

Prior residency and the stability of dominance relationships in pairs of Green Swordtail fish,

Xiphophorus helleri (Pisces Poeciliidae).

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Abstract

The stability of dominance relationships between pairs of male Green Swordtail fish was followed daily for 20 consecutive days. In one experimental sample composed of 21 pairs, dominance of one of the fish had been favoured on the first day by giving the fish prior familiarity (prior residency) with the aquarium where it was to meet an intruder. In a control sample composed of 12 pairs, two intruders met in an unfamiliar aquarium. It was expected that the advantage given to the dominant by familiarity with the aquarium on the first day would disappear as the subordinate acquired in turn familiarity with the milieu. In comparison with pairs composed of two intruders, this would show up by more frequent inversions of the initial dominance relationship in pairs composed of a prior resident and an intruder. Only two inversions occurred over the 20 days of follow up and they occurred equally in the experimental (5%) and control (8%) samples. These results confirm the great stability of dominance relationships in dyads and invalidate the hypothesis that the prior residency advantage would decay as the subordinate became familiar with the aquarium. Unexpectedly, 13 of the 66 (20%) fish died over the 20 days. Death equally occurred in both samples but 12 (92%) cases implied initial subordinates. The exception was an initial dominant which had become the subordinate pair member three days before death. Various hypotheses are suggested to account for the selective deaths of subordinates.

Key-words: Prior residency, temporal stability of dominance/subordination relationships, death of subordinates, Green Swordtail fish, *Xiphophorus helleri*.

Introduction

Familiarity with the surrounding in which the meeting takes place favours dominance in the individual over one in a place which is unfamiliar to him. Thus, the advantages of a three hour familiarization period with the future meeting place were clearly demonstrated in the Green Swordtail for individuals of equivalent size which had been put in isolation for 18 hours beforehand (Zayan, 1975a, 1965b, 1976; Beaugrand and Zayan, 1985). In these studies, the opponents were equally manipulated and simultaneously introduced into the place of residence of one of the two fish. Residency effect can therefore not be attributed to differences in manipulation or even to the fact that an opponent had been present in the residence at the time the other fish was introduced. Prior residency can thus correspond to the opponent's greater familiarity with the environment in comparison to the other partner, or even to the fact that the intruder must become familiar with the additional environment of the resident. So, "prior residency" is expressed through a very revealing tendency of the resident to dominate over the intruder. Under these conditions where dominance is favoured from the outset by a familiarity with the environment, one would expect this advantage to disappear as the intruder in turn gains in familiarity. In comparison with a control group made up of pairs of intruders, this advantage should make itself known with more frequent subsequent dominance relationship inversions in the case of pairs composed of one resident and one intruder.

In captivity, hierarchies formed by *Xiphophorus* have the reputation of remaining unchanged for small groups of two to three subjects for three weeks (Noble, 1939; Braddock, 1945) or for even for longer periods of up to six months (Noble and Borne, 1938, 1940). However, the conditions under which stability has been examined are, in general, precarious. The effectives relied upon were usually very scarce: one to three pairs at most were followed, rarely more than four social units (Braddock, 1945, 1949; Zayan, 1974). The composition of each social unit also greatly varied: some studied pairs of males, others mixed groups of three (rarely larger groups) male and/or female or even immature fish. Non-systematic observation was most often the rule, not to say anecdote. The species studied varied, *X. helleri*, *X. maculatus*, or hybrids between them being studied in aquarium.

The results obtained thus varied according to the species and composition of the social unit. In general, stability is of relatively short duration. Pairs of *X. helleri* and hybrids showed greater stability (mean of two weeks) than *X. maculatus* (one week). Social units composed of two *X. maculatus* males were noted by Braddock (1945, 1949) to be more stable (5.8 days) than units of composed of three (2.9 days) and four males (1.5 days). Female (and/or immature) pairs had a tendency to show greater stability (9.9 days) than pairs of males (5.8 days).

No study had actually followed the daily evolution of the dominance relationship in a significant number of pairs of *X. helleri*, and for several consecutive days; and data on pairs is required before turning to the study of larger group dynamics.

The goal of the present study is thus to keep track of the stability of dominance relationships in pairs of Green Swordtail for 20 days. Pairs initially composed of one resident and one intruder will be compared to others composed of two intruders. We expect that more inversions will be produced in the case where dominance is originally favoured by prior residency.

