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DETERMINANTS OF DOMINANCE IN MALE STICKLEBACKS (GASTEROSTEUS ACULEATUS L.)

by

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Introduction

Encounters between adult male sticklebacks in reproductive condition usually lead to aggresive interactions. When a territorial male, i.e. one defending an area around its nest, meets a rival inside his territory, the owner of the territory will inexorably attack the intruder and practically always the intruder will promptly flee and leave the territory. If, however, the intruder is prevented from fleeing *e.g.* because he is enclosed in a glass tube, the territory-owner keeps attacking him with some persistence and intensity. This situation has been used as an "aggression test" to measure the aggressiveness of territorial males (VAN IERSEL, 1958; SEVENSTER, 1961; *etc.*). In such tests a male of bright colouration and standard size is put in a standard glass tube (which inevitably causes some darkening and fading of the colouration!) and presented for a few minutes to the male to be tested, at a standard distance from the nest and (by various means) at a standard height above the bottom. Variations may be imposed by the nature of the research in question. In any case the number of bites delivered at the tube towards the intruder or "test male" is counted and taken as a measure of the aggressiveness of the male concerned (at the site and time of the test). Other behaviour elements can be incorporated in the outcome of a test. In spite of some disadvantages (SEVENSTER, 1961) the method has yielded useful data in many studies of stickleback behaviour (SEVENSTER-BOL, 1962; MUCKENSTURM, 1968,

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1979; PEEKE *et al.*, 1969; HUNTINGFORD, 1976; ROWLAND, 1982; WOOTTON, 1971, *etc.*). In the experiments here presented, a modification of the standard method has been used.

The aggressiveness, as measured by such tests, declines with increasing distance from the nest (VAN IERSEL, 1958). Consequently males introduced into an area already occupied by a territorial male, will tend to build a nest, if they succeed at all, in settling at the greatest possible distance from the nest of the first occupant (VAN DEN ASSEM, 1967). Once two neighboring territories have been established, overt fighting between the two males gradually wanes and is replaced by threatening displays and other ambivalent behaviours at the border (VAN DEN ASSEM & VAN DER MOLEN, 1969), but these will not be considered in this paper.

There is one interesting form of fighting, however, with which we will be occupied in some more detail. This is the "spine-fighting", as described by VAN IERSEL, 1953, in which two males circle around each other rapidly, often with open mouth and with spines erected. A description is also found in WOOTTON, 1976, who calls it "roundabout fighting" to avoid the suggestion that the spines are actually used to hit the opponent. This suggestion is the more plausible since usually only the ventral spine directed towards the opponent is erected. Actually, however, it has never been seen that the opponent was even touched by the spine. In this roundabout fighting then, the two fishes seem to chase one another, each going for the other's tail. The fast circling which ensues may continue for many minutes without interruption, there being obviously an extremely stable and delicate mutual adjustment of the fishes' movements. Intense and persistent roundabout fighting is seen especially when two rather aggressive males meet in a situation where neither has priority over the other. In the wild (personal observations by one of us, P.S.) it is commonly observed between adjacent territories when a sharp boundary has not been established yet and a strip of no man's land is still being disputed. Further, in the general turmoil after a predator or a human observer has chased off the entire population for a while so that the returning males have to reestablish their territories. Similar intensive disputes with roundabout fighting occur in the commotion during or after an outbreak of nest raiding in which a number of neighbouring males took part. Finally, roundabout fighting is occasionally seen in the wild when for some reason an obstacle separating the territories (row of plants, stone, *etc.*) has disappeared. In a similar way it is easily provoked in the laboratory by suddenly removing an opaque partition which separated two nest-owning males. This almost invariably releases fights with fre-

quent and prolonged bouts of roundabout fighting. In such experiments still another, extremely rare, form of fighting was observed on some occasions and in one of them repeatedly. As far as we know, this has not been described so far. The two males suddenly seize one another by the mouth and remain more or less motionless for a while with the jaws interlocked like in the "mouth-fighting" of Cichlids. This "mouth-fighting" in the three-spined sticklebacks is also shown in a film on animal behaviour by SIELMANN (in the French version: "Comportements innés et acquis")[1]).

