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The influence of recent experiences on the conquest of territory in Padogobius martensi (Teleostei, Gobiidae)

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Zoologia. — The influence of recent experiences on the conquest of territory in Padogobius martensi (*Teleostei*, Gobiidae) ^(*). Nota di GILBERTO GANDOLFI E GIUSEPPE NOTARBARTOLO, presentata ^(**) dal Socio S. RANZI.

RIASSUNTO. — Nelle competizioni per la conquista di un territorio individuale tra due *Padogobius martensi* (Teleostei, Gobiidae), di dimensioni simili ed uguale sesso, il pesce che ha avuto una recente esperienza di vittoria su un conspecifico di taglia minore ha una probabilità significativamente più elevata di prevalere nei confronti di quello che ha avuto una recente esperienza di sconfitta da parte di un conspecifico di taglia maggiore. Nelle competizioni tra individui di sesso diverso, studiate fuori dal periodo riproduttivo, il risultato è influenzato, altre che dalle recenti esperienze dei pesci, anche dalla maggiore aggressività dei maschi. Avendo avuto cura che le esperienze subite dai contendenti prima della competizione per il territorio non comportassero danni di tipo fisico, è possibile confermare, anche nel caso di questa specie, che condizionamenti di tipo sociale possono influire sul livello di aggressività.

Among the various factors that influence the aggressiveness of an individual, the effect of previous submissive or dominant experiences play an important role in the establishment of dominance hierarchies. Studies on mammals [I, 2, 3, 4, 5, 6], on birds [7], on teleostean fish [8, 9] and on invertebrates [I0, II, I2] have shown that positive or negative experiences can respectively increase or diminuish the chances an individual has of subsequently being the dominant member of a pair or a group. In the species studied in the above-mentioned experiments, the social structure can be defined as Etkin's [I3] "social dominance" (corresponding to Schjelderup–Ebbe's "peck order" [I4]) or "partial dominance". Whereas in social dominance there is an organization based on individual recognition which leads to a decrease in conflict within the group, once the social rank of each member has been established, this occurs at a lesser degree in cases of partial dominance. It is a question of two different levels of organization in animals that live in groups.

Regarding teleostean fish there is substantial agreement between the results [8] on the green sunfish, *Lepomis cyanellus*, and those [9] on the anabantoids *Trichogaster trichogaster* and *Macropodus opercularis*. In both cases, reversal of dominance in pairs of fish of the same size took place after one or both of the fish had undergone appropriate experiences with conspecific individuals. On the contrary, in pairs of young male *Xiphophorus* hybrids (*X. helleri* \times *X. maculatus*), there was no reversal of dominance even after

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the dominant member had undergone submissive experience with a larger partner [15]. A further example of aggressive behaviour being modified by previous social experiences is given by the anabantoid *Betta splendens* [16]. The male that has undergone submissive experiences gives an operant response reinforced by its own image in a mirror with significantly less frequency than the male with dominant experiences.

The aim of the present study is to control the effect of positive and negative experiences in a species in which aggressive behaviour is not related to the establishment of hierarchies but to individual acquisition of a territory, the conquest and defence of which is a means of subdividing the available resources among the individuals living in a given area.

In our experiments we used *Padogobius martensi* ⁽¹⁾, a small teleostean fish which is very frequent in some rivers of the Po basin. We chose this species for its great adaptability to small aquaria, and its marked territoriality and aggressiveness. Some of our specimens were caught in streams near Milano and the others in the Taro river. The fish were kept in an irregularly shaped fiberglass holding tank (bottom area 2.2 m^2). In order to imitate its natural habitat, the water was 10–15 cm deep and the bottom was covered with sand and large pebbles. A filter driven by a centrifugal pump (480 litres per hour) purified the water and created a slight surface current. The fish were fed daily with live *Tubifex* and dried food. Alternate 12-hours periods of light and dark were regulated automatically. The water temperature was kept between 12 and 15°C.

The experiment began with the daily removal of about 20 fish of similar size from the holding tank. Under anesthesia (Sandoz MS 222 at a concentration of I : 15,000), the sex was determined from the shape of the genital papilla, which is conical in the male, and rather blunt in the female, as in other species of the same family [18, 19, 20]. The length of the fish was measured, and six pairs of fish were chosen, allowing a difference in size between members of a pair not exceeding I mm. The caudal fins were clipped in different places for the purpose of identification, and subsequently each fish was isolated in a small container till the effect of the anesthetic had worn off.