Methods

Subjects and equipment

We had at our constant disposal in the laboratory, about 1,200 adult males of the species *Xiphophorus helleri* bought at least one month earlier from the same distributor (5D Tropical Inc., Plant City, Florida, USA). These males were distributed in 9 batches of 100-150 individuals of mix sex into large 165 litre tanks measuring 90x50x40 cm each. For the purpose of the present experiment, the adult males were taken from the tanks in as random a fashion as possible.

The isolation, engagement of pairs, as well as their existence as a pair throughout the 20 days of the experiment necessitated the use of 40 identical glass aquariums measuring 30x30x15 cm and containing 13.5 litres of water each. The bottom of each aquarium was covered with 2 cm of gravel and assorted objects (shells, pieces of plastic, coloured rocks) were spread out unevenly over the gravel in order to encourage the eventual recognition of the fish's milieu of residence. Each aquarium was provided with oxygen by an air rock.

Once a day, in the morning, before observation, about 1 cm³ of dehydrated food (TetraMin Staple Food) was distributed to each pair. In addition, the same volume of live food (Tubifex) was fed to each pair once a week.

Research outline

The research was comprised of two samples or independent groups. The experimental group (**Res-Int**) was made up of 21 pairs of Green Swordtail. The individual that dominated at the end of the first day's encounter had been given a three hour prior residency over its now subordinate opponent. The control group (**Int-Int**) was formed of 12 pairs of Green Swordtail in which one member dominated the other. Neither group was familiar with the surroundings of the first encounter.

From the moment they were placed in the test aquarium, the pairs were left together in this area for 20 consecutive days. Each day, it was determined through direct observation which of the two fish dominated the other. Our criterion for a dominance relationship was met when one fish of the pair (the dominant one) succeeded in chasing its opponent six times without it being threatened, attacked or bitten in turn, and without it fleeing at the approach of the said opponent.

Size measurement

We took three measurements of each fish (to a precision of 0.5 mm): (1) the body length - the distance between the tip of the snout and the tip of the caudal fin; (2) the length of the sword - the distance between the tip of the caudal fin and the outside of the sword; (3) flank height - the greatest distance between the root of the dorsal fin and the root of the gonopodium. These measurements were taken before pair formation and measurements were obtained while the fish remained in the aquatic environment. With the aid of a mobile, mesh partition, the fish was gently immobilized against the inside glass wall of the aquarium. The anatomical positions which correspond to the aforementioned measurements were rapidly marked on the glass with a felt marker. After the fish was freed we used with a ruler to measure the distance between the marks left on the glass.

Procedure

On the first day, the fish were captured in the stocking aquariums, measured with precision and described so they could be easily recognized by the observer. Each fish was then placed in isolation in an aquarium for 17 hours.

On the second day, the pairs were formed. First of all, the fish were caught and placed in small plastic tumblers containing water from their aquarium of destination. Fish meant to meet each other are then inserted simultaneously into an aquarium. In the case of the experimental group (**Res-Int**), this aquarium was the one in which one of the individuals had spent 17 hours in preliminary isolation. This aquarium was therefore unknown to its partner. The members of the control group pairs (**Int-Int**) were not familiar with the aquarium in which their meeting was scheduled to take place. In any case, fish meant to meet each other came from different stocking tanks and did not know each other. Moreover, the two individuals were required to be of equal size, with a difference between each measurements not exceeding 10%.

Once put into the aquarium, the pairs were observed for three consecutive hours or until the dominance criterion was reached. The stability of dominance relationships was then followed daily for the next 19 consecutive days

Results

After 27 meetings between a resident and an intruder of equal size, in which the resident proved itself victorious, 21 experimental pairs were formed. These results confirm the advantage obtained by a familiarity with the environment between opponents having been subjected to a short period of preliminary isolation (Beaugrand and Zayan, 1985).

The primary importance was to eliminate differences in opponent size as the main explanatory factor in the outcome of the conflicts between residents and intruders. To do this, we compared the sizes of the winning residents to that of the losing intruders for each one of the three measurements taken: body length, flank height and sword length. The results of *t* tests for separate measurements indicated that the winners were not significantly larger in any of the measurements (body: $t=0.50$, sword: $t=0.81$, flank: $t=0.45$, $df=40$). It was the same for the pairs of intruders: the winners were not systematically favoured by size (body: $t=0.43$, sword: $t=0.59$, flank: $t=0.58$, $df=22$).

