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# Differences between the reproductive biologies of *Tripterygion tripteronotus* and *T. delaisi* (Pisces, Perciformes, Tripterygiidae): the adaptive significance of an alternative mating strategy and a red instead of a yellow nuptial colour

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## Abstract

This paper contributes to the understanding of the evolution of alternative mating strategies by comparing morphological, ecological and ethological aspects of the reproductive systems of two closely related fish species studied near the marine biological station "STARESO" at Calvi, Corsica, between March 1982 and May 1985. The Mediterranean breeding areas of *Tripterygion tripteronotus* and *T. delaisi* partly overlap. The red territorial males of *T. tripteronotus* defend territories in the upper 6 m of the water column and the yellow territorial males of *T. delaisi* breed between a depth of 3 and 40 m. Small male *T. tripteronotus* possess relatively large gonads exhibit "sneaking" behaviour, while small male *T. delaisi* do not participate in mating. *T. tripteronotus* expends more effort in reproduction than *T. delaisi*. This is expressed in larger gonads, a higher density of and stronger competition for nest sites, and a longer breeding season and shorter spawning bouts with a higher fertilization rate in the former species. We hypothesize that the sneaking strategy of non-territorial male *T. tripteronotus* evolved in response to competition for nest sites in the shallow, upper water layers, which are limited in depth, but contain a good food supply. The depth restriction is imposed by the light-reflecting properties of the red territorial males. We suggest that the evolution of *T. tripteronotus* began with the appearance of a red morph of *T. delaisi* after the invasion of this latter species into the tideless Mediterranean Sea.

## Introduction

Two closely related demersal fish species of the genus *Tripterygion* inhabit the rocky littoral of Mediterranean shores. *T. tripteronotus* is endemic to the Mediterranean and occurs in the upper 6 m of the water column. *T. delaisi* lives between 3 and 40 m depth and occurs also in the Eastern Atlantic Ocean. Size ranges are similar in both species; the maximum length of adult males is about 70 mm (Abel 1955, Zander and Heymer 1970, Wirtz 1980). Both species display territorial breeding characteristics. Territorial males have a black head and a conspicuously coloured body, in *T. tripteronotus* such males are red, while *T. delaisi* males are bright yellow. In contrast, the colour pattern of females and non-territorial males of both species is cryptic: grey-brown, with five dark dorso-ventral bands between head and tail. Only a triangular, caudally directed extension of the caudalmost band of *T. delaisi* makes it possible to distinguish between the non-territorials of the two species.

The general pattern of breeding behaviour in territorial males is similar in the two species. Each male defends an area of about 1 m$^2$; a smaller area of about $20 \times 20$ cm within the territory is used as the nest site. Gravid females swim to a nest site where the colour and courthship display of the males initiates spawning behaviour. The eggs are attached one by one to algae in the nest. Males fertilize each egg whilst displaying trembling motions side by side with the female.

Small males with ripe gonads, strongly resembling females, occur in both species. The behaviour of these non-territorial males is strikingly different between the species. Those of *Tripterygion tripteronotus* dwell around established territories, where they frequently try to fertilize eggs by stealthily approaching spawning females and releasing clouds of sperm. Such sneaking behaviour is only rarely displayed by small male *T. delaisi*, who do not usually participate in mating (Wirtz 1977, De Jonge and Videler unpublished a).

We were interested in the adaptive significance of the alternative male mating strategy displayed by *Tripterygion tripteronotus*, and therefore compared demographical, ethological and ecological aspects of the reproductive systems of these two closely related sympatric species. Hypotheses on their phylogenetic history are discussed.

## Materials and methods

Our research area was the rocky littoral near the marine biological station "STARESO" at Calvi, Corsica. *Tripterygion tripteronotus* and *T. delaisi* were observed and collected by SCUBA diving between 0 and 18 m depth. Behavioural data were recorded by means of underwater tape-recorders, writing pads, and stopwatches. Dry diving suits made it possible to remain several hours under water even at temperatures as low as 12 °C. Data were collected during four successive years: between March and September 1982 and 1983, during April and June 1984, and in May 1985.