As might be predicted from the above, roundabout fighting is also frequently seen, when two nest-owning males are introduced simultaneously into a strange area which is not large enough to accommodate two territories. One male will become "dominant", and eventually build a nest, the other will give up fighting and become the "subordinate" or "inferior", hiding somewhere or keeping quiet so as not to elicit attacks from the dominant.

What determines the outcome of this type of contest? What decides who is going to be dominant? These are the central questions with which we are concerned in this article.

Material and methods

For the research reported, sticklebacks were caught from brooks in the neighbourhood of Vaassen (the Netherlands), where a population of the non-migratory forma *leiura* (BERTIN, 1925) is found. From these wild-caught specimens several generations were bred in the laboratory for use in an extensive program of genetical selection on aggressive behaviour. The results of the selection experiments will be published elsewhere and can be disregarded in the context of this article. The fish were kept under highly standardised conditions: three weeks after fertilisation the young were isolated in small plastic aquaria of 34 x 17 x 20 cm with sand, a few plants and some nest material. Temperature was kept at 18-20°C and the light schedule at 16 hours light against 8 hours dark. Food was provided twice a day and consisted of live *Tubifex* worms, live *Artemia*, live *Chironomus* larvae and frozen *Mysis* or *Artemia*.

Aggression test.

After nestbuilding (at an age of $3^1/_2$ to 6 months) the aggressiveness of the males was assessed by means of an aggression-test. In these tests a rival male was enclosed in a plexiglass cell of 20 x 6 x 6 cm, which was hung against the front of the aquarium, *i.e.* at a distance of 10 to 30 cm from the nest of the male to be tested. If the nest concerned was close to the frontpane the test cell was presented at the greatest possible distance from the nest site. The cell was left there for at least 5 minutes. If the experimental male did not approach the test male within this period, the cell was removed, but if he did the subsequent behaviour was recorded for 5 minutes from then on. The outcome of a test can be expressed as the percentage of time spent biting or bumping at the test male. In this article the mean score of four weekly tests in four successive weeks is used as an assessment of the territorial aggressiveness of an individual experimental male.

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Dominance test.

After this assessment of their territorial aggressiveness males (n) were tested in pairs as to their dominance relationships. All the possible combinations of 2 males: $\frac{n(n-1)}{2}$, were submitted to a so called dominance test, in which both males were taken out of their home tank and simultaneously introduced in a strange aquarium of the same size (34 × 17 × 20 cm) and similarly planted. Since this size corresponds roughly to the size of a minimal territory (van den Assem, 1967) rival situations, in which both males succeed in settling, were excluded. Usually a clear cut dominance of one fish over the other was established within 10 minutes after their introduction; the dominant one attacking and chasing the other, "inferior" male. Often the dominant male started searching and collecting material for nest building. The inferior, when not fleeing, stayed immobile most of the time, lying on the bottom or floating at the surface. Moreover the inferior underwent a temporary fading of its colouration. Preliminary tests had shown that this dominance relationship once established will not be reversed in the same test. Occasionally the tests remained 'undecided" for a long time: the pairs were then observed for at least 15 min., but usually much longer. After the test both males were put back in their own aquarium, and were briefly stimulated with a ripe female in a glass tube (4.5 cm in diameter). During this stimulation the colouration of the males became more intense, and could be classified on a four-point scale, according to its brightness:

1. Bright: intensely red, practically no black pigmentation.
2. Fair: much red on throat and ventral region. Caudal region with more or less pronounced black pigmentation.
3. Moderate: some red on throat only.
4. Dull: no sign of red.

The males were usually exposed to two dominance tests a day (separated by at least 4 hours), seldom to only one but never to more than two. All the males were individually marked by means of clipping the tip of the dorsal and/or ventral spines in various combinations. So far no effects on behaviour have been found to correlate with this spine clipping.

Results

When individuals taken from a batch of isolated territorial stickleback males are submitted to dominance tests pairwise and in all possible combinations, it appears that the males can be arranged in a linear order of dominance. Only occasionally exceptions to linearity are found (such as A dominant over B, B over C, but C over A). The rank of a male in the linear order reflects in a quantitative way his capacity to become dominant over others, and this capacity will be called for the sake of brevity his "dominance" or "rank".