Inversions

An inversion of the dominance relationship was noted when the individual of one pair that dominated on day d became the subordinate member of the pair on day $d+1$. Only two inversions were produced during the 19 days that followed the initial encounters. One inversion was produced on the 13th day in group **Res-Int** and the other on the 17th day of observation in group **Int-Int**. In both cases, the former subordinate became the dominant of the pair and stayed that way until the end of the experiment. Therefore, these results do not support the hypothesis claiming that the advantage brought on by prior residency diminishes with time and gives way to dominance inversions. To the contrary, they clearly indicate that the dominance relationship initially established between two individuals maintains itself several days for several days afterwards.

Mortalities

Twelve cases of death occurred during the 20 days of observation: eight in the **Res-Int** group and five in the **Int-Int** group. Statistically, there were no more deaths in one group than in another. Except for in one case, all the deaths were associated with the subordinate pair member on day 1. The exception refers to an individual dominant on day 1 which turned subordinate on the 14th day, then died three days after the inversion of the relationship.

Discussion

Prior residency

The present research confirms the advantage that prior residency brings at the time of conflicts between *X. helleri* having size differences not greater than 10%. As might have been expected, this advantage is not momentary. The fact that the dominance inversion cases were not more frequent in the **Res-Int** sample than in the **Int-Int** one justifies our rejection of the hypothesis that prior residency lessens with time. On the contrary, the dominance originally favoured by prior residency or familiarity with the meeting-place is maintained for several days afterwards, despite the fact that in the meantime the intruder has acquired a comparable familiarity with the environment. Even though prior residency gives a certain advantage, *X. helleri* is not a territorial species. The dominance-subordination relationships in *X. helleri* do not show any sign of the reversibility that had been demonstrated by DeBoer and Heuts (1973) for *Hemichromis bimaculatus*. These authors showed that a dominance relationship could be inversive depending on the type of residence in which the encounter was carried out. In *X. helleri*, once the initial dominance is established between two individuals it persists even if the former subordinate is resident and it takes in its former dominant as the intruder (Zayan, 1974, 1975b; Beaugrand and Zayan, 1985).

The stability of

dominance-subordination relationships

The present research well illustrates that the initial dyadic dominance-subordination relationships between *X. helleri* males are temporally stable. As we are showing, these relationships can be maintained for 20 consecutive days. Inversions are particularly rare between pairs. This confirms the less systematic observations of Noble (1939), Noble and Borne (1938, 1940), Braddock (1945) and Zayan (1974). It is plausible that individual recognition ensures this stability. As we have shown in a preceding work (Beaugrand and Zayan, 1985), familiarity with the opponent (and the recognition of its previous status) is more important than familiarity with the environment when accounting for dominance in this species. Individual recognition would act as a bias against the inversion of established dominance relationships, a social factor which Landau (1951) introduced to account for the stability in animal hierarchies.

Mortalities

We noticed that in almost 40% of the pairs, the subordinate member died before the 18th day. The fact that it was always the subordinate member is particularly significant. Given the unexpected nature of these mortalities in relation to the objectives of the present research, we were neither watchful of the behavior, nor conducted post mortem or biological tests that might have permitted a better understanding of the cause of these deaths. Here we can only put forward a series of hypotheses which might be put to the test at the time of later more rigorous studies. **(1)** Lack of food: This explication is improbable since food remnants had to be regularly siphoned out of the experimental aquariums. **(2)** The previous state of health of the subordinates: It is possible that some fish became subordinates of the pair due to a poor initial state of health, a state that was then worsened during the experiment. **(3)** Injuries resulting from the conflict: Bites received during fights or subsequent chases, although not apparent to the observer, could have brought on death several days later. **(4)** Stress of being the subordinate: As Beaugrand et al. (1984) reported for small groups of *X. helleri* --- and we have noticed it in

informal observations in the present research when looking for the attainment of the daily dominance criterion --- the majority of dominant males systematically pursue and without interruption subordinates of the same aquarium. It is well known that animals subjected to stress present greater pathogenic risks to sickness and parasites (e.g., Hannes et al., 1984; Beden and Brain, 1982; Rasa and Vandenhoovel, 1984). In short, any of the factors already mentioned could have combined and thus contributed to the selective death of the subordinates.

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