For morphometric measurements, specimens of both species were collected outside the area used for behavioural studies. Fish were killed with an overdose of MS222 (Sandoz, Basel). The total length, mass of body and gonads and the number of ripe eggs in the ovary were recorded. We tried several techniques for age determination, using otoliths and hypural plates, but failed. Fish were collected about once a month during the first and second year of this study.

The study of behaviour required individual recognition of fish belonging to populations of both species in the study area. Fish were caught after anaesthesia with quinaldine, colour-marked under water, and released on the same spot where they had been trapped. We used subcutaneous injections of Alcian Blue suspended in artificial sea water, which produced small but clearly visible blue spots. Fishes were individually colour-coded, using different numbers of spots along the left and right side of the body. A total of 164 fish were marked: 61 territorial and 41 non-territorial males of *Tripterygion tripteronotus;* and 45 territorial and 17 non-territorial males of *T. delaisi.* The markings remained for over a year on some specimens, allowing us to recognize individuals the following season and to renew the colour marks. The same individuals could thus be followed during successive years, which allowed us to study their development and to estimate age ranges.

The daily research routine included visiting territories inside the research area. At each such visit, we recorded the presence and identity of the territorial male, the presence of females and non-territorial males (sex determination of non-territorial individuals was based on behavioural differences), and of interactions between territorial males and intruding males. A total of 3900 such records were made, including 2100 on 57 different territories occupied during the period of investigation by 105 *Tripterygion tripteronotus* males, and 1800 records on 59 territories occupied by 67 *T. delaisi* males.

Nest sites within the territories were studied in more detail by comparing characteristic features of 9 nest sites of *Tripterygion tripteronotus* with 21 of *T. delaisi.* We examined the depth, type and degree of algal and faunal cover, the shape of the rocky underground and exposure to sunlight. The density of nest sites of the two species was determined by counting the number of sites of *T. tripteronotus* in an area of 230 $m^2$ between 0 and 3 m depth and of *T. delaisi* in an area of 290 $m^2$ between 3 and 7 m.

Food supply between territories at 0.5, 4 and 10 m depth was compared by collecting the overgrowth covering an area of 15 $cm^2$ within two territories at each depth. The number of potential prey items (determined from gut-content studies, Zander 1982) in these samples was used as a measure of the food supply available to the territorial males.

To study interspecific competition for nest sites, we recorded the number of interactions between territorial males and intruding males of the other species, and the ownership changes between males of the two species.

To determine the level of intraspecific competition, data were collected on the number of interactions between territorial and intruding males and on the frequency of changes of ownership. In addition we performed two experiments, one in May 1985 and one in June 1983, when we removed territorial males and closely followed subsequent occupation of the nest sites.

Our comparison of the mating and spawning behaviour of the two species is based on several recordings. Observation times varied between 10 and 70 min, and totalled 22 recording hours for *Tripterygion tripteronotus* and 10 h for *T. delaisi.*

The reproductive success of territorial males could not be determined directly. Instead, as an index of reproductive success, we defined mating activity as the number of times males were seen mating during our daily visits, expressed as a percentage of the total number of observations. We excluded males who kept a territory for less than 10 d and those who were absent during more than 20% of the observations from this analysis, and did not count mating activities of males who started to breed late in the season.

## Results

### Demography

#### *Comparison of body lengths*

Fig. 1 compares the body lengths of territorial and non-territorial males and females of *Tripterygion tripteronotus* and *T. delaisi.* Variation in length within each of the six groups of fishes arose from a combination of three factors: (1) the fishes belonged to different year-classes (marked individuals were recorded over three successive years); (2) they were caught at different times between March and September; (3) the natural variation in length between fishes of the same age.

Territorial males were, on average, significantly larger than non-territorial males and females (Mann-Whitney *U*-test, $p < 0.001$). Although the frequency distribution of body length between the territorial males Fig. 1 A and D suggests an interspecific difference, this difference was not significant (Mann-Whitney *U*-test, $p > 0.3$).

