Inversion of initial dominance relationships following the interchange of roles of resident and intruder within pairs of male swordtail fish (*Xiphophorus helleri*)

Claude Goulet*) and Jacques P. Beaugrand

Département de psychologie, Université du Québec à Montréal, Montréal, C.P. 8888, Centre Ville, Québec H3C 3P8, Canada

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*) Corresponding author

E-mail: Rana@UQAM.ca

Abstract

This experiment consisted of 75 different pairs composed of two male adults *Xiphophorus helleri* meeting each other twice. On the first occasion, one of the fish was familiarized with the meeting place for 3h (resident) while its opponent was familiarized with another aquarium (intruder). Upon dominance of one individual over the other, the pair members were separated and returned to their respective home groups for 168 hours (7 days). After this period of separation, the same pair members were reunited and met while roles had been reversed: the initial resident became the intruder, and the initial intruder was given prior-residency. Individuals in the initial resident role defeated the initial intruder in a significant majority of cases (76%). On their second meeting, the newly established dominance relationship was noted in favour of the new resident in a significant majority of cases (82%), and in a reversed direction as compared to the initially established dominance order. This shows that prior-residence is a powerful determinant of dyadic dominance outcome in *Xiphophorus* males when fish show minimal size differences.

Keywords: Inversion of dominance; Prior residence; Swordtail fish; *Xiphophorus helleri*

1. Introduction

Two sets of individual properties appear to determine dominance outcome in dyadic encounters of male Green swordtail fish (*Xiphophorus helleri*): A first set would comprise properties which are static or change very slowly in time, e.g., size, strength, fighting ability, and possibly, latent aggression. These properties are probably largely a function of the genetic make up of the concerned individuals and their constitution. A second set would comprise more dynamic factors, i.e., factors which fluctuate much more rapidly in time, such as recent experience of dominance and subordination, familiarity with the meeting place, knowledge of the opponent, evaluation by the animal of coveted resources, strategic position, etc. For convenience only, the first set will be referred to as static factors, as opposed to the second set which we will call dynamic factors, admitting that this distinction is arbitrary since dynamic or experiential factors can be influenced by latent biophysical part of static factors and vice-versa. These static and dynamic factors appear to combine and to determine which opponent will become the dominant of a pair (Beaugrand & Zayan, 1985; Beaugrand et al., 1991, 1996).

In order to illustrate the importance of a given dynamic factor in affecting dominance, one usually varies only the factor of interest, while equalizing individuals on all nuisance factors. Nuisance factors are those which could potentially contaminate or spoil the presumed relationship existing between the independent variable and the dependent variable. In the case of prior residency, dyadic encounters in which pair-members are carefully matched or equalized on all known and relevant nuisance factors such as familiarity with each other, size/weight, colour morph, sexual gender, maturity, age, recent experience and history, handling are staged. The fish are then isolated for periods of e.g., 2, 3, 18, or 24 hours into separate aquariums, which they are presumed to become familiar with. The experimental variable is then introduced by randomly deciding which of the matched opponents will serve as resident and which will serve as intruder. Encounters are then staged between the future resident and the future intruder

