

Alternative styles in the European wrasse, *Symphodus ocellatus*: boldness-related schooling tendency

Sergey V. Budaev

Laboratory of the Behaviour of Lower Vertebrates, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninsky Prospect, 117071 Moscow, Russia

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Synopsis

Underwater field observations in a non-reproductive period revealed enormous variation in schooling tendencies among individual European wrasses, *Symphodus ocellatus*. The fish occupying vegetated habitats displayed much more pronounced schooling tendencies than those from open areas. Sixteen solitary and schooling males were caught with a small seine and observed in a novel environment. The former individuals turned out to be much more bold and active than the latter in this test, which would suggest lower fear and higher exploratory tendency. It was hypothesized that the bolder wrasses might appear as territorial nest-builders in the reproductive period, whereas the shyer ones are likely to play sneaky and satellite tactics.

Introduction

Schooling behaviour of fishes is acknowledged as an anti-predator mechanism of fundamental importance (Radakov 1972, Magurran 1990). But, regardless of the substantial progress in understanding ultimate causation mechanisms, relatively less is known about proximate factors and, particularly, motivational systems involved in it. However, these may be crucial, even with respect to the evolutionary issues. For example, common motivational and neural basis may cause genetic correlations imposing constraints on the evolutionary processes. On the other hand, a particular behaviour controlling system may constitute the motivational basis of alternative styles, which may be, in turn, subjected to frequency- or density-dependent selection (e.g. Wilson et al. 1994 for shyness-boldness). Furthermore, direct motivational link may constitute the basic mechanism maintaining an appropriate bal-

ance between behavioural styles (see Magurran & Seghers 1991 for a discussion of schooling and aggression).

The analysis of individual differences is particularly suitable to disentangle the motivational constraints, as one can easily investigate whether and to what extent the behaviour of individuals is consistent and predictable across a range of situations. Moreover, individual differences in behaviour become recently of substantial interest as a 'hot topic' of behavioural ecology (Clark & Ehlinger 1987, Magurran 1993).

In the present study I examined patterns of individual variation in the schooling tendencies amongst the European wrasses, *Symphodus ocellatus* Forskål, as well as the relationships between individual schooling tendency and behaviour in a novel environment.

European wrasse, a small Mediterranean shore fish, seems particularly suitable for this sort of study

because it employs alternative male mating styles, so that territorial and accessory individuals may be distinguished (Taborsky et al. 1987). In addition, the novel environment test is often used to determine the level of boldness in fish, which is known to play an important role in determining aggression, dominance, territoriality, schooling, parasite fauna etc., (Huntingford 1976, Huntingford et al. 1990, Wilson et al. 1993).

Materials and methods

Field observations

The field studies took place in a non-reproductive period, July–August 1992, within the location of Maliy Utrish biological station (Black Sea, Northern Caucasus). The main study area represented a gently sloped pebbled shallows devoid of vegetation, descending from the surf zone down to, approximately, 2 m. It was followed by shallows covered by dense weeds (mainly *Cistoseira* sp.) spreading down to 5–7 m depth. Thus, two distinct habitats were inspected in this study; these are referred below as ‘pebbled’ and ‘vegetated’ respectively.

All underwater observations were made through video-taping by an experienced SCUBA observer in the following manner. A diver, swimming quietly along a shore, randomly selected one individual wrasse. Immediately he turned on his video camera-recorder and traced the fish with it during approximately 2 minutes. It was hardly possible to trace the fish for longer amount of time, as they sometimes swam out of the visual field and were lost (all unusually short observations were discarded then), and one might expect the fish to be more afraid of an exceedingly tenacious observer. The wrasses never formed very large schools (a typical size was about 20–50 subjects), and to avoid possible artefacts, only one individual was selected from each school. However, on the whole the selection procedure was informal and, therefore, some biases were likely to occur. It was also impossible to estimate the size and sex of fish during the observations. The fish never demonstrated any apparent fear or avoidance of the observer, skin-divers being quite common in

this habitat. All observations were performed between 10:00 and 13:00 h when the wrasses were reasonably active in terms of locomotion and foraging. The number of individuals whose behaviour was recorded and analyzed in the pebbled and vegetated habitats was 18 and 27, respectively

After returning to Moscow the behaviour of fish was transcribed from the TV monitor and ciphered onto a personal computer using a specially written software which accepted keystrokes as codes for particular behaviour patterns (Budaev 1995). The analysis was made separately for the fish observed in the pebbled and vegetated sites.