*Tripterygion delaisi* females were, on average larger than those of *T. tripteronotus* (50.1 and 45.5 mm, respectively), and this difference was significant (Mann-Whitney *U*-test, $p < 0.001$). The histograms in Fig. 1 C and F differ in shape: *T. delaisi* females displayed a slight peak in the 39 to 43 mm

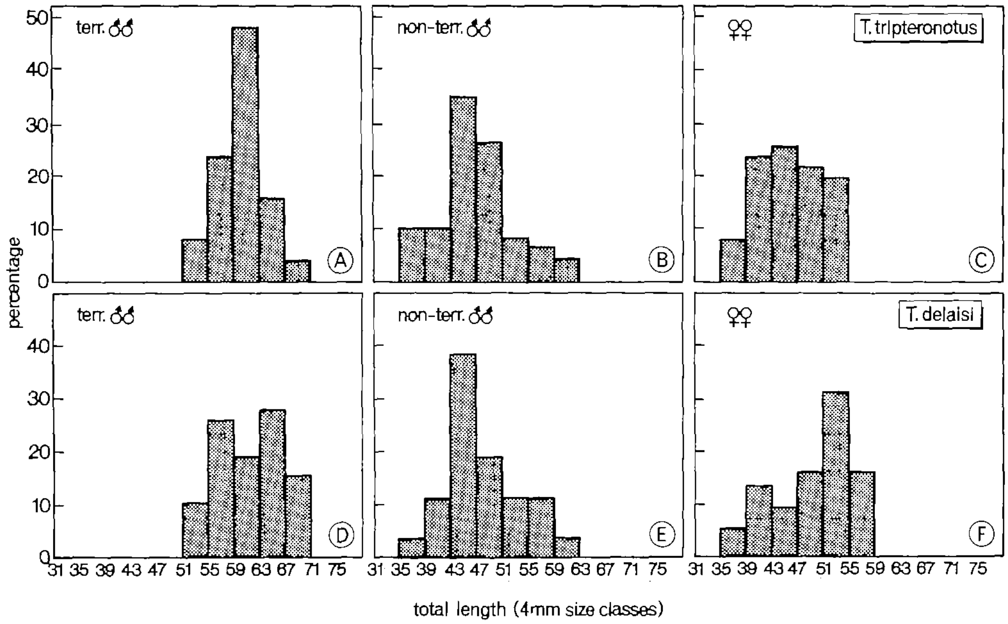

**Fig. 1.** *Tripterygion tripteronotus* (A–C) and *T. delaisi* (D–F). Frequency distributions of body length of territorial males (A, D), non-territorial males (B, E), and females (C, F). (A) $n=50$, $x=59.7\pm3.4$ (SD) mm; (B) $n=49$, $x=46.3\pm5.8$ (SD) mm; (C) $n=50$, $x=45.5\pm4.8$ (SD) mm; (D) $n=57$, $x=60.8\pm4.9$ (SD) mm; (E) $n=26$, $x=47.3\pm5.6$ (SD) mm; (F) $n=74$, $x=50.1\pm6.7$ (SD) mm