by first catching them and introducing both simultaneously into the aquarium of the future resident. In most cases, i.e., 75%, the resident is found to defeat the intruder in *Xiphophorus*, which is interpreted as a genuine prior-residence effect (Zayan, 1975a, 1975b, 1976; Beaugrand & Zayan, 1985; Beaugrand & Beaugrand, 1991; Beaugrand et al., 1996). However, one may ask why the advantage given by familiarity is not stronger, and why in the remaining 25% of cases the intruder was successful in defeating the resident. Having the same individuals meet again on the next day after having reversed their roles would only lead to the finding that the same individual which dominated the day before now dominates again, but this time as the intruder! Quite evidently such a result could be explained by individual recognition, since the relationship which was first installed in favour of the previously resident pair member now persists even when roles are subsequently reversed. Similar questions spontaneously arise while testing for persisting effects of prior-dominance experiences of victory/defeat. Why did the individual which obtained victory in the first encounter not also obtained victory in the subsequent encounter? The general answer is invariably that all nuisance variables were not appropriately neutralized. In order to neutralize nuisance variables there exists two general approaches depending on whether the factor was identified or not, and if it can be measured or not. A first technique is to keep their level constant or equalize it; this is the case with e.g., sexual gender and size/weight. These factors can be measured, and it is well known that they can potentially affect dominance outcome. A second technique is to cast the subjects at random into the various treatments or, as in the prior residence example, into the available roles of resident and intruder. Such an approach relies on the law of large numbers to equalize treatments or roles on irrelevant variables. With numbers of subjects as low as 20 pairs per condition, it is reckless to believe that randomness will do the expected job. In addition to increase effectives, the power of experiments could be ameliorated by the use of an intra subject design to decide between genuine effects due to a given studied dynamic factor, or to spurious effects composed of uncontrolled static and dynamic factors.

To illustrate the use of a within design, prior residence was chosen as a dynamic factor. Prior residence is here defined as familiarity with the surrounding in which the meeting takes place, a factor which has been reported to favour dominance in the resident over an intruder which was unfamiliar with the meeting place. Thus, the advantages of a 3-hour familiarization period with the future meeting place were demonstrated in *Xiphophorus* for individuals of equivalent size which had been put in isolation for 18 hours beforehand (Zayan, 1975a, 1975b, 1976; Beaugrand & Zayan, 1985). In these studies, the opponents were equally handled and simultaneously introduced into the aquarium of residence of one of the two fish.

The solution examined in the present research was to use the same opponents but in reverse roles of resident and intruder in two successive encounters separated by 7 days. Pilot studies we carried out suggest that one week of separation is sufficient to make the two successive outcomes independent from one another. Upon their reunification, the opponents fight as if they had never met each other, and the previously dominant pair member does not systematically reinstate dominance over its prior subordinate when size differences are minimal.

Since in the present research the same individuals will be repeatedly used and occupy the resident and intruder roles on alternate occasions, fish will thus provide almost perfect replicas of themselves, allowing to subtract those properties, which have not changed from one role to the other, i.e., especially static factors. If prior residence is the genuine causal factor, it will clearly reveal itself as a reversal of dominance outcome from the first meeting to the second, most certainly induced by the reversal of roles experimentally induced upon the opponents.

2. Methods

2.1 Subjects and material

A pool of more than 500 adult swordtail fish was constantly available in the laboratory. They were bought from the same breeder (5*D* Tropical Inc., Plant City, Florida 33566, USA) and maintained in heterosexual groups of 100-150 individuals in nine large communal tanks of 165 litres (90 x 50 x 40 cm). Home groups were composed of 5 adult males and 4 adult females selected at random from the communal tanks. These groups were kept in 52 litres (60x30x30) glass tanks for one month before the beginning of the experiments. All 40 glass aquariums used in the present experiments were identical (30 x 15 x 15 cm) and contained 13.5 litres.

2.2 Size measurement

Size measurement was obtained before the establishment of home groups and the formation of pairs. A specially designed aquarium was used to measure the fish. Using a mesh partition that could be moved freely by hand, the fish was gently cornered and immobilized against the front glass of the aquarium. Its length, height and sword length were then rapidly transferred on the front glass with a soft pen. After having released the fish, distances between markings left on the glass were measured using a ruler. Three size measurements were thus obtained on each fish: *(1)* its total length, from the snout to the end of the caudal fin; *(2)* its flank height, from the base of the dorsal fin to the origin of the gonopodium; and *(3)* its sword-length, from the distal end of the middle rays of the caudal fin to the tip of the sword. A precision of 0.5 mm was used throughout. Opponents were paired according to their general appearance, to the form of their body which had to be of a similar morph, as well as to their lateral surfaces which had not to exceed a 5% difference. The lateral surface of each fish was obtained by adding its sword-length to the product of its total length and flank height. Beaugrand & Zayan (1985) found that lateral surfaces calculated in this way, showed a 5% mean error when

compared to that measured using a planimeter. Moreover, these authors have shown that lateral surface was significantly more correlated to dyadic dominance outcome than standard length in *Xiphophorus*.