A priori there are two extreme possibilities to explain the origin of such an order of dominance among animals which have not met before.

a. Originally the capacity to gain dominance is practically identical in the males concerned, and it is a matter of chance who is going to win and who is going to lose in a first test, when both males are still unexperienced. However, winning in this first test increases the chance of winning in

subsequent tests, whereas losing increases the chance of losing again. In this way it could be assumed that the experience of individuals would accumulatively determine their eventual ranks.

b. The capacity to gain dominance is, from the beginning, a characteristic of each individual animal, as determined by its condition. In the extreme form of this view there would be no influence of experience in previous tests.

In reality it appears that both views are relevant. In order to disentangle the effects of previous experience from those of the individual condition special experiments were carried out.

Experience.

The influence of experience is revealed by experiments in which males were given different experiences immediately before a dominance test. Some males, arbitrarily chosen, were put in the territory (= tank) of another male and left there for 15 minutes. All of them were defeated and chased about until they were taken out again: experience of inferiority. Other males were left in their own territories (= tanks) and were given another male as an intruder for 15 min. All of these were victorious and chased the intruder until he was taken out: experience of dominance. Both groups were then given dominance tests with an unexperienced rival and the outcome in Table 1 shows that experience plays an absolutely decisive role in such tests. Awaiting further evidence, we take it for granted that "experience" can be taken in its usual behavioural sense, though in the case of inferiority it is just conceivable that the experience involved some degree of physical damage which might be responsible for a defeat in the dominance test. All we can say is that physical damage was not visible.

The influence of experience, even in less extreme circumstances and over longer time lags, is apparent from an analysis of the scarce deviations from linearity in the order of dominance. In Table 2 data are presented from 7 groups (used in our genetical selections) in which the order of dominance was determined. As we have explained, nearly always some tests are found in each group which do not fit the linearity of the dominance order. In the 7 groups of Table 2 a total of 23 tests with aberrant, "wrong", results was found. We can leave out 3 of them because they were first dominance tests, and therefore involved unexperienced males. Of the remaining 20 tests, however, 8 can be ascribed to "wrong" inferiority as a result of experience with inferiority in the preceding test against one of the three most dominant males in the group.

TABLE 1. Effect of imposed experience on a male's success in a dominance test against an unexperienced male

Experience of	Test against unexperienced ♂		
	dominant	inferior	undecided
Dominance	5	0	0
Inferiority	0	7	1

(Fisher test, $p<0.01$).

TABLE 2. Number of tests deviating from linearity ("wrong" tests) and number of undecided tests (no aggression or flight within 15 min. after introduction)

Group	Number of ♂♂	Number of tests	"Wrong" tests		Undecided tests	
			n	%	n	%
A	8	28	1	3.6	0	0.0
B	12	66	7	10.6	0	0.0
C	14	91	3	3.3	2	2.2
D	10	45	4	8.9	0	0.0
E	16	120	5	4.2	16	13.3
F	10	45	3	6.7	2a	4.4
G	10	45	0	0.0	5	11.1

A: generation 0; B, D, F: generation 1, 2 and 3 of DH-line; C, E, G: generation 1, 2 and 3 of DL-line; a: males still roundaboutfighting after 45 min.

This seems convincing evidence that a severe defeat temporarily decreases a male's dominance, apparently over an interval of 4 hours or more.

Genetical factors.

Experience is not the only factor determining the order of dominance. Evidence that other factors are involved is found in our genetical selections. The 7 groups of males in Table 2 represent generations of selected lines. Group A is a sample of the unselected populaton from which we started, groups B, D and F represent the successive generations of a line selected for high dominance (DH), whereas C, E and G represent the line of low dominance (DL). In Table 2 it is seen that the number of "wrong" tests is larger in the DH-line than in the DL-line. At the same time "undecided" tests in which no aggression or flight was seen within 15 minutes, were only found in the DL-line: the 2 "undecided" tests in the

TABLE 3. Spearman rank correlation coefficient between dominance rank and territorial aggression score

Group	Correlation rank-aggression
A	0.25^{ns}
B	0.07^{ns}
C	0.51^{*}
D	-0.09^{ns}
E	0.16^{ns}
F	0.40^{ns}
G	0.68^{ns}

(* = $p<0.05$, ns = $p>0.05$).

TABLE 4. Spearman rank correlation coefficient between dominance rank and colouration score

Group	Correlation rank-colouration
D	-0.67^{*}
E	-0.78^{**}
F	-0.61^{*}
G	-0.71^{*}

(** = $p<0.01$, * = $p<0.05$).

