Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri:*

effects of body size and prior dominance

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Abstract. The relative contribution of prior experience and of size asymmetries to the determination of dyadic dominance between unfamiliar individuals was examined using pairs of green swordtail fish, *Xiphophorus helleri.* Three experiments were conducted to assess the extent to which superiority in size could override potential handicaps resulting from prior experience. These results indicated that prior experience accounted for dyadic dominance when the size advantage of a previously subordinate over a previously dominant opponent was less than 25 mm^2. However, as the lateral surface of the subordinate fish increased, neither previous experience nor size differences clearly accounted for the outcome of dyadic conflict. Even when the size advantage of subordinate opponents was in the 126-150 mm^2 range, size differences did not adequately explain the outcome. In conflicts between large previously subordinate and smaller dominant fish, there was evidence for an inverse linear relation between the effects of size and the likelihood of establishing dyadic dominance. In general, males with prior experience as subordinates had to be at least 40% larger than a previously dominant fish to win a significant proportion of conflicts. These results indicate that prior agonistic experience and body size effects can be additive when at the advantage of one opponent. These factors can also cancel each other out when in opposition, at least when size differences are not extreme. The results also confirm the main effect of both factors as well as their interaction in the determination of conflict outcomes for *X. helleri.*

Body size is most often identified as the best cue for gauging resource holding power (Parker 1974) in animal conflicts. Size correlates naturally with strength and size is presumed to be an important factor accounting for conflict outcome in fish, with the larger individual usually winning in *Xiphophorus* spp. (Collins et al. 1967; Beaugrand & Zayan 1985). However, size is not always a reliable indicator of resource holding power because of transitory changes in motivation or physiological state that may indirectly influence the outcome of conflict (Clutton Brock & Albon 1979; Robertson 1986). Although animals may rely on alternate means of conflict resolution when such means are available (Barnard & Burk 1979), when contestants are closely matched in size, the potential cost associated with errors of assessment of relative size and strength may be high.

Resource holding power can also be affected by factors related to the history of two contestants. Among experiential factors, prior dominance experience seems to account for increases in resource holding power, while recent subordination seems to produce decreases in resource holding power (Francis 1983; Beaugrand & Zayan 1985; Beacham & Newman 1987). Differences in familiarity with the area in which the contest occurs (Zayan 1975; Henderson & Chiszar 1977), as well as prior cognizance of the opponent (Zayan 1974) can also have decisive roles in conflicts.

Beaugrand & Zayan (1985) combined several of these experiential factors in a predictive model of dyadic conflict outcome. They showed that when size differences between opponents are limited, experiential factors fully account for dominance outcomes in pairs of green swordtail fish, *Xiphophorus helleri.* In testing this model, contests were arranged to manipulate experiential asymmetries while keeping size differences between rivals to a minimum. Nevertheless, the research revealed that size differences still accounted for 10% of the total variance in observed conflict outcomes. The investigators suggested that size differences might emerge as a more salient determinant of dominance when differences were great and clearly perceptible. What happens when these factors interact to affect resource holding power, each providing potentially conflicting cues? Clarifying how these factors combine to influence resource holding power requires experimental comparison of experiential asymmetries with varying degrees of size asymmetries.

Beacham (1988) has recently shown that when the asymmetry of weight is small, prior experience may override the influence of weight in conflicts between pumpkinseed sunfish, *Lepomis gibbosus*, pairs. When the asymmetry was greater than 80%, size superseded prior experience. We investigate the relative contribution of prior experience and body size in the determination of dominance in male X. *helleri.* In addition to extending the broad principles of Beacham's findings to another fish species, we propose a combinatory function for predicting conflict outcomes in terms of prior experience and size asymmetries.

GENERAL METHODS

Subjects and Material

A pool of more than 1200 adult X. *belleri* vas constantly available in the laboratory. All fish were purchased from the same breeder (SD Tropical, Plant City, Florida). They were maintained in mixed groups of 100-150 adult and immature males and females in nine large communal tanks each containing 165 litters of water and measuring 90 x 50 x 40 cm. When they were to be used for an experiment, adult males were selected from these communal tanks. They were captured as randomly as possible with the use of a mesh net placed on the floor of the tank, which, when raised, captured most of the fish in the tank. All dyadic conflict bouts were staged in 40 identical glass aquaria measuring 30 x 15 x 15 cm that contained 13.5 litters of water.