2.3 Design

The experiment consisted in having 75 different pairs composed of two adult males meet twice. On the first occasion, the future resident fish was familiarized for 3h with the meeting place where it stayed in isolation. During that time, its opponent , the future intruder, was familiarized for 3 hours with another aquarium. The two fish were then netted, and each put for 3 minutes into distinct small plastic transfer boxes before being simultaneously poured into the aquarium to which the future resident was familiar. Upon agonistic dominance of one individual over the other, the pair members were separated and returned to their respective home groups for 168 hours (7 days). After this period of separation, the same pair members were reunited and met while roles had been reversed: the initial resident became the intruder, and the initial intruder was given prior-residency. Reunification occurred in an aquarium different from the one that served for the initial meeting. Both residents and intruders were always equally and simultaneously handled. Fish were observed for a maximum of 60 minutes to determine which fish agonistically dominated the other. Agonistic behaviours were observed and served to decide which male dominated the other. We considered that a dominance relationship had been established when one fish was successful in chasing its opponent on six occasions without being threatened, attacked, or bitten in turn. This criterion has been validated by Beaugrand & Beaugrand (1991).

   After the maximum period, when dominance remained unclear, pair members were separated and returned to their home group. Their data were not considered in further analyses. This happened in only 9/85 pairs.

3.0 Results

Two-tailed statistical tests were used throughout. Binary categories were compared using the Binomial test (Z-Binomial test, in Siegel & Castellan, 1988). The probability of a given frequency repartition under the null hypothesis was specified, as in e.g. $p=.5$, where $q=1-p$.

Results are illustrated as an arborescence in Figure 1. As can be seen, there were four possible equiprobable outcomes in such a situation: RR, residents won alternately; RI, initial residents won both encounters; IR, initial intruders won both encounters; and II, intruders won alternately. Upon their initial encounter, residents defeated intruders in 76% of cases, which is more than can be expected by chance (Z-Binomial test, $p=.5$, $n=75$, $x=57$, $P<.0001$). When these 57 pairs met again 7 days later after their respective roles had been interchanged, the new-residents defeated the new-intruders in 82.5% of pairs, which is again statistically significant (Z-Binomial test, $p=.5$, $n=57$, $x=47$, $P<.0001$). Overall, prior-residence thus favoured dominance alternately in succession in 47 of the 75 pairs (63%) making outcome RR significantly more frequent than explainable by chance alone (Z-Binomial test, $p=.5$, $n=75$, $x=47$, $P<.0001$, B-test). Outcomes RI and IR total 25 cases; they corresponded to the same pair member becoming dominant on two successive occasions. This outcome did not occur more frequently than expected by chance (Z-Binomial test, $p=.5$, $n=75$, $x=25$, $P<.3$). Outcome II, which corresponds to victories obtained by males in the alternate role of the intruder occurred on only three occasions, much less than by chance alone (Z-Binomial test, $p=.5$, $n = 75$, $x = 3$, $P=.0001$).