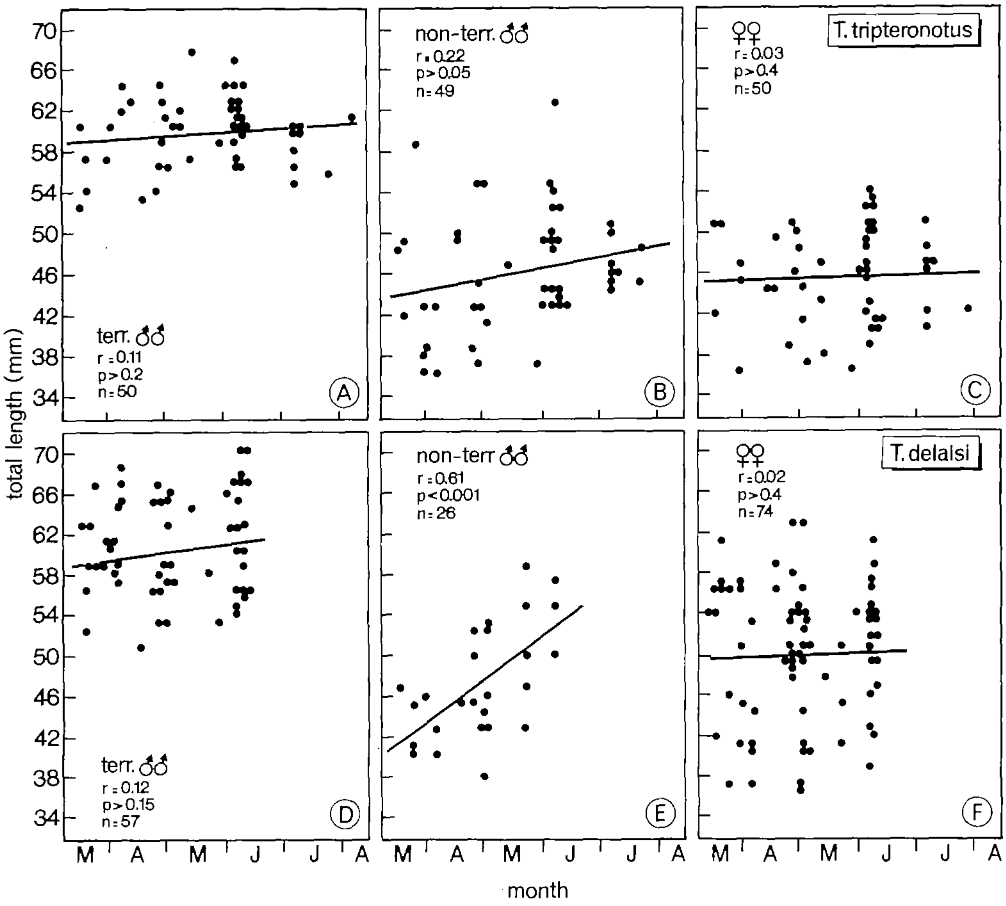

**Fig. 2.** *Tripterygion tripteronotus* (A–C) and *T. delaisi* (D–F). Length of males and females during reproductive seasons of 1982 and 1983

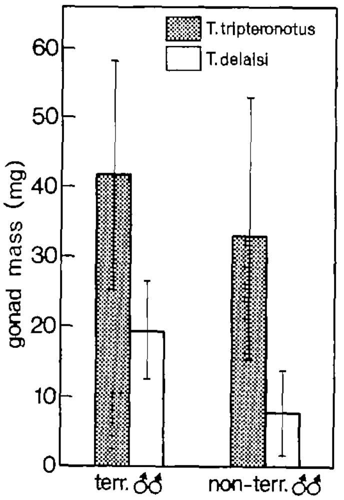

**Fig. 3.** *Tripterygion tripteronotus* and *T. delaisi*. Mean gonad mass (±SD) of males

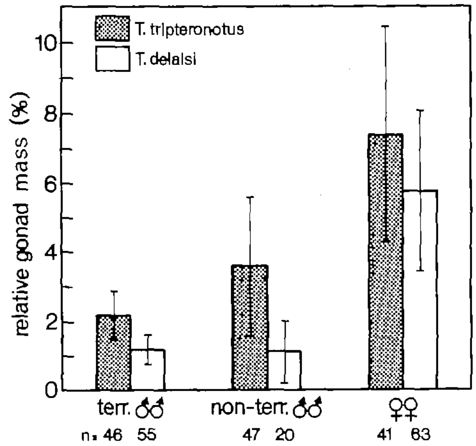

**Fig. 4.** *Tripterygion tripteronotus* and *T. delaisi*. Mean relative gonad mass (gonad mass as % of body mass) (±SD) of males and females

class and a larger peak between 51 and 55 mm. Female *T. triperonotus* apparently do not grow larger than 55 mm.

The average length of non-territorial males was not significantly different between species, size distribution was similar, with maximum numbers occurring in the 43 to 47 mm length-classes.