Size Measurements

Three size measurements (with precision of 0-5 mm) were obtained for each individual: (I) total length, from the snout to the end of the caudal fin; (2) flank height, from the base of the dorsal fin to the origin of the gonopodium; (3) sword length, from the end of the middle rays of the caudal fin to the tip of the sword. Males were paired according to differences in their lateral surfaces. The lateral surface was obtained by adding the sword length to the product of total length and flank height. Calculated in this way, Beaugrand & Zayan (1985) found that lateral surface showed a 5% mean error when compared with lateral surfaces measured using a planimeter. Moreover, these authors have shown that lateral surface had a significantly greater correlation to dyadic dominance outcome than the standard length in X. *helleri*.

Size measurements were obtained before pairs were formed. We used a specially designed aquarium to measure the fish. The aquarium had a mesh partition that we could move freely about to immobilize a fish against the front glass of the tank. We then rapidly marked its length, height and sword length on the front glass with a felt tip pen. After having released the fish, we measured distances between markings on the glass using a ruler.

General Procedure

The three experiments were conducted in succession. All had a common general procedure consisting of two consecutive phases.

Pre experimental phase

Prior social experiences of dominance or subordination were gauged on the first day: we measured two fish from different communal tanks and isolated them for 2 h in separate pre-experimental aquaria. We used only fish that were unfamiliar with each other and showed a difference in lateral surface of between 0 and 10 mm^2. We then simultaneously introduced both opponents into a third aquarium, where they remained together for the next 12 h. During this period, we observed social interactions from behind blinds. We noted which fish was dominant. However, if dominance was still not clear after 12 h, the encounter was considered null and was terminated.

Experimental phase

On day 2, we formed new pairs by recombination of opponents who experienced prior dominance or subordination on day I. In forming pairs, we selected fish that were unfamiliar with one another and sufficiently different in size so that they could correspond to one of the treatments scheduled for that day. Depending on the treatment, the fish had similar or divergent prior dominance experience. We simultaneously introduced the opponents into an unfamiliar aquarium of the same type as that used in the previous phase; we then observed them for a maximum of 1 h or until one clearly dominated its opponent, whichever came first.

In both phases, the selection of fish pairs was computer assisted. Using a database manager, we constantly monitored information concerning each fish, noting communal tank of origin, body measurements, previously visited aquaria and prior dominance experience. A program then applied this information and computed specific directions concerning the pairing of specific opponents. The program also randomly assigned pairs to the various available aquaria.

We considered a dominance relationship as being established when the dominant fish was successful in chasing its opponent on six occasions without having been threatened, attacked or bitten in turn. At the experimental phase, we took care to separate contestants or to return them to communal tanks as soon as the dominance criterion had been fulfilled. No detectable injury occurred during the experiments.

EXPERIMENT 1

Methods

In experiment 1, five types of encounters were staged (see Table I), each type corresponding to one independent experimental treatment or sample. Sample 1, 2 and 3 correspond to the encounter of a previously dominant and a previously subordinate opponent. In samples 4 and 5, two previously dominant fish or two previously subordinate fish were paired. Except for sample 1, a difference of at least 100 mm^2 (range of 100-250 mm^2) was maintained between their respective lateral surfaces. In sample 1, we kept size differences below 50 mm^2, i.e. opponents were considered to be of equivalent size.

Table I. Conflict outcomes of experiment 1

Sample	*N*	Encounter between fish 1 and fish 2	Difference range in lateral surface (mm^2)	Winning frequency		Binomial *P*-value
				Fish 1	Fish 2	
1	14	Equal dom and equal sub	0–50	14	0	<0·01
2	12	Large dom and small sub	100–250	11	1	<0·01
3	15	Small dom and large sub	100–250	1	14	<0·01
4	14	Large dom and small dom	100–250	13	1	<0·01
5	12	Small sub and large sub	100–250	1	11	<0·01

Sample size (*N*, number of pairs) is indicated. In sample 1, a prior dominant fish (dom) encountered a prior subordinate (sub) of nearly equal lateral surface. In sample 2, the dominant fish was larger (between 100 and 250 mm^2) than the prior subordinate opponent.