It was important to eliminate size as a nuisance variable in the present study and to show that RR inversions occurred independently of size. Resident pair members obtaining victory were advantaged in size in 28 cases out of the 47 in the initial encounters, which does not significantly depart from chance alone (Z-Binomial test, $p=.5$, $n=57$, $x=28$, $P=.5$). In 10 other cases, opponents were of equal size. Considering only pairs in which the resident won in the first encounter, new-residents which won the subsequent encounter were more frequently the smaller pair member (Z-Binomial test,

p=.5, n=47, x=34, *P*<.0015), clearly indicating that size was not at stake on the second meeting since smaller individuals became more frequently the dominant pair members. In general, winners were not significantly larger than losers neither on the initial encounters nor on the subsequent one (Avova F=.0001, df=1/148, *P*=.99). Of the 18 residents which lost on their first encounter, 9 were smaller and 9 larger or equal than their intruder opponents, which is not significantly more frequent than expected by chance (Binomial test, *p*=.5, n=18, x=9, *P=.5*). One can thus conclude that size did not play a significant role in the present study, leaving the obtained effects to either prior-residence, or to unidentified nuisance variables.

4. Discussion

The goal of the present study was to show that it is possible to reverse dyadic dominance outcome by reversing roles of resident and intruder in *Xiphophorus*. The goal was achieved in the following steps. Knowing that 3 hours of residency in the meeting place was sufficient to influence dyadic dominance outcome, such an advantage was given to one of the opponents of independent pairs. It was noted that the individual in the resident role defeated the initial intruder in a significant majority of cases (76%). The experiment was repeated using the same opponents after a week of separation while reversing their respective roles as resident and intruder. Again, in a significant majority of cases (82%) the newly established dominance relationship favoured the new resident, in a reversed direction as compared to the initially established dominance order.

This study demonstrates that prior-residence, defined as an asymmetry between two individuals, one being familiar for 3 hours with the meeting site (residency) and the other one not being familiar (intrusion), is a powerful determinant of dyadic dominance outcome in male *Xiphophorus* when they show minimal size differences (less than 5% in lateral surfaces). This unequivocally confirms previous findings about familiarity with the meeting site in male *Xiphophorus* rivals (e.g., Zayan, 1975a, 1975b, 1976; Beaugrand & Zayan, 1985; Beaugrand & Beaugrand, 1991; Beaugrand et al., 1996).

The present research also provides for the first time an idea of the importance of nuisance factors in experiments such as the present one where an experiential factor is tested. For instance, while showing that 47 out of 75 (i.e., 62.7%) of double outcomes were most probably influenced by prior residence, it nonetheless revealed that in the remaining 28 encounters (i.e., 37.3%) the outcome was due to uncontrolled factors qualifying in the context of the experiment as noise or error. In 25 out of all 75 initial pairs, the same individual won twice in succession. This can be due to some unidentified static factor(s) and/or even to dynamic ones, which played an important role since they determined more than 33.3% of all issues. As we have mentioned in the result section, size can be eliminated as reasonable explanation here. However, other undetermined static factors might account for this. For instance, "latent aggression" probably plays an important role to decide which opponent will dominate in *Xiphophorus*. Goulet & Beaugrand (2001) have found that "latent aggression", measured as aggressive scores to successive mirror tests, was highly stable in time and significantly correlated with victory in male *Xiphophorus* pairs: the male that showed higher scores to mirror pre-tests systematically defeated its opponent, whatever its familiarity with the meeting site.

In the present research, three double outcomes (IR: 4%) could be explainable by uncontrolled dynamic nuisance factors. These are cases initially won by the intruder, but lost on the subsequent encounter while the same individual was now advantaged as resident. Uncontrolled dynamic factor(s) such as e.g., handling, abrupt change in health or mood since the last meeting, or to experience received in the home aquarium during the period separating the two successive meetings, could account for such a paradoxical results in which prior residency was repeatedly found to be a disadvantage. It is rather improbable that changes in a static factor could account for this result.

The present research would have benefited from a control group in which two intruders having met each other previously would encounter again one week later. Such a control group would have given an estimate of the spontaneous change in

dominance outcome from a first encounter to a second using the same individuals and without the influence of familiarity. Further studies are required to assess the stability of latent factors in their determining role of dominance. This could be done by repeatedly reverse respective roles, as in a time series.

