of prior residence in fish which are first tested as intruders (and defeated by a resident), and then tested as residents in their (pre-) experimental tank where they can challenge their former dominant opponent, disadvantaged by intrusion. Individual recognition thus inhibits reversible effects of prior residence upon (aggressive) dominance and imposes, instead, stability of initial α-ω relations. Successive recognition of a former despot actually inhibits territoriality, defined as systematic dominance reversal (inversion) between two individuals becoming alternately residents (Zayan, 1975b). It is interesting to note that repeated alternations of territories (residence areas) do not favor the probability of recording dominance reversals in *Xiphophorus* pairs (Zayan, 1975c, 1976) and small groups (Heuts, 1968). Social status resulting from sequences of contests won/lost between pair-members, can be continuously determined by cognitive processes such as familiarity with the initial residence area and familiarity with particular dominant individuals or subordinates. Dominance stability or reversibility depends upon the relative importance of each pre-experimental factor at the time a duel occurs.

Finally, our model was qualified as experimental in order to avoid confusion with theoretical models of dominance. Most of them are formal (logical or mathematical), which entails that they can always be empirically interpretable but never involve experimental testing. Typical examples of these theoretical models are Landau's (1951a, b, 1953, 1965, 1968) and Rapoport's (1949a, b, 1950) probabilistic and combinatorial representations of hierarchical structures. We consider them relevant to further elaboration of models on dominance establishment in fish, since they purport to refer to animal societies and did not ignore Murchison's work on fowl. We believe that experimental models should eventually achieve a combination of experimental laws and of purely theoretical models, as, for example, the stochastic or deterministic automata theory applied to dominance probabilities expected after repeated duels between symmetric and/or asymmetric opponents. Although theoretical models of hierarchy formation are much too general to be empirically tested (or even to suggest any specific predictions), they could be helpful if connected with results like those of the present experiment. Thus, Landau has formally examined the necessary and sufficient conditions for the formation of strictly linear aggressive hierarchies in animals. He concluded that linearization is possible only if several asymmetries exist between individuals and have some decisive effect, even if a minimal one. Moreover, two additional

mechanisms would make it possible to obtain a hierarchical order from a series of dyadic encounters (Landau, 1951b). The first mechanism would be the determinant influence of social experience of dominance and subordination; the second mechanism would be the existence of a bias against inversions of the α-ω relations once they are established between two group-members. According to the author, a hierarchy could result from tournaments in which each individual carried out successive contests against each other member of the group (see Chase, 1974, for a critical examination of this hypothesis); as a matter of fact, this is how Murchison (1935a to f) obtained a linear dominance hierarchy after experimental planning of all possible pair encounters. However, Landau rightly points to the fact that in this case duel outcomes are not independent of each other: for each of the opponents in the group the outcome (victory or defeat) of a given contest influences the outcome probability of the next duel. Dominance frequencies being statistically dependent events, the outcome of later duels could be fairly explained by the agonistic history of an animal, i.e., by the relative frequencies of its *previous* gains and *losses.* Landau postulated that the probability of an individual's winning of a contest is a linear function of the number of group-members it has already defeated. The author also examined several alternatives for the determination of outcome probabilities by recent establishment of dominance relations, as Rapoport did for triadic encounters. The order in which duels will occur in the round-robin tournament appears to be essential in this respect, to the point at which linear orders may or may not result from particular sequences of dyadic encounters. The number of asymmetric and of symmetric opponents which are successively encountered is also essential: stochastic dependence between dominance outcomes, as well as linearity of the hierarchy, should be maximized in cases where a subordinate individual encounters successive opponents which were previously dominant, and in cases where a dominant animal encounters successively previous subordinates. This asymmetry with respect to previous α and ω experiences should determine divergent dominance frequencies in group-members encountering for the first time. Of course, individual recognition will increase the respective advantage and disadvantage in former α and ω conspecifics which happen to encounter each other again; it is very likely that it will also increase the stability and degree of linearity of the dominance hierarchy.

   Even if dominance establishment is only considered at the level of dyadic encounter and not at the level of group hierarchy, Landau and the present authors tend to emphasize the determinant part played by asymmetries. This conception tends to support a definition of dominance as a relational, instead of as an individual (intrinsic) property or state. It was important to arrive at the conclusions that such a property could qualify potential (conditional, dispositional) dominance, and that it could be experimentally produced by controlling the individual states of potential aggressiveness and/or fear. Moreover, the experiential/cognitive aspects of social asymmetries suggest that aggressiveness and dominance are more in the order of attributes than of biophysical properties, i.e., are properties that an individual attributes to a potential opponent.

ACKNOWLEDGMENTS

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