Results

The results and statistics are summarized in Table I. When the size difference was in the 0 50 mm2 range, prior social experience alone decided conflict outcome. In sample 1, previously dominant individuals defeated previously subordinate opponents in all 14 staged duels. When the difference in size was in the 100-250 mm^2 range (samples 2 to 5), size imbalance accounted for dominance. The larger individuals systematically defeated the smaller opponents, despite the asymmetry resulting from respective prior experiences. Comparison of samples 3 and 1 clearly illustrates the effects of prior experience asymmetry and size. In sample 1, size differences were within the 0-50 mm^2 range and previously dominant fish defeated previously subordinate fish. In sample 3, we allowed an advantage of 100-250 mm^2 for the previously subordinate fish. The handicap of being a subordinate meeting a previously dominant fish was no longer evident and size clearly determined the outcome.

EXPERIMENT 2

Methods

The aim of the second experiment was to establish to what extent size could compensate for a lack of prior experience. We followed the same procedure as in experiment I, with the only difference being that all staged conflicts took place between a previously dominant and a previously subordinate fish, the latter having the greater size. The range of superiority in lateral surface of previously subordinate fish was 1-25 mm^2 in sample 1. We then increased the size differential by steps of 25 mm^2 for each successive sample, up to 126-150 mm^2 in sample 6 (see Table II).

Table II. Conflict outcomes of experiment 2

Sample	*N*	Difference range in lateral surface (mm^2)	Winning frequency		Binomial/*Z* *P*-value
			Small	Large	
1	23	1–25	19	4	<0·01
2	21	26–50	11	10	NS
3	21	51–75	14	7	<0·05
4	19	76–100	8	11	NS
5	20	101–125	8	12	NS
6	20	126–150	8	12	NS
1, 2, 3 (pooled)	65	1–75	44	21	<0·01
4, 5, 6 (pooled)	59	76–150	24	35	NS

Results

When the size predominance of the previously subordinate fish was small, i.e. in the 1-25 mm^2 range (sample 1, Table II), the previously dominant fish won significantly more often. Pooling the results of samples 1, 2 and 3 suggests that prior experience significantly accounted for dominance when the difference did not exceed 75. As size predominance in the previously subordinate individual became larger than 75 (samples 4 6), prior experience was of less importance; size superiority quashed the handicap of prior social experience and neither asymmetry clearly explained the outcome.

EXPERIMENT 3

Methods

The purpose of experiment 3 was to study the interaction between size and prior experience asymmetries in the 154-300 mm^2 range. The procedure used in this third experiment was identical to the one described in the previous experiments. We staged five types of conflicts between previously dominant and subordinate opponents. Pair members were unfamiliar with each other and the test area. As in experiment 2, the previously subordinate pair members were larger in lateral surface than their previously dominant opponent. The size advantage varied between 20 and 40 mm^2 in sample 1, and between 151 and 175 mm^2 in sample 2. We then increased it at each interval by 25 mm^2 up to a maximum of 226-250 mm^2 in sample 5 (see Table III). We used a larger sample for sample 1 because we expected the corresponding size asymmetry to be in the zone where size would override prior experience asymmetry; increasing N contributes to a stabilizing variance, and thus can allow the detection of a minimal, but reliable, treatment effect (Kirk 1968).

Table III. Conflict outcomes of experiment 3

Sample	N	Difference range in lateral surface (mm^2)	Winning frequency		Binomial/Z P-value
			Small	Large	
1	43	20–40	26	17	NS
2	21	151–175	7	14	<0·05
3	20	176–200	5	15	<0·01
4	20	201–225	3	17	<0·01
5	20	226–250	4	16	<0·01
2, 3, 4, 5 (pooled)	81	151–250	19	62	<0·001

Results

The results appear consistent with those obtained in the two previous experiments. A slight advantage in size (sample 1: 20-40 mm^2) did not statistically account for the dominance displayed (Table III). Previously dominant fish won 60% of conflicts. In samples 2-5, as size became more predominant, it negated the effects of prior experience. In general, with an advantage greater than 151 mm^2, the larger previously subordinate fish won more frequently. The pooled results of samples 2-5 were also highly significant (19 versus 62; Table III), thus confirming the importance of size greater than 151 mm^2.

POOLED DATA

The three experiments ended at overlapping intervals in time during the summer months and therefore we felt justified in combining samples 1 and 3 of experiment 1 with all samples of experiments 2 and 3. In all of these 273 pairs, a previously dominant individual had met a previously subordinate opponent of nearly equal or larger size.

