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Asymmetrical Effects of Prior Winning and Losing on Dominance in Sticklebacks (*Gasterosteus aculeatus*)

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BAKKER, TH. C. M., FEUTH-DE BRUIJN, E. & SEVENSTER, P. 1989: Asymmetrical effects of prior winning and losing on dominance in sticklebacks (*Gasterosteus aculeatus*). *Ethology* 82, 224—229.

Abstract

Reproductive male three-spined sticklebacks, *Gasterosteus aculeatus* L., without fighting experience, were given either an experience of dominance or an experience of inferiority. They were then tested for their ability to dominate an inexperienced male in a dyadic combat either a) immediately following the experience treatment, b) 3 h later or c) 6 h later. The effect of prior losing proved to be stronger and more prolonged than that of prior winning. The influence of non-experimental factors, and possible causes for this asymmetrical effect are discussed.

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Introduction

Several studies have investigated the effects of prior experience (dominance or inferiority) on pre-existing dominance relationships. Relatively few studies have concentrated on the effects of prior experience on the probability of winning during the establishment of new dominance relationships. These effects are likely to be of more importance in many natural settings (BEACHAM & NEWMAN 1987). With few exceptions (e.g. on mice: BEVAN et al. 1960) the latter studies were done on teleost fishes: the blue gourami *Trichogaster trichopterus* (FREY & MILLER 1972), the paradise fish *Macropodus opercularis* (FRANCIS 1983, 1987), the three-spined stickleback *Gasterosteus aculeatus* (BAKKER & SEVENSTER 1983), the sword-tail *Xiphophorus helleri* (BEAUGRAND & ZAYAN 1985), and the pumpkinseed sunfish *Lepomis gibbosus* (BEACHAM & NEWMAN 1987).

A clear asymmetry in the effects of winning and losing on the outcome of future contests was shown by these studies. In *Macropodus opercularis*, *Xiphophorus helleri*, and *Lepomis gibbosus* prior experience of dominance did not change the probability of winning future contests relative to inexperienced males (isolates), while prior experience of inferiority significantly decreased that probability. In *Trichogaster trichopterus* prior experience of dominance increased the probability of winning (but see FRANCIS 1983 for criticism on the experimental design of FREY & MILLER 1972), but this effect was less than that of prior experience of inferiority. In *Gasterosteus aculeatus*, BAKKER & SEVENSTER (1983) showed an effect of prior experience on the probability of winning. In contrast with the other studies, these preliminary experiments on sticklebacks suggested a symmetry in the effects of prior winning and losing (BAKKER & SEVENSTER 1983). However, there is no obvious reason why in sticklebacks the effect of prior winning on dominance should be different from that in other fish species. In the present study therefore the experiments of BAKKER & SEVENSTER (1983) are repeated with greater numbers of fish to verify their suggestion and extended to get some idea of the time span of experiential effects on dominance.

Methods

The sticklebacks used for this study were bred from parents from an anadromous population collected at Den Helder (Netherlands). This population is polymorphic with the three lateral plate morphs (i.e. forma *trachura*, *semiarmata* and *leiura*) present. The offspring were raised in groups of about 200 fish (bred from about 10 males and 20 females) under laboratory conditions (16L/8D; 18–20 °C). Before reaching sexual maturity (at 4–5 months), they were transferred to winter conditions (8L/16D; 10–12 °C) and kept in a non-reproductive condition until required. This procedure guaranteed that the fish had no or little experience of aggressive social interactions. Before the start of the experiments, non-reproductive males were transferred to summer conditions (16L/8D, 18–20 °C) and housed singly (physically and visually isolated from neighbours) in plastic tanks (34 × 17 × 20 cm) (see BAKKER 1986). They were fed twice a day on live and/or frozen food. They were used for experiments in the first two months after completion of their first nest.

The males were given one of the following three treatments at random: experience of dominance (68 males), experience of inferiority (29 males), or no experience (97 males). A male was given an experience of dominance by introducing another reproductive male in his own tank or by introducing him simultaneously with another reproductive male, which had recently experienced inferiority, into an unfamiliar tank (same size as their home tanks). Observations were made of both fish for a period of 15 min after the last bite of the 'inferior' male to verify this status and to ensure that no dominance reversal took place (see BAKKER & SEVENSTER 1983 for a description of dominance tests). In all cases this verified dominance relationship occurred within 60 min after introduction. A male was given an experience of inferiority by introducing him into the tank of another reproductive male. The experience of inferiority also lasted 15 min after the last bite of the inferior male. The males that were given no experience were either left alone in their home tanks or transferred to an unfamiliar tank (same size as their home tank) for a similar period of time as for the other two treatment groups. They served as opponents to test the effects of prior dominance or inferiority. One or two days prior to the treatment, the males were either marked by clipping the tip of one of the dorsal or ventral spines or sham-marked by similar handling but without actually clipping the spines.