The following behaviours were easily distinguishable on the TV screen and recorded: moving (**move**), hanging in midwater (**stop**), feeding (**feed**) as well as hiding in shelters and among weeds (**hide**). In addition, the percentages of time the fish spent in schools (no more than 0.5 m from other conspecifics) were also registered.

The distributions of individual schooling tendencies (i.e. the percentages of time spent in schools) were examined separately for the pebbled and vegetated habitats. Here I inspected possible discontinuity (multi-mode patterns) in the distributions, which would indicate clear-cut alternative styles. The differences in these distributions, as well as in mean scores were also analyzed. In addition, I examined the correlations between the percentages of time individuals devoted to the above behavioural units and the percentages of time they spent in schools.

Because of strong biases in the distributions, the significance of differences was tested with Mann-Whitney U test; and, to test correlations, Spearman rho statistic was applied (Sokal & Rohlf 1981).

Experimental analysis

The experiments were conducted during August 1993 at the same location as the field observations. Twenty individual wrasses were caught for the experiments using a small flat square seine (1 × 1 m) as is described below.

The seine was left to lay freely on the bottom at the edge of the pebbled habitat (approximately 1.5

m depth), so that the experimenter was able to observe it all the time. As soon as an individual or a school of wrasses appeared just above the seine, I pulled a cord to lift it rapidly. Thus, it was quite easy to determine, whether the subject captured has been swimming in a school or individually, the fish being thereby classified into solitary and schooling subsamples. However I did not catch the fish in ambiguous cases, for example, when two simultaneously entered the area above the net from different sides. In total, eight solitary and twelve schooling male wrasses were captured (standard length 6.0–8.2 cm, overall median 7.2 cm).

Only 8 schooling fish were randomly selected for the present experiments to ensure equal group sizes ($N = 8$). The individuals were maintained in two 100-litre tanks at temperature 18–20°C and natural photoperiod. They were feed every day with broken molluscs. The wrasses were given one week to adapt to the laboratory conditions, after which the experiments started.

The novel environment test was administered to each individual. The test apparatus used was a long aquarium (120 × 30 × 20 cm). It consisted of two compartments: smaller ('home', 20 × 30 × 20 cm) and larger ('test', 100 × 30 × 20 cm) separated by an opaque partition with a sliding door in it (2.5 × 2.5 cm, 1 cm above the bottom). The test compartment was lit by a single 60 W bulb suspended 1 m above the water surface. All individuals were tested in mornings (10:00–11:00 h). To reduce the possibility of confounding transient motivational states with individual traits, the fish were given equal (*ad libitum*) amounts of food in the evening before testing, and I did not feed them just before the testing. Thus, all individuals were, presumably, equally hungry. Also, to attend stress attenuation, the temperature in the novel environment was maintained on the same level as in the rearing aquariums.

Initially an individual fish was gently transferred to the home compartment for 10 minutes, after which period the door to the adjacent compartment was opened. Consequently I recorded the latency with which the fish emerged in the adjacent novel (i.e. test) compartment. In case the individual had not emerged within 10 minutes, I placed it for 5 minutes into an opaque bottomless plastic cylinder col-

oured white (so-called start-box) standing directly in the test compartment. This was done to diminish possible handling stress.

As soon as the fish found itself in the novel compartment (or the start-box was lifted), the first test session begun. It continued 20 minutes, during which period the behaviour of the tested fish was transcribed as observer's comments on an audio cassette recorder.

After this first test session, the fish was captured and released back to the home compartment. Ten minutes later the door was opened and the second test session was conducted, the procedure being exactly the same as for the first session. This was done in order to gain an additional evidence that the wrasses were really exploring the novel environment, since the initial locomotor activity is typically reduced as it becomes more familiar (although the decrease of locomotion may also reflect decline of the tendency to escape; yet, the latency to freely enter a novel area is typically less confounded, see Russell 1983 for more discussion). Only solitary individuals were tested two times, schooling ones being administered only the first session.

All these observations were made through a small window in a blind separating the experimental apparatus from the observer to prevent unnecessary disturbances of the fish. Immediately after the last test session the standard length of each wrasse was measured.

The following behaviour patterns were recorded: freezing at the bottom (**frz**), moving (**move**), hanging in midwater (**stop**), and attempts to get through the glass walls of the tank (**esc**). The boldness was defined according to Wilson et al. (1993, 1994) – a fish can be called bold if it is active in the novel environment (presumably, explores it), rather than retreats or freezes (indicative of shyness).

Consequently, the records of the observer's comments were ciphered onto a personal computer using slow cassette play-back and the event-recording software mentioned above. The time budgets of particular individuals were analyzed in this study, that is, the percentages of time the animals displayed the above behaviour patterns.