A given difference in surface area between two opponents can influence outcome in a manner that depends on the absolute value of their respective sizes. To avoid such a scaling effect, we worked out a dimensionless ratio (Gold 1977) similar to that used by Beacham (1988) for weight in his study.

The size differential *(d)* between contestants was expressed by a percentage of the smaller (and previously dominant) individual's lateral surface (LS):

d=(large LS-small LS / small LS) x 100

Since dominance was a categorical variable (win/ lose) and we wanted to predict the proportion of success, logistic regression seemed appropriate. We used the Logistic Regression computer program from BMDP (Engelman 1988) to regress the 273 size differential scores onto their corresponding dominance outcome. The result shows that *d* can adequately predict dominance outcome (X^2= 38.82, *df=1, P<0.001)*. The Brown goodness-of-fit test indicates that the obtained logistic model is appropriate for the data (X^2 =1.22, *df*= 2, *P* < 0.54; Fig. 1).

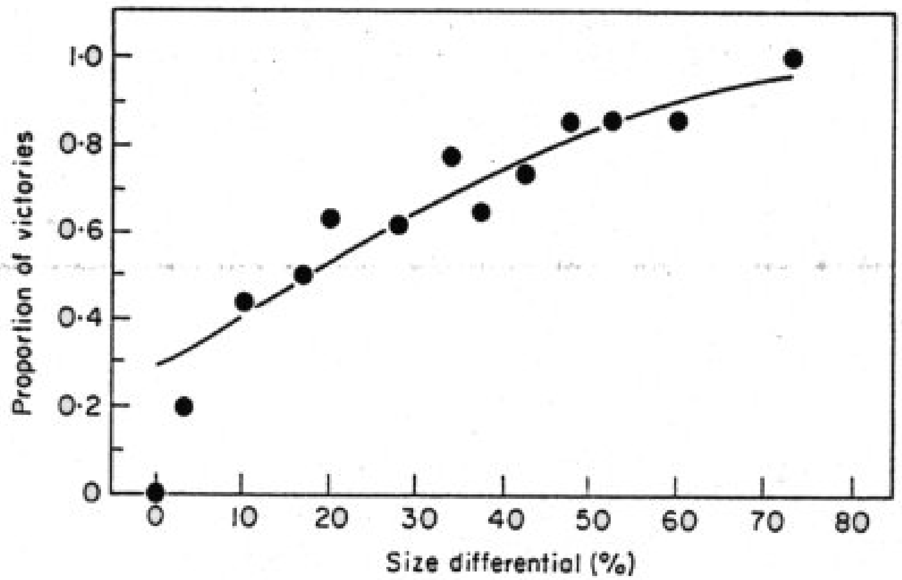

Figure 1. Logistic function $Y=\exp(U)/(1+\exp(U))$, where $U=0{\cdot}9194-(0{\cdot}052846\,d)$. Points represent the proportion of conflicts won by the prior subordinate at successive 5% *d*-intervals.

For visual comparison, we calculated the proportion of victories of the previously subordinate fish at successive d intervals and superimposed them on Fig. 1. As one can see, the logistic function is quite ineffective when size differences are small. However, we consider it sufficiently adequate for an initial approximation. Figure 1 summarizes the results: as size differential increases in favor of that of the previously subordinate, the ability of the latter to defeat the smaller dominant increases in an almost linear fashion.

DISCUSSION

Weapons, body size and information about a previous encounter with an opponent (i.e. individual recognition) are most frequently mentioned as the principal indicators of resource holding power (Maynard Smith 1982; Turner & Huntingford 1986). Parker (1974) recognized that prior experience could contribute to resource holding power. He noted that successful fighting experience markedly increased the readiness for escalation and explained this effect in terms of experience increasing resource holding power.

The question asked here was how two factors, potentially contributing to individual resource holding power, interacted, especially, when influencing resource holding power in an antagonistic manner. Our results confirm the importance of both size and prior experience differences in the determination of conflict outcome. Size is especially impressive when opponents have had equivalent prior experiences of dominance or subordination, thus confirming the findings of Beacham (1988). Prior experience asymmetry determines future dominance when size differences are small, again confirming a now well established regularity (Beaugrand & Zayan 1985; Beacham & Newman 1987; Beacham 1988).