DH-line are different, for here the competing males after 45 minutes were still involved in roundabout fighting. We are not going to venture upon a specific explanation of these phenomena, but in any case such differences in selected lines point to a partly genetical basis of the outcome of the dominance tests. Our genetical analysis, reported elsewhere (BAKKER, in prep.), amply confirms this conclusion: under our experimental circumstances heritability of dominance is high. Obviously experience is not the only factor determining dominance. Other, partly genetical, factors must be involved.

Aggression.

It seems a plausible assumption that territorial aggressiveness, as measured in the aggression tests, will be involved. In Table 3 the relevant data are found: the correlation of the score in the aggression tests (expressed as % of test time spent biting or bumping at the intruder) with

TABLE 5. Influence of experience on the dominance of the brighter coloured male in a dominance test

Experience of the two ♂♂		Number of dominance tests in which brighter ♂ becomes		Ratio
		dominant	inferior	
no	no	14	1	14.0
+	—	49	3	16.3
—	—	20	4	5.0
+	+	19	8	2.4
—	+	3	3	1.0

no no: neither of the males has experience; + —: the brighter has won, the duller has lost in the previous test; — —: both have lost in the previous test; + + : both have won in the previous test; — + : the brighter has lost, the duller has won in the previous test.

the dominance (number of rank in the linear order of dominance) is presented for each group separately. The correlation is erratic, varies between groups and is not significant in most groups. The conclusion must be that territorial aggression may play a role, but certainly does not fully predict an animal's rank in the dominance order.

Colouration.

Another factor influencing dominance was suggested to us by a striking difference in colouration between the two lines selected for high and low dominance. The mean score on our colouration scale was higher (= duller!) for the low line DL as compared to the high line DH, especially in the later generations. A closer analysis reveals that even within generations there is a significant correlation of ranknumber and colouration (Table 4), the brighter coloured males being the more dominant.

Further analysis of the dominance tests in these same groups brings to light the interaction of the male's colouration with the nature of his experience in the preceding dominance test, as summarized in Table 5. When both males are unexperienced (as is the case in first dominance tests) the brightest male is almost certain to win. Similarly when the brightest male has won in his previous test and the dullest has lost his last contest, the brightest also wins. If experience in the previous test has been the same for both, the brighter male still has a good chance to win, especially if both have lost the previous encounter. When colouration is counteracted by experience the influence of colour seems to be outweighed by experience, though unfortunately the number of cases is rather too small to be conclusive. As an addition to Table 5, finally: if

TABLE 6. Incidence of roundaboutfighting (+ R) in relation to colouration and experience as the fraction of tests in which R occurs (for DH-line)

Colouration dominant-inferior	Experience				
	no	+ +	— —	+ —	— +
1-1	—	4/4	—	0/1	—
1-2	1/1	5/7	0/2	1/8	1/1
1-3	1/1	—	0/1	—	—
1-4	—	—	0/2	0/1	—
2-1	1/1	2/2	0/2	1/2	1/1
2-2	4/4	7/8	2/11	1/10	4/4
2-3	2/2	—	0/2	0/4	—
2-4	1/1	—	0/2	0/3	—
3-3	—	—	—	—	—
3-4	—	—	—	—	—
4-4	—	—	—	—	—
Total	10/10 100.0%	18/21 85.7%	2/22 9.1%	3/29 10.3%	6/6 100.0%

no: neither has experience; + + : both have won in the previous test; — —: both have lost in the previous test; + —: the dominant has won, the inferior has lost in the previous test; — + : the dominance has lost, the inferior has won in the previous test. Under colouration the score of the dominant is listed first.

there is no difference in colouration between the two males, the previous winner will in general win against the previous loser: 24 out of 30 tests (ratio 4.0).

So the two factors obviously interact in a predictable manner and each by itself is an important determinant for the outcome of a dominance test. It would seem that this outcome for the greater part can be accounted for by the three factors mentioned: colouration, experience and aggressiveness. In the following paragraph some more details in confirmation of this picture will be presented.

Roundabout fighting.