Body-length data related to time of capture during the breeding season are presented for each of the six groups in Fig. 2. Again, there is considerable scatter due to year-class differences and natural variation, but a few trends can be identified. The territorial males of both species and the non-territorial males of *Tripterygion tripteronotus* showed a slight, but not statistically significant, length increase during the summer. Females displayed no correlation between length and time of year. Only non-territorial male *T. delaisi* exhibited a significant ($n=26$, $r=0.61$, $p<0.001$) trend of increasing body-length (~14 mm 100 $d^{-1}$) during the reproductive period. Apart from these measurements, the growth rate of non-territorial male *T. tripteronotus* was established from ten marked individuals which were recaptured 58 to 112 d after marking. Their length increased at a rate of 6.5±1.5 (SD) mm per 100 d.

### *Differences in gonad mass*

All fishes captured during the breeding season possessed mature gonads. Gonad size decreased gradually towards the end of the spawning season until, in winter, they were in the resting stage. Fig. 3 shows that the mass of the testes of territorial *Tripterygion tripteronotus* males was only slightly larger than that of the non-territorial males of this species (Student's *t*-test, $0.02<p<0.05$). The testes of *T. delaisi* territorial males were significantly larger ($p<0.001$). Fig. 4 expresses the relative gonad mass as a percentage of body mass for both species. The relative gonad mass of non-territorial male *T. tripteronotus* was larger than that of territorial males (Student's *t*-test, $p<0.001$), whereas male *T. delaisi* displayed no significant difference (Student's *t*-test, $p>0.2$). The testes of both territorial and non-territorial male *T. tripteronotus* were heavier than those of the territorial males of *T. delaisi*, whether measured relative to body mass or not (Student's *t*-tests, $p<0.001$).

The gonads of the two male types of both species differ in morphology. Territorial males possess a large mesorchial gland in the gonads. This structure is less developed in non-territorial males (De Jonge et al. unpublished b). Since the mass of this gland is equal in both species, the differences in gonad mass between the species must be due to different amounts of spermatogenetic tissue.

Female *Tripterygion tripteronotus* had a significantly larger relative gonad mass than female *T. delaisi* (Fig. 4. Student's *t*-test, $p<0.001$), and their ovaries contained more eggs. On average we found 134 mature eggs in *T. tripteronotus* females ($n=41$) and 113 in *T. delaisi* ($n=63$).

### *Differences in ratio territorial and non-territorial males*

The proportion of males among the randomly caught non-territorial fishes was higher for *Tripterygion tripteronotus* (48.1% males; $n=52$) than for *T. delaisi* (21.7% males; $n=69$). There was no indication that non-territorial *T. delaisi* males concentrated outside the sampling area, so, assuming a similar longevity for males of both species, this difference may indicate that young *T. delaisi* males become territorial earlier in their life history than *T. tripteronotus* males. If so, the ratio of non-territorial to territorial males should be lower in *T. delaisi* than in *T. tripteronotus*. There are some indications that this is the case. Non-territorial fishes were collected in the vicinity of six *T. tripteronotus* territories and eleven *T. delaisi* territories. The ratio between territorial and non-territorial males was 6:5 for *T. tripteronotus* and 11:3 for *T. delaisi*.

### *Age-ranges of males and females*

Although the exact age of the fishes could not be determined, observations of marked individuals revealed that:

(1) males can be territorial for two (observed for *Tripterygion tripteronotus*, $n=5$; and *T. delaisi*, $n=3$) and even three (*T. tripteronotus*, $n=1$) successive years; (2) "sneakers" of *T. tripteronotus* may remain non-territorial for at least two years ($n=3$); (3) females can attain 3 yr of age (*T. delaisi*, $n=1$). Unfortunately, no data on non-territorial male *T. delaisi* were available.