We knew from Beaugrand & Zayan (1985) that, within reasonable size differences, prior experiences of dominance or subordination could fully account for a conflict outcome. Our study, by opposing prior experience to various degrees of size asymmetries, is capable of providing a more precise formulation of the degree of interaction between size and prior experience. The function obtained shows the following interesting properties. (1) The relation between the size differential and dominance outcome is linearly proportional within the range studied. When the size differential is small, the likelihood that a previously subordinate fish will defeat a smaller previously dominant opponent is very low. As the size differential increases, the likelihood increases progressively, in a manner that is, at first glance, linearly proportional. (2) Prior dominance experience and size asymmetries influence conflict outcome through an additive . Unfavorable prior experience can be offset by superiority in size. However, when the size superiority is considerable, size camouflages any prior experience advantage of the opponent over its partner. (3) The compensation process is gradual when examined at the aggregate level, i.e. for several conflicts analyzed together. There is apparently no threshold effect in the population that could demonstrate that, at a given size difference, most or all small opponents would immediately concede victory to the larger one.

To our knowledge, Abbott et al. (1985), and, more recently, Beacham (1988) are the only ones who have systematically manipulated both size difference and prior experience of fish opponents. Abbott et al. (1985) investigated the interaction between experience with an opponent and an opponent's relative size in contests between juvenile steelhead trout, *Salmo gairdneri.* They provided apparently contradictory prior experience and body size cues by supplementarily feeding the subordinate fish in an established dominant/subordinate pair to increase its size relative to its dominant. They found that previously subordinate fish that were supplementarily fed never became dominant although they did reach a size great enough to exert dominance in initial encounters between unfamiliar control pairs. However, it is important to note that not only were experimental and control samples unequally manipulated in their research, but that Abbott et al. (1985) repeatedly tested the members of the same pair. They attributed social stability within pairs to experience from prior contests. However, it is evident from previous work carried out by Beaugrand & Zayan (1985) that their fish re established dominance on the basis of individual recognition, rather than on prior experience alone.

Frey & Miller (1972) reported that the majority of blue gouramis, *Triclrogaster trichopterus,* with previously subordinate experience were unable to dominate smaller standard rivals (up to 10% smaller in body length) that had been isolated. Francis (1983), Beaugrand & Zayan (1985) and Beacham & Newman (1987) have shown that fish that have been isolated are equivalent to fish having received prior dominance experience. Frey & Miller's observations are thus consistent with the result of to present study and that of Beacham (1988).

Their isolated fish, being equal to our previously dominant fish, were able to systematically defeat larger subordinate opponents. Beacham (1988) conducted a study very similar to the present one. He staged dyadic contests between small pumpkinseed sunfish having experienced prior dominance and large previously subordinate fish. The relative difference in weight was used to pair individuals as opposed to surface area, as in the present study. His results and the present ones are remarkably consistent. When a weight difference was relatively small, a ratio of between 20 and 40%, prior dominance experience not only compensated for this disadvantage in weight, but still determined conflict outcome (Beacham 1988). He also found a zone of 40-80% weight difference in which weight predominance was overridden by a disadvantage in social experience. In these cases, previously dominant and subordinate fish had the same chance of winning. Previously subordinate fish also had to show more than 100% in weight superiority over their previously dominant opponent to be in a position to defeat them.

One word of caution is in order about a methodological limit in the present research that may preclude drawing a straightforward inference about the exact role of experience in determining . Indeed, some unspecified individual attribute such as fighting skill, may account for the fact that the winner in the pre experimental encounter is also more likely to dominate during the second encounter. Such a confound could have been avoided by imposing prior experience rather than by merely selecting the dominant and subordinate fish in terms of pre experimental results. There are a variety of ways to manipulate dominance or subordination by using size and prior residency asymmetries. Such a manipulation could permit assessment of the effect of the experience itself, unconfounded by pre existing individual differences in dominance capacity. However, sufficient evidence already exists concerning the effects of prior experience under various experimental conditions, including rigged contests (e.g. Thinès & Heuts 1968; Francis 1983). In the present context, the selection of winners and losers seemed more natural than the imposition of prior experience. Our objective was to better understand the formation of hierarchies through the study of dyads. It seems to us that potential participants in real social hierarchies naturally sort themselves out according to dominance/submission; they seldom have the opportunity to experimentally control past histories of their opponents through rigged contests.

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