One member of each pair was designated at random as TA, and the other as TB. Each TB-fish was placed for 24 hours in a little aquarium inhabited by a large (70-75 mm) male *P. martensi* (A-fish), whereas each TA-fish was placed for the same period with a small (30-35 mm) *P. martensi* (B-fish) taken from the holding tank. The twelve identical acquaria $(20 \times 35 \times 20 \text{ cm})$ used for this purpose were made of glass with steel supports, with a sand bottom and a filter. In order to avoid the possibility of physical damage

(I) Padogobius martensi (Günther) (= Gobius fluviatilis Bonelli). A careful examination of the morphological, meristic, and morphometric characteristics of this fish let us maintain the old specific nomenclature despite the controversial fact that Berg [17] considered all fresh-water species of Gobiidae of the Rodano-Padano district to be synonymous with Padogobius panizzai (Verga).

from repeated attacks, a plate of opaque plexiglass, propped against one of the shorter sides of the aquarium and immersed several centimeters in the water, provided a hiding place for the fish that would be expelled from the bottom. In any case, the difference in size between the TB-fish and A-fish on one hand, and the TA-fish and B-fish on the other, was so great that, not only did the larger fish dominate as expected, but in most cases it did so without fighting. At the aggressive displays of the larger fish, the smaller one recognized its inferior status immediately or at least after a single attack. Since the territory was limited to the bottom, the fish that took possession of it usually did not attack the other when hiding behind the plexiglass plate or staying against the walls of the aquarium.

After 24 hours, tha TA- and TB-members of each pair were simultaneously transfered into plexiglass aquaria of the same size as the preceding ones. Anyway, differences in detail (i.e. they lacked the steel supports and the siphon of the filter and had a lighter sand on the bottom) were enough to differentiate the new territory with the one in which the fish had just experienced victory or defeat.

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Comparison of size (mean length) of fish with positive (TA) and negative (TB) experience in the four experimental series.

	$\begin{array}{ c c c } MM & Series \\ TA(\mathcal{J}) & TB(\mathcal{J}) \end{array}$		FF S TA(우)	Series TB(♀)	MF S TA(3)	Series TB(♀)	FM Series	
Mean length (mm)	49.81	49.66	50.66	50.47	46.22	4631	46.62	46.44
Standard deviation	±8.13	±8.20	± 9.05	±8.92	± 7.86	± 7.71	± 7.38	±7.30
<i>t</i>	0.049 (*)		0.043 (*)		0.056 (*)		0.031 (*)	
d.f	30		30		30		30	
(*) <i>p</i> > 0.05.	i e se			÷		·		

Altogether 64 pairs of *P. martensi* were tested, consisting of 4 series of 16 pairs: MM series (male TA and male TB), FF series (female TA and female TB), MF series (male TA and female TB), FM series (female TA and male TB). The experiments took place at least four months before the mating season of *P. martensi*, in order to exclude the complication of courting during the tests.

The outcome of the encounters between the TA- and TB-fish was easily established. After a period of ritualized fight with aggressive displays and reciprocal attacks, the more aggressive fish drove the weaker one from the bottom. The latter was forced to remain attached to one of the walls of the aquarium by means of its pelvic fins. In only few cases was there an unclear

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outcome or no immediate aggressive behaviour, and this occurred only in FF series. In such cases, *Tubifex* were given to stimulate aggression, and an increase in combativeness ensued immediately.

There was not any significant difference in size between the TA- and TB-fish of the same pair (Table I) or between the fish that eventually conquered the territory and the excluded ones (Table II). Supposing that the previous experiences of TA- and TB-fish had no effect on the outcome of their subsequent encounter, as the paired fish were almost identical in size, the probability of either fish conquering the territory should be the same. The amount of the 64 experimental encounters permit us to reject this hypothesis and to conclude in favour of a significant effect of the preceeding experiences. In fact, out of 64 winners, 45 had just undergone positive experiences and 19 negative (p = 0.009).

TABLE II.

Comparison of size (mean length) of fish that conquered the territory (W) and those that were defeated (D) in the four experimental series.

	MM Series		FF Series		MF	Series	FM Series	
	W	D	W	$\mathbf{D}^{(1)}$	W	D	W	D
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Mean length (mm)	49.75	49.72	50.62	50.50	46.25	46.28	46.47	46.59
Standard deviation	±8.13	±8.21	±9.02	± 8.95	±7.83	± 7.74	± 7.33	± 7.34
t	0.029 (*)		0.021 (*)		0.034 (*)		0.002 (*)	
d.f	30		30		30		30	
(*) <i>p</i> > 0.05.		• .	-	,-î		· · ·		

Considering the four experimental series separately, further information can be gleaned. Whereas the effect of recent social experiences on subsequent encounters between two males (MM series) or two females (FF series) is clear-cut, encounters between fish of different sexes are influenced by the difference in aggressiveness between males and females. In the MM series, the territory was won by 12 TA-fish and 4 TB-fish (p = 0.038); in the FF series, by 13 TA-fish and 3 TB-fish (p = 0.011); in the MF series, by 13 TA-fish and 3 TB-fish (p = 0.011); and in the FM series, by 7 TA-fish and 9 TB-fish (p = 0.773). Table III gives the length of the opponents and the results of their aggressive encounters.