Males that were given a prior experience of dominance or inferiority were tested for their ability to dominate a randomly chosen male that had been given no prior experience. Length differences between the males were small and never exceeded 12%. Moreover, contestants were chosen irrespective of length in order to avoid possible influences of differences in body size on test outcome. In sticklebacks such an influence was found by ROWLAND (1989), but not by others (VAN DEN ASSEM

1967; SARGENT & GEBLER 1980; BAKKER 1986; FITZGERALD & KEDNEY 1987). The dominance tests occurred in tanks ($34 \times 17 \times 20$ cm) unfamiliar to both contestants and lasted 15 min after the last bite of the inferior male. The effect of prior experience of dominance was tested immediately following that experience (37 males) or 3 h later (31 males). The effect of a prior experience of inferiority was also tested immediately following that experience (9 males) or 3 h later (9 males). Since the effects of prior experience of inferiority were clear-cut and in agreement with the results of BAKKER & SEVENSTER (1983) (see Results), we kept the number of males tested low and included a third group that was tested after a waiting period of 6 h (11 males). The males that were tested after waiting, were returned to their home tanks after the experience treatment. As the outcomes of dominance tests with males that were given a prior experience of dominance in their home tanks or in an unfamiliar tank were similar, these were combined in the analysis.

Results

The results showed a clear asymmetry in the effects of prior experience of dominance and inferiority on the outcome of dominance tests against inexperienced males (Fig. 1). Both opposing forms of prior experience had an effect on the probability of winning against an inexperienced male immediately following such experiences. A prior experience of inferiority had a stronger effect: it reduced the probability of winning from 0.5 to 0. A prior experience of dominance had less effect: the realized probability of winning after such an experience increased to 0.65. Moreover, the effect of a prior experience of inferiority was more long lasting than that of a prior experience of dominance. Whereas the effect of a prior experience of dominance was undetectable after 3 h,

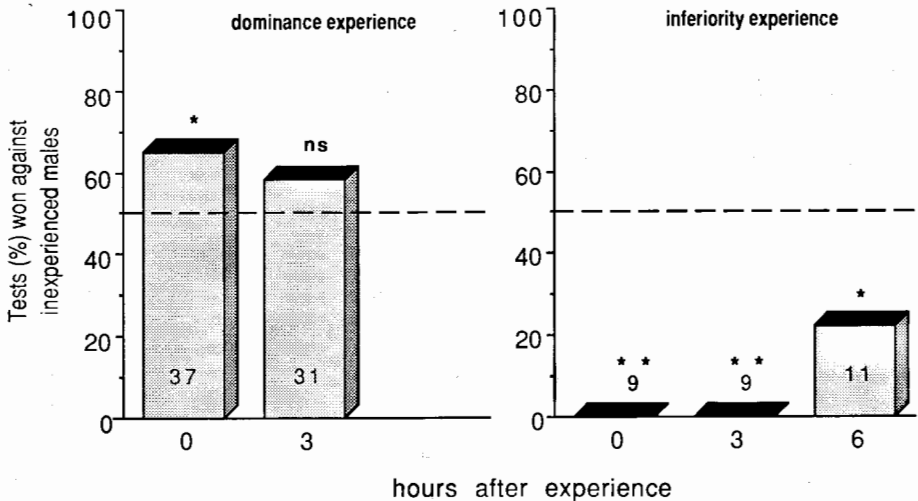


Fig. 1: Test results of dyadic combats between inexperienced males and males that had been exposed to experience of dominance or inferiority immediately, 3 or 6 h before the test. Numbers of males in each treatment group are indicated in or above the appropriate columns. ** $p < 0.01$, * $p < 0.05$, ns $p > 0.05$; p-values are for the one-tailed Chi-square goodness-of-fit test or binomial test of the null hypothesis indicated by the dotted line (i.e., no experiential effect on dominance, so half of the inexperienced males would win against experienced males)

the effect of a prior experience of inferiority was still demonstrable after 6 h, although there seemed to be some recovery. Unpublished preliminary experiments performed after longer time-intervals seemed to suggest that the effect of a prior experience of inferiority disappears after 24 h (3 out of 5 males win against an inexperienced male).