Because of very small sample sizes, nonparametric Mann-Whitney and Wilcoxon tests were ap-

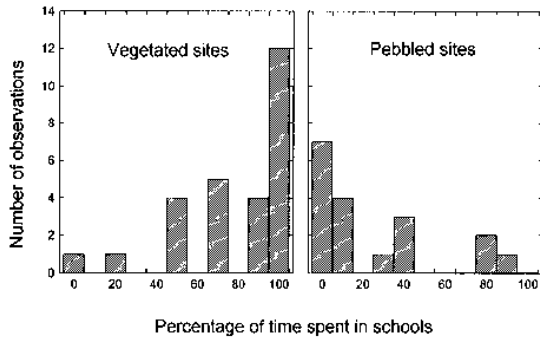


Figure 1. Frequency distributions of the percentages of time individual wrasses spent in schools in the vegetated and pebbled (open) habitats. Medians and quartiles (Q_{25} and Q_{75}) are, respectively, 95.4% (72.7–100.0) and 17.5% (5.5–46.2).

plied. Additionally, randomization tests were also used (involving 1000 random permutations per comparison), however because they gave exactly the same results, I do not report these here.

Results

Field observations

The percentage of time spent in shoals varied enormously between individuals, ranging as much as from 0 to 100% in pebbled as well as in vegetated sites. Additionally, in both cases the distributions were characterized by excessive skewness (1.11 left skewed, -1.64 right skewed, respectively). Furthermore, in the vegetated habitat the distribution showed extreme kurtosis (2.42), with the mode equal to 100% (frequency of mode $N = 12$). No conspicuous discontinuity of the distributions was observed, however, regardless of the very long tails (Figure 1). Bearing in mind the large differences between the distributions, no wonder that the mean percentages of the time devoted to schooling behaviour differed significantly between these two sites (Mann-Whitney test: $U = 55$, $p < 0.0001$, $N = 18 + 27$).

Examination of the Spearman correlation coefficients (Table 1) revealed high positive correlations between the schooling tendency (percentage of time spent in schools) and the percentage of time devoted to apparent feeding.

Furthermore, profound negative correlations between the schooling tendencies and active locomotion (**move**) as well as hanging (**stop**) were observed at the pebbled sites. In contrast, at the vegetated areas, the tendency to hide rather than locomotion, showed significant negative correlation with the schooling tendency.

Bearing in mind that at the vegetated areas the distribution of the schooling time has shown extreme skewness and kurtosis, one might expect that the correlation coefficients might not reflect correctly the relationships in regards to the subjects that made up the long left tail of the distribution. In other words, the weight of numerous schooling individuals in determining the correlation coefficient was too large, as compared with less common solitary ones. To cope with this problem, I dichotomized the whole sample into two subgroups with the cut-off point 65%. Thus, schooling ($N = 21$, have spent $> 65\%$ of time in schools) and solitary ($N = 6$, have spent $< 65\%$ of time in schools) subsamples were derived. In this case, the former fish showed significantly less tendency to active locomotion (**move**) than the latter (medians are, respectively, 34.5 with $Q_{25} = 25.6$ and $Q_{75} = 46.2$ versus 51.6 with $Q_{25} = 44.5$ and $Q_{75} = 66.3$; Mann-Whitney test: $U = 26$, $p = 0.031$).

Thus, in both sites solitary fish tended to be more active in terms of their locomotion.

Table 1. Spearman correlation coefficients between individual schooling tendencies (percentage of time spent in schools) and several behaviour units recorded during the field observations. The data analysis was conducted separately for the pebbled (open) and vegetated habitats.

Behaviour pattern	R_s	t	p
Pebbled ($N = 18$)			
move	-0.66	-3.54	0.003**
stop	-0.62	-3.19	0.006**
feed	0.66	3.48	0.003**
hide	-0.20	-0.82	0.427
Vegetated ($N = 27$)			
move	-0.31	-1.62	0.118
stop	-0.31	-1.63	0.116
feed	0.59	3.66	0.001**
hide	-0.46	-2.60	0.016*

Asterisks indicate significance levels: * $p < 0.05$; ** $p < 0.01$.

Experimental analysis

Solitary and schooling individuals did not differ in their standard length (Mann-Whitney test: $U = 24$, $p = 0.399$, NS, medians, respectively 7.3 and 7.0 cm). However these two groups turned out to differ enormously in their behaviour in the novel environment (Table 2). In general, solitary individuals devoted approximately 50% of time to active locomotion, whereas schooling ones demonstrated a very strong tendency to freeze at the bottom of the aquarium. Only 2.7% of total time did they spend in active swimming. It is not surprising, that all these profound differences were highly statistically significant.