The conspicuous roundabout fighting described in the introduction is frequently seen in dominance tests. Since the persistent circling is highly symmetric in that both males are as it were constantly attacking one another with equal intensity, the occurrence of such fights seems to imply that the two males are well-matched. This is supported by the nature of the situations in which it occurs (see introduction). Its occurrence in the dominance tests, appears to be directly related to the experience of the

TABLE 7. Incidence of roundaboutfighting in relation to colouration and experience (for DL-line)

Colouration dominant-inferior	Experience				
	no	+ +	— —	+ —	— +
1-1	—	0/1	—	—	—
1-2	1/1	4/4	0/1	0/3	0/1
1-3	0/1	1/1	0/2	1/1	—
1-4	—	—	0/2	0/4	—
2-1	—	2/3	—	—	—
2-2	1/2	5/12	0/4	1/9	1/2
2-3	1/1	2/3	0/4	0/5	—
2-4	3/5	5/7	0/3	1/14	0/1
3-1	—	0/1	—	—	—
3-2	—	1/1	—	0/1	1/1
3-3	1/1	—	—	0/3	—
3-4	0/2	—	0/1	—	—
4-2	—	0/1	—	—	—
4-3	—	—	0/2	0/1	—
4-4	—	—	0/2	0/1	—
Total	7/13	20/34	0/21	3/42	2/5
	53.8%	58.8%	0.0%	7.1%	40.0%

Legends: see Table 6.

male eventually losing the contest. If this loser had lost also in the previous test roundabout fighting is rare, but if he had won in the previous test or had no experience yet, roundabout fighting becomes very likely: Table 6 for DH-line, Table 7 for DL-line. There appears to be very little influence, if any, of colouration. Nevertheless, the incidence of roundabout fighting is higher among brightly coloured males than among duller males, but this can be ascribed to the large number of + + combinations (both males have won the previous test) among the brighter males.

Comparison of Tables 6 and 7 reveals a difference in the incidence of roundabout fighting between the selected lines. The overall frequency of roundabout fighting in the DH-line is 39/88 (44.3%), and in the DL-line 32/115 (27.8%). The difference is significant at the 5% level: χ^2-test. When "undecided" tests and "undecided" previous tests are also taken into account, the difference becomes even more pronounced (40/90 against 34/165), because of the many undecided tests in DL.

Finally there is a relation between the occurrence of roundabout fighting and the mean duration of the dominance tests, *i.e.* the mean time it takes before dominance is established. When roundabout fighting oc-

TABLE 8. Incidence of roundaboutfighting (+ or -R fights) and mean duration of decision (in sec.)

Test	Mean duration of decision	
	D + F	E + G
+ R fights (first tests)	1000.0	501.4
+ R fights	315.0	212.4
- R fights	41.0	120.4

curs, the duration of the test is much prolonged: Table 8. Especially in first encounters roundabout fighting can be long-continued. This phenomenon is most obvious among the males selected for high dominance (DH).

Discussion

First of all in this discussion, some remarks on our use of the words "dominance" and "rank" are in place. The concept of the linear dominance hierarchy was developed by SCHJELDERUP-EBBE (1922) for chickens. It applies and should be restricted to a group of individuals living (constantly or part of the time) in a common area, and recognising one another individually. When groups are too large, stable hierarchies are not established, because individual recognition fails and disputes continue (SCHJELDERUP-EBBE, 1922).

Such stable hierarchies, in the stricter sense, are not found in the three-spined sticklebacks. Some sort of hierarchy was described by VAN DEN ASSEM (1967) in a stable situation with a number of rivalling territorial males. He found a general, positive correlation between the size of the territory and the number of attacks initiated by the owner of that territory. Those with the largest territory were seldom attacked by their neighbours, those with the smallest territory did not initiate attacks and were continuously on the defensive.

For the moment, these hierarchies should be well distinguished from the linear order of dominance as we have used, though they do probably correspond to some extent. Between tests, we kept the males in isolation and, in the tests, each individual male was confronted with another particular individual only once. So individual recognition was ruled out in our concept of dominance. Confrontations were unique and the rank of a male in our linear order of dominance was purely determined by the

number of confrontations in which he won and in which he lost. It does not seem unlikely, however, that this order of dominance would be reflected in the hierarchy of a rival situation like those described by VAN DEN ASSEM (1967).