A comparison of series MF and FM shows a significant difference in the results (p = 0.033, Fisher exact probability test), from which it can be seen that males with a previous positive experience dominate females with a negative experience more often than females with a positive experience dominate males with a negative experience.

TABLE III.

Total length (mm) of fish with positive (TA) and negative (TB) experience, and fish that took possession of the territory ^(*) in each pair of the four experimental series.

Pair	MM Series		FFS	Series	MFS	Series	FM Series	
no.	TA(3)	TB(3)	TA(♀)	TB(Q)	TA(3)	TB(♀)	TA(Q)	$\mathrm{TB}(\mathcal{J})$
I	52.5 (*)	53.0	47 · 5 ^(*)	47.0	43.5	43·5 ^(*)	44.0 (*)	44.0
2	58.0 (*)	58.0	49.0 (*)	49.0	50.0 (*)	50.5	54.0	54.0 (*)
3	41.5	4 ¹ ·5 ^(*)	52.0 (*)	51.0	45.0 (*)	44.0	56.0	55·5 ^(*)
4	62.5	62.0 (*)	50.0 (*)	49.5	54.0 (*)	54.5	48.0 (*)	47.0
5	67.0 (*)	67.0	51.0	50.0 (*)	42.0 (*)	42.0	52.0 (*)	53.0
6	61.5 (*)	61.5	57.0 (*)	57.0	46.0 ^(*)	46.o	56.0	55·5 ^(*)
7	44.0 (*)	44 · 5	48.0 (*)	48.5	40.0	40 5 (*)	43.0 (*)	42.5
8	40.0 (*)	39.5	44.0 (*)	45.0	41.5 (*)	41.5	38.0	37 · 5 ^(*)
9	46. o (*)	45.5	41.0 (*)	40.5	36.0 (*)	36.0	40.0	40.0 (*)
10	45.0 (*)	45.0	38.0 (*)	37 · 5	59.0 (*)	58.5	38.5 (*)	39.0
II	47.0 (*)	46.0	40.5	40.5 (*)	34·5 ^(*)	35.0	36.0	36.0 ^(*)
I 2	43.5	42.5 (*)	70.0 ^(*)	69.0	65.0 ^(*)	64.5	61.0 ^(*)	60.5
13	49.0 (*)	48.5	58.5 (*)	58.5	46.0	46.0 ^(*)	44.0	44.0 (*)
14	48.0 ^(*)	48.0	60.5 ^(*)	60.5	47 · 5 ^(*)	48.0	48.0	47 · 5 ^(*)
15	47.0	47 · 5 ^(*)	62.5 (*)	62.5	44·5 ^(*)	45.0	42.0 ^(*)	42.0
16	44.5 (*)	44.5	41.0	41.5 (*)	45.0 (*)	45 · 5	45 · 5	45.0 (*)

The conclusion that can be drawn about *P. martensi*, i.e. a significant influence of recent experiences on the conquest of territory, closely resembles those [9] regarding anabantoids. It is more difficult to compare our data with observations on *Xiphophorus* hybrids [15], or on *Lepomis cyanellus* [8] since the latter two studies deal more with modifications of pre-established hierarchies than with the conquest of a given social rank after recent experiences of the individual fish. It is known that hierarchies are very stable, always requiring individual recognition. The results of Thines and Heuts [15] probably hinge on this fact. On the other hand, it is also understandable that, in certain circumstances, the rank order can be changed, as in the experiments of McDonald, Heimstra and Damkot [8], who conclude that the most important factor involved in the change of the hierarchy was the negative experience to which the previously dominant fish was subjected.

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The experiments, not involving physical injuries to the fish during the pre-test experiences, showed that in *P. martensi*, as in other species, social conditioning can influence the degree of aggressiveness of an individual. As we already pointed out, *P. martensi* differs from the other species used in experiments, in that there are not dominance-subordinance relationships but rather individual possession of territory, from which all other members of the same species are excluded. The territoriality is not exhibited only by males, the females also competing in our experimental conditions.

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