## Breeding biology

### *Nest sites*

The nests of both species are usually located in places hidden from direct sunlight. Our analyses shows that the species display no difference in preference with respect to type of rocky substrate. In an area of 230 $m^2$, 40 *Tripterygion tripteronotus* nests were found between 0.5 and 3 m depth, an average density of 17 100 $m^{-2}$. The depth range of *T. delaisi* nest sites was between 2 and 40 m, with an average density of 10 100 $m^{-2}$ (based on 29 nests in an area of 290 $m^2$ between 3 and 7 m).

The algal cover of *Tripterygion tripteronotus* nests consisted mainly of 0.5 to 2 cm-long brown algae (*Cystoseira* sp.). The algae in the nests of *T. delaisi* were usually shorter (0.2 to 0.6 cm), and shared the space with sponges. Examination of the gut contents of both species confirmed that small crustaceans are the main food items of tripterygions (Zander 1982). The average number of potential food items in the territories ranged from 681 $dm^{-2}$ at a depth of 0.5 m to 326 $dm^{-2}$ at 10 m.

Interspecific competition for nest sites can be expected in areas between 2 and 3 m depth. We never observed a change of species in any territory during one breeding season but, in four successive years, we saw three *Tripterygion tripteronotus* territories occupied by a *T. delaisi* male and two *T. delaisi* territories occupied by a *T. tripteronotus* male at the start of a new season.

Intraspecific competition for nest sites is most common among *Tripterygion tripteronotus* males. During 1392 daily visits, we saw seventeen agonistic interactions between territorial males of *T. tripteronotus* and only four during 1291 visits to *T. delaisi* territories. The difference is significant (chi-square for two independent samples $=5.94$, $p<0.01$).

We removed males of both species from their territories, and observed the re-occupation of the nest sites by new territorial males. Fig. 5 shows that within one day of removal of the males 60% of the nest sites of *Tripterygion tripteronotus* and 10% of the nest sites of *T. delaisi* had been re-occupied. This situation remained virtually unchanged during next week of observation. Thus, it can be concluded that more potentially territorial *T. tripteronotus* males are present in the vicinity and that the competition for *T. tripteronotus* nest sites is higher than for *T. delaisi*. This is supported by the observation that shifts in territory ownership occur more frequently in *T. tripteronotus*: during one season 3 out of 11 nest sites of *T. tripteronotus* were occupied by one male, 4 by two males in succession, 3 by three males, and 1 by four males. In contrast, 12 out of 15 *T. delaisi* nest sites were occupied by one male and only 3 by two males in succession.

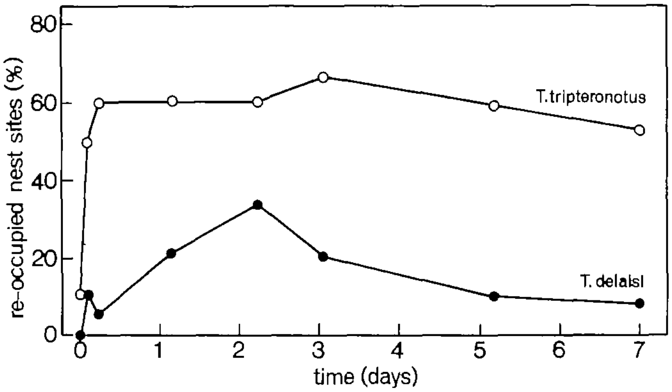

**Fig. 5.** *Tripterygion tripteronotus* (o, $n=20$) and *T. delaisi* (•, $n=29$). Percentage of nest sites re-occupied during 7 d following experimental removal of territorial males

We followed the re-occupation of the nest sites from one season to the next over four successive years. At the start of a new season, *Tripterygion tripteronotus* re-occupied an average of 50% of the old territories and *T. delaisi* only 30%: this also indicates a lower availability of suitable nest sites for *T. tripteronotus*.

### *Reproductive season*

The breeding season of the *Triperygion tripteronotus* population lasted about 5 mo, two months longer than that of *T. delaisi*. In both species, spawning activity started in the middle of March. After this time, spawning frequency increased rapidly. The spawning season for *T. delaisi* ended abruptly in June. Within 14 d all territorial males lost their breeding colour and left their territories. The *T. tripteronotus* population showed a more gradual decline and spawning had finished by the end of August.