It was shown that the colouration of a male three-spined stickleback is an important determinant of his rank in the order of dominance. For the moment we leave aside the unlikely possibility that an unknown factor predictably correlated with colour is responsible for the male's rank. SEMLER (1971) however studied the effects of artificially coloured males on females in courtship. Encouraged by his article we did a few pilot experiments with males artificially coloured according to his recipe. In 14 dominance tests one of the males randomly chosen was painted red with with nail-polish (Yves Rocher, Papaye CO854202), the other was treated with colourless polish (Carmen): in 8 of the tests the red male won, in 2 the colourless, and 4 tests were undecided. The tests were still unsatisfactory: the colour was rather too flashing, the paint came off during the tests and the fish seemed to be ill affected. Yet, the evidence seems to support our conclusion that colour as such is the effective factor. This reminds us of the classical examples of colour as an indicator of social status. MARLER (1955) proved experimentally that the difference in colour between the sexes in the chaffinch (*Fringilla coelebs* L.) is responsible for the difference in dominance in mixed flocks. Similarly in the Harris sparrow (*Zonotrichia querula*) variations in the amount of black on throat and crown are important determinants of social status (ROHWER, 1975), but there is an interaction with the accompanying behaviour. If subordinates were dyed and given larger black bibs, their social status did not increase. Instead they were attacked and persecuted. If testosterone was administered to subordinates, their status did not increase either. Only if subordinates were both dyed and injected with the hormone, their social status dramatically increased (ROHWER & ROHWER, 1978). The congruence between the behaviour and the colouration appeared to be the crucial factor. The colouration in itself seems to elicit aggression in the conspecific opponents, but if supported by the appropriate behaviour its intimidating effect has the upper hand.

A similar situation seems to obtain in the three-spined stickleback. In several studies the "releasing" effect of the red belly has been emphasized strongly (TER PELKWIJK & TINBERGEN, 1937; TINBERGEN, 1948, a.o.): dummies with a red underside were attacked more frequently and more intensively by a territorial male than dummies without any red. But there are also many reports of similar investigatisons where an eliciting ef-

fect of the red colour could not be demonstrated (PEEKE *et al.*, 1969; MUCKENSTURM, 1968, 1979). Recently ROWLAND (1982) repeated such dummy presentations once more and convincingly demonstrated an intimidating effect of red dummies as compared to grey dummies. Consequently the latter were attacked more. This is in agreement with an explanation given by SEVENSTER (1949) for similar phenomena in the ten-spined stickleback, *Pungitius pungitius* (L.). In this species males in reproductive condition become dark, or even almost black. Dark dummies released most bites in territorial males, as compared to other colours, but absolutely pitch-black dummies did not release as much biting in some males. It was not that these males did not pay much attention to such dummies, but they were obviously inhibited to approach them, so that it was conluded that an intimidating effect of black in these tests outweighed the releasing effect. This principle might well account also for the disagreement in the reports on the three-spined stickleback (see ROWLAND, 1982). The intensity of the colours used on the dummies cannot be read from the publications concerned. Some of TINBERGEN's early paraffin dummies are still available in our laboratory. They were painted with shellack and powder of various colours. This produced a rather transparent, soft colour without striking contrasts. From some illustrations in the literature we get the impression that other authors may have used dummies with more saturated colours and more marked contrasts, and therefore may have increased their dummies' intimidating effects. Somehow future workers in this field should make an effort to specify their dummies in this respect as accurately as possible. The experience of the males may be another source of variation in dummy experiments as our data in this article would seem to predict. Whether the experimental male has been exposed to conspecifics or has been raised in isolation, whether he has been provoked to fight a dummy before or alternatively has been beaten up with a dummy, may have consequences for his future reactions to dummies. This has not been investigated in a standardised way, but seems to follow from many observations. The most extreme form of the influence of experience on later reactions to dummies is the conditioned reaction to the green tip of a rod (courting or fighting as the case may be) in sticklebacks (SEVENSTER, 1968, 1973). Finally there are quite a few males which fail to react to dummies for reasons not even vaguely understood.