6.0 References

Beaugrand, J.P., & Beaugrand, M., 1991. Prior residency and the stability of dominance relationships in pairs of green swordtail fish *Xiphophorus helleri* (Pisces, Poeciliidae). Behavioural Processes, 22, 169-175.

Beaugrand, J.P., Goulet, C., & Payette, D., 1991. Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri*: Effects of body size and prior dominance. Animal Behaviour, 41, 417-424.

Beaugrand, J.P., Payette, D., & Goulet, C., 1996. Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri):* interaction of body size, prior dominance/subordination experience, and prior residency. Behaviour, 133, 1-17.

Beaugrand, J.P., & Zayan, R., 1985. An experimental model of aggressive dominance in *Xiphophorus helleri* (Pisces, Poeciliidae). Behavioural Processes, 10, 1-52.

Goulet, C., & Beaugrand, J.P., 2001. Relation between prior agonistic intensity upon subsequent aggressive levels in winners and losers of dyads of male Green swordtail fish (*Xiphophorus helleri*). Behavioural Processes (in press).

Siegel, S. , & Castellan, N.J. Jr., 1988. Nonparametric statistics for the behavioral sciences. 2nd edition, McGraw-Hill.

Zayan, R.C., 1974. Le rôle de la reconnaissance individuelle dans la stabilité des relations hiérarchiques chez *Xiphophorus* (Pisces, Poeciliidae). Behaviour, 49, 268-312.

Zayan, R.C., 1975a. Modifications des effets liés à la priorité de résidence chez *Xiphophorus* (Pisces, Poeciliidae) : le rôle de l'expérience immédiate de dominance et de soumission. Revue du Comportement Animal, 8, 296-311.

Zayan, R.C., 1975b. Défense du territoire et reconnaissance individuelle chez *Xiphophorus* (Pisces, Poeciliidae). Behaviour, 52, 266-312.

Zayan, R.C., 1975c. Modifications des effets liés à la priorité de résidence chez *Xiphophorus* (Pisces, Poeciliidae) : le rôle des manipulations expérimentales. Z. Tierpsychol., 29, 463-491.

Zayan, R.C., 1976. Modifications des effets liés à la priorité de résidence chez *Xiphophorus* (Pisces, Poeciliidae), le rôle de l'isolement et des différences de taille. Z. Tierpsychol., 41, 142-190.
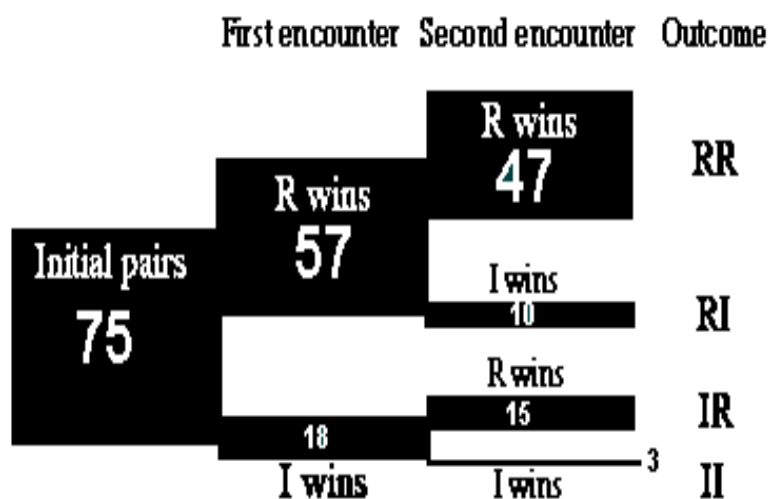

Fig. 1. Relative frequencies of victories in encounters between a resident (R) and an intruder (I). On the second encounter, initial R became I and vice-versa. Thus, outcome RR corresponds to 47 pairs in which the males in the R roles systematically obtained victory over the fish in the I roles.