No one schooling individual emerged in the novel compartment within 10 minutes, allowed by the present experimental design. In contrast, 5 out of 8 solitary wrasses entered the adjacent unknown compartment within 18 s to 2 min.

The behaviour of solitary individuals differed in the two consecutive exposures to the same novel aquarium. Specifically, the median percentage of time devoted to active locomotion (**move**) decreased from 53.2% ($Q_{25} = 40.7$, $Q_{75} = 57.0$) to 39.5% ($Q_{25} = 20.3$, $Q_{75} = 46.1$), which was significant (Wilcoxon test, $T = 2$, $p = 0.025$). The tendency to freeze increased extremely (from 15.3 to 44.6), but not significantly (Wilcoxon test, $T = 7$, $p = 0.124$, NS) because of large overlap.

Discussion

The results indicate that individual European

wrasses differ profoundly in their tendencies to join conspecific schools. Furthermore, at the vegetated sites the fish showed significantly higher schooling tendencies than at the pebbled ones. However, there may have been some observational biases, associated with possibly haphazard sampling; and, in addition, the shy fish, most likely to escape from any approaching diver, may have been underrepresented in the data. Also, strictly speaking, the differences between individual wrasses in field would be confounded by sex, size, transitory motivational state, and must not be completely ascribed to the levels of boldness.

The most interesting finding, however, is that individuals characterized by higher schooling tendencies (at least those captured from the border of the pebbled site) exhibited enormous freezing when tested in a novel environment. Low-schooling wrasses, in contrast, showed much more active behaviour in this test, and only these individuals (although not all) entered freely a novel adjacent compartment. The behavioural differences cannot be attributed to differences in the fish size.

Both the differences revealed in the field and in the laboratory experiments were rather striking and seem to indicate that the possible observational biases and immediate motivational states were not important.

Similar results were obtained by Wilson et al. (1993) in their studies of the shyness-boldness continuum in the pumpkinseed *Lepomis gibbosus*: the bolder individuals showed lower tendency to swim in close proximity of other conspecifics. In addition, profound behavioural differences were recently discovered (Ehlinger & Wilson 1988, Ehlinger 1990)

Table 2. Differences between the solitary and schooling fish in their behaviour in a novel environment. The table presents median percentages of time the fish displayed particular behaviour units. Lower (25%) and higher (75%) quartiles are given in parentheses.

Behaviour pattern	Solitary subgroup	Schooling subgroup	Mann-Whitney test	
			U	P
move	53.2 (40.7–57.0)	2.7 (0.6–7.2)	7	0.009**
stop	5.7 (2.8–6.6)	0.0 (0.0–0.02)	4	0.003**
frz	15.3 (10.5–23.6)	96.1 (70.3–97.2)	3	0.002**
esc	12.0 (5.3–16.1)	0.0 (0.0–0.2)	3	0.002**

N = 8, asterisks indicate significance levels: ** $p < 0.01$.

in the bluegill sunfish, *Lepomis macrochirus*, which seem to accord with the present wrasse data in that the fish living in vegetated habitats were characterized by significantly lower mobility than those from open-water areas.

Motivational factors

It is frequently assumed (Russell 1973, Walsh & Cummins 1976) that freezing indicates a state of excessive fear and stress. This behaviour is commonly observed in many fish species in an aversive restricted environment, for instance, a novel aquarium (Figler & Evensen 1979, Csányi et al. 1985). Freezing may reflect fear arising when a normally schooling fish has established that conspecifics cannot be found, which may be illustrated by the common observation that an individual dropped out of a school is likely to hide and freeze (e.g. Magurran & Pitcher 1987).

Locomotion, on the other hand, is argued (Walsh & Cummins 1976, Russell 1983) to reflect spatial exploration. Most often, it will decrease with repeated exposures to the same novel environment (Warren & Callaghan 1976, Mikheev & Andreev 1993) as it was observed in the experiments with bold fish. In addition, the latency to enter an unknown adjacent compartment represents a very relevant test of exploratory behaviour, unconfounded by the tendency to escape (Russell 1983). However, it is known that in stressful situations the basic exploratory tendency may be interfered with by fear (Russell 1973).

Therefore, the present results imply that the schooling tendency may be motivationally associated with fearfulness. This is in accord with the important antipredatory function of schooling behaviour (Radakov 1972, Magurran 1990) as well as with more pronounced schooling and risk-avoidance tendencies typically reported for fish living in stocks under high predation pressure (see Magurran et al. 1992 for a review).