The average duration of the territorial periods was 46.2 d (24.7 SD, $n=22$) for *T. tripteronotus* males and 47.1 d (24.3 SD, $n=29$) for *T. delaisi*. The longest period spent in anyone territory was 108 d for *T. tripteronotus*, and 82 d for *T. delaisi*. The first occupants of a *T. tripteronotus* nest site remained for an average of 57.5 d (25.6 SD), significantly longer than succeeding males, who remained for an average of 32.6 d (15.7 SD) (Student's $t=3.62$, DF$=20$, $p<0.01$).

### *Spawning behaviour*

The duration of a spawning bout was usually shorter for *Tripterygion tripteronotus* than for *T. delaisi*. In *T. tripteronotus* we observed three complete spawning bouts which lasted for 37, 42 and 73 min, while for *T. delaisi*, we recorded two bouts which lasted longer than 100 min. Wirtz (1978) found similar differences between these species; he reported a range of 23 to 85 min for *T. tripteronotus* and 45 to 105 min for *T. delaisi*.

If undisturbed, females spawn all mature eggs in one bout, as demonstrated by dissecting females directly after spawning. Males fertilize eggs whilst displaying trembling motions side by side with the female. Such fertilization behaviour is significantly more frequent in *Tripterygion tripteronotus* than in *T. delaisi*. During spawning bouts, an average of 11.0 (4.3 SD) fertilizations per 10 min for *T. tripteronotus* and 6.4 (3.2 SD) for *T. delaisi* were counted (Student's *t*-test, $p < 0.001$).

We defined mating activity as the number of times territorial males were seen mating expressed as a percentage of the total number of observations. Mating activity varied strongly (between 0 and 30% in both species). The number of males with no mating activity was lower in *Tripterygion tripteronotus* (3.4% of the total individuals involved) than in *T. delaisi* (20%); 15.1% of *T. tripteronotus* males and 5.4% of *T. delaisi* males were absent during more than 20% of our visits. We observed that unsuccessful male *T. tripteronotus* left their territories and displayed "sneaking" behaviour.

"Sneakers" interrupted the spawning of territorial male *Tripterygion tripteronotus* an average of 12.5 $h^{-1}$. Sneaking behaviour in non-territorial male *T. delaisi* was very rare, we observed it only twice during 10 h of observation of spawning pairs. This striking difference in mating behaviour between the non-territorial males of the two species was also reflected in the number of such individuals which dwelt around the territories during spawning: 47% of non-territorial male *T. tripteronotus* stayed within a territory at a distance of $< 0.5$ m from the nest site, compared to only 19% of non-territorial male *T. delaisi*.

We observed some *Tripterygion tripteronotus* sneakers which took on a nuptial colouration and became territorial in the course of one breeding season, and others at the beginning of the following season.

## Discussion and conclusions

This study shows that the length distribution of males in both *Tripterygion* species is similar. The weight of the testes are however, markedly different. The larger testes of both types of *T. tripteronotus* males compared to those of *T. delaisi* males probably results from sperm competition between sneakers and territorial males in the former species. Sneakers, and consequently sperm competition, are virtually absent from *T. delaisi*. The relatively large testes of *T. tripteronotus* sneakers compared with those of territorial males of the same species might be due to selection for sneakers with large testes. Large testes enable sneakers to release great amounts of sperm instantaneously on the spawning ground, which could increase their fertilization success. A relationship between testes size and spawning strategy has also been reported for labrids (Robertson and Warner 1978, Warner and Robertson 1978, Warner and Lejeune 1985) and bluegill sunfishes (Gross and Charnov 1980).

Sneaking male *Tripterygion tripteronotus* probably develop testes at the expense of growth during the breeding period. This could cause a delay in their transition to territorial status, since only large males appear to be capable of establishing a territory. All small male *T. tripteronotus* possess large testes and, in a number of cases, we observed them change to territorial colours. Therefore, we assume