Discussion

The effects of prior experience on dominance in sticklebacks are in agreement with the asymmetrical effects of winning and losing in other fish species (see Introduction). In *Gasterosteus aculeatus*, a prior experience of dominance enhances the probability to dominate over an inexperienced male. This seems to contrast with the absence of such an effect in *Macropodus opercularis* (FRANCIS 1983, 1987), *Xiphophorus helleri* (BEAUGRAND & ZAYAN 1985), and *Lepomis gibbosus* (BEACHAM & NEWMAN 1987). However, in these studies the fish were isolated after the experience treatment for periods of 24, 3, and 1.5 h, respectively. Our fish were subjected to dominance tests immediately following the dominance experience. This raises the possibility that the increased chance of winning is not due to an experiential effect of prior dominance, but to a "warm-up" effect of the previous fighting experience (e.g. THRESHER 1978) or to behaviour or brightness of coloration associated with the previous dominance status. The males were transferred directly from a dominance treatment into a dominance test. Some of the males might not have noticed in the first instance that they faced a different opponent and continued to attack the opponent. In most dominance tests performed in this study, we scored which of the two contestants initiated the dominance fight by delivering the first bite. This revealed that eventual winners initiated the fight significantly more often than eventual losers (first bite by eventual winner in 60 tests and by eventual loser in 29 tests; χ^2 test, one-tailed, $p < 0.001$) (see also FITZGERALD & KEDNEY 1987).

Another factor that might have contributed to the enhanced chance of winning in males with a previous dominance experience is the brightness of their coloration. Winning a fight causes a temporary increase in the brightness of coloration, whereas a temporary fading and darkening of coloration is evident in losers (BAKKER & SEVENSTER 1983). Although the experiments were randomized with respect to the males' brightness of coloration as assessed before the experience treatments, a dominance experience immediately before the dominance tests probably made these males on average more brightly coloured than their opponents which had been given no prior experience. In a previous study (BAKKER & SEVENSTER 1983) we showed that the brightness of coloration is an important determinant of dominance in sticklebacks, probably through an intimidating effect on rivals (ROWLAND 1982). However, the males used in that study originated from a freshwater population. Brightness of coloration seems a less important determinant of dominance in males from the anadromous population used in the present study (BAKKER & FEUTH-DE BRUIJN in prep.; see also FITZGERALD & KEDNEY 1987 and ROWLAND 1989). The suggestion that a dominance experience immediately preceding dominance tests had a stronger effect in the study of BAKKER & SEVENSTER (1983) than in the present study, might be

ascribed to the above-mentioned population differences in the importance of brightness of coloration as a determinant of dominance.

The non-experiential factors that might have influenced the dominance ability of males immediately following a dominance experience, might also have been operative (in opposite direction) in males that were given an inferiority experience immediately preceding a dominance test. However, in the latter case the influence of non-experiential factors is overruled by experiential factors; 3 h after the experience treatment (the influence of non-experiential factors is then ruled out), the probability of winning is still 0.

Why are the effects of prior winning and losing asymmetric? The symmetry in experimental design might lead one to expect similar, but opposing effects of prior winning and losing on the probability of winning during the establishment of new dominance relationships. There are two factors that show an asymmetrical relationship with the two opposing experience treatments: physiological and conditioning factors. Numerous studies in several vertebrates have investigated the complex changes in endocrine and/or brain biochemistry that accompany social experience. These showed asymmetrical effects of winning and losing on the physiological mechanisms involved, in that winning and losing make partial demands upon different systems and if identical systems are involved, winning effects are not simply opposite changes of a magnitude similar to losing (see e.g. review by HUNTINGFORD & TURNER 1987 and references therein).

There is also an asymmetry in the learning situations associated with winning and losing (e.g. FRANCIS 1983). The eventual loser plays the decisive role in terminating the dominance fight. This has implications for learning in the two contestants. The inferior male may learn to associate fleeing (the operant response) with stopping the fight (which might be a positive reinforcement if the received bites are perceived as aversive stimulation), whereas for the dominant male the fight suddenly stops. This also stops the noxious stimulation of received bites by the inferior male, but in the dominant male this event is unrelated to preceding behaviours. Experimental psychologists create an analogous situation by a yoked-control procedure, which STADDON (1983) described as: "... Animal A is given contingent access to an activity. In equilibrium, the contingent activity for animal A occurs at a certain rate with a certain temporal pattern. The activity is then permitted to animal B, the yoked animal, at exactly the same time as animal A makes it available for himself. Thus, both animals get the same frequency and temporal pattern of access to the activity, but it is dependent on an instrumental response in one case (A), but independent of the animal's behavior in the other (B)...". For the dominant male the learning situation in a dominance fight can be compared with the situation of a yoked control in an operant conditioning experiment.

Acknowledgments

B. BOONSTRA, Th. van ES, E. C. FLACH, C. P. GROSHART, J. van der LINDEN, P. MENGARDUQUE, R. SCHIPPER, W. SMIT, H. W. de SWART, and W. TWISK assisted in collecting the data. Dr. K. KORTMULDER provided helpful discussion of the ideas on learning. Dr. G. S. LOSEY and two anonymous reviewers made useful criticisms.

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Received: June 24, 1988

Accepted: April 5, 1989 (W. Pflumm)