The intimidating effect of the colouration may well account for the consistent correlation of rank with colour in our dominance tests (Table 4). When in a first dominance test two unexperienced males are

simultaneously placed in the strange tank, which is new to both, the brightest male is generally the first to attack the other, duller one, and is then usually going to win. Since there is no experience (leaving aside the confrontation with the test male in an aggression test) and since the correlation of dominance with aggressiveness is but erratic, the most likely explanation seems to be that the duller male is intimidated by the sight of his bright opponent, whereas the latter is not (as much) intimidated by the sight of the duller one. Consequently one would expect the brighter male to initiate the attack. From then on experience becomes an additional factor in the rest of the encounter and in later encounters. The detailed course of the behaviour in the dominance tests has yet to be studied (with more easily recognizable individuals!) before this explanation can be confirmed. However, the overall effect of colour and experience as the result of an interaction of two separate factors is well established by the data in Table 5.

The possible role of aggressiveness, as assessed in our aggression tests, is more difficult to trace in the available data. For one thing, the analysis is handicaped by the uncertain relationship of colouration and aggressiveness: Table 9. In one line (DL) the two factors seem to be correlated (though not significant) and the brighter males tend to be more aggressive. In the other line (DH) no such correlation can be demonstrated. Since the groups, even within DL, are not at all homogeneous the evidence remains inconclusive, but in any case the correlation, if any, is not very important. Therefore we have tried to play off colour against aggressiveness like we did with colour and experience.

In Table 10 first dominance tests are arranged according to the difference in colour of the two males and/or to their difference in aggressiveness. When colours are different, it appears that with one exception the brightest always wins the contest, even when he has the lowest score for aggressiveness (4 out of 10, in 2 cases aggression scores are equal). Even when colours are equal, it seems that aggressiveness does not decide the outcome of a contest: in 1 out of 3 cases the most aggressive wins, but in the other 2 the aggression scores are equal, and in 2 more cases the contest remains undecided, even though in 1 case there is a pronounced difference in aggressiveness.

Though further evidence is certainly needed, our final conclusion is that aggressiveness as defined and measured by us, plays an almost negligible role in determining the outcome of a dominance test, which is easily masked by colour and experience. This conclusion is in agreement with the fact that our genetical selection for dominance has not brought

TABLE 9. Spearman rank correlation coefficient between territorial aggression score and colouration score

Group	Correlation aggression-colouration	
D	+ 0.35	+ 0.00 (DH-line)
F	- 0.51	
E	- 0.26	- 0.36 (DL-line)
G	- 0.69	

All coefficients are not significant.

TABLE 10. Possible influence of territorial aggression score on the outcome of first dominance tests (Groups D, E, F and G)

Colouration		Aggression	
dominant	inferior	dominant	inferior
1	2	31.8	60.3
2	4	38.2	62.0
3	4	24.7	59.5
2	3	27.9	41.6
2	4	32.9	34.6
2	1	52.6	45.4
1	3	70.6	44.7
2	4	72.1	6.1
2	4	30.0	10.2
2	4	44.6	43.3
2	4	57.6	26.7
2	3	47.2	27.2
1	2	50.8	7.4
2	2	62.2	48.7
2	2	57.7	59.4
2	2	45.4	47.7
Undecided			
2	2	43.3	37.7a)
2	2	35.6	18.7b)

a: males still roundaboutfighting after 45 min; b: no sign of aggression after 20 min.

about a clear shift in aggressiveness, but has caused a conspicuous change in colouration.

In the introduction "mouth-fighting" was described. It was a surprise to find that this rare type of fighting was observed on several occasions in the dominance tests of DH and DL, but always in connection with

roundabout fighting. Remarkably, both types of fighting showed little, if any, influence of colouration, but were strongly dependent on the experience of the eventual loser. It has already been mentioned that roundabout fighting is more frequently observed in the DH line. For these regularities no explanation can be offered.

Summary

When two males of the three-spined stickleback (*Gasterosteus aculeatus* L.) in reproductive condition are placed in a tank of small size, one becomes dominant over the other in a very short time. In this way a group of isolated reproductive males were tested pairwise on their capacity to become dominant. It appeared that the males could be arranged in a linear order of dominance. Their rank was to some extent correlated with their territorial aggressiveness as assessed in other tests. Their experience in previous dominance tests played a more important role. The brightness of their colouration, however, was probably the most consistent and decisive determinant of dominance. The interaction of colour and experience could be traced in the outcome of the dominance tests. The occurrence of roundabout fighting is discussed.

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