However, there may not be a single general and unitary dimension of shyness-boldness. For example, the behaviour of fish in other situations may be relatively independent and situation-specific. On

the other hand, one could find several general and independent dimensions of temperament in fish associated with different proximate causal mechanisms. For example, in the pumpkinseed *L. gibbosus*, two independent 'shy-bold continua' were discovered (Coleman 1995): one which was pronounced in response to a potentially dangerous object and another, more prominent with an innocuous one. Likewise, the ongoing research on the guppy, *Poecilia reticulata*, reveals the similar pattern, with two independent, consistent and general temperamental dimensions: one associated with activity, exploration and schooling tendencies, and another, made up of fear and escape (Budaev unpublished data). Therefore, further studies are needed, specifically exploring the behaviour of wrasses in a wider range of situations and involving a multivariate analysis.

Ecological considerations

The benefits of group living in animals have been discussed many times. In general, both easier detection of food and predator avoidance (due to 'many eyes', dilution effect and confusion effect) are now conceived as the principal advantages of group living (see reviews of Pulliam & Caraco 1984, Clark & Mangel 1986).

Recently, however, substantial interest in potential costs of schooling behaviour has appeared (Pitcher et al. 1986, Magurran & Bendelow 1990, Magurran & Seghers 1991), which points to a trade-off between resource defence and predator avoidance.

In this way, a solitary wrasse must devote substantially greater portion of time than a schooling one to scanning for possible predators, which thereby would reduce the time devoted to foraging and feeding. But, on the other hand, higher locomotion and exploratory behaviour might allow this fish to explore a larger area per unit time and consequently give a better chance to find a more profitable patch (yet, the present data indicate that the wrasses were more actively foraging in schools, although little can be said about its efficiency). There exists also an indication that schooling may invite rather

than decrease predation since schools are more visually conspicuous than individuals (Clifton & Robertson 1993). Additionally, solitary individuals will not suffer from competition with other conspecifics, nor will be exposed to their manipulations and exploitation. An interesting possibility is that the bold solitary wrasses may be opportunistic scroungers (Giraldeau et al. 1994, Ranta et al. 1996, also see Clifton 1991), themselves exploiting the food discovered by the shyer and schooling fish; in particular, because foraging schools are visually conspicuous and boldness is often associated with higher competitive ability (Huntingford et al. 1990), the necessary prerequisite for stable producer-scrounger pay-off equilibrium (Ranta et al. 1996).

The negative correlation between the schooling and hiding tendencies observed in the vegetated habitats may illustrate the trade-off between feeding and predator avoidance, as the solitary fish are presumably exposed to a higher risk of being eaten. Therefore the fact that these individuals strongly preferred open areas close to the surf zone may be associated with absence of predators there (personal observation). Yet, in both habitats the predation pressure is rather low. Perhaps, it might be more difficult for any predator to approach its prey undiscovered at the open area, as compared with the vegetated one. However, the habitat preferences may reflect also different foraging modes just in the same way as for the bluegills (Ehlinger & Wilson 1988, Ehlinger 1990, see above), the shy and schooling individuals being adapted to search for cryptic prey typical for weeded habitats.

What are the possible effects of the boldness on other salient behavioural styles in the European wrasse, assuming it represents a relatively stable and situation-general trait? One important candidate is the male mating style.

As many other labrid fishes, the European wrasse is known to employ alternative mating styles. Typically, normal territorial nest-builders, sneaky (kleptogamic) males, satellites tolerated by the nest-builders and non-reproductive individuals (Fiedler 1964, Taborsky et al. 1987) are distinguished, although, unlike some other related species, hermaphroditism is not observed in *S. ocellatus* (Warner & Lejeune 1985). Little is known about the

behaviour of fish which uses alternative style in the non-reproductive period, however. Nevertheless it was suggested (Huntingford 1976, 1982, Huntingford et al. 1990) that individual level of boldness profoundly influences the willingness to display aggression, propensity to take risks in presence of predators, social dominance and competitive ability. Furthermore, it was shown (e.g. Magurran & Seghers 1990) that under an immediate risk of predation male guppies, *Poecilia reticulata*, tend to switch to the sneaky mating behaviour, and this was much more pronounced in fish from populations suffering from higher predation pressure (which exhibit shyer behaviour). Therefore, it may be hypothesized that the bold wrasses, displaying also a tendency to be solitary, would employ the territorial nest-building rather than sneaky behaviour in the reproductive period. This hypothesis is supported also by the observed facts (Taborsky et al. 1987) that territorial males frequently attack and expel accessory ones (mostly sneaky) from the nest, or take other nests over. However, future longitudinal studies are necessary to test this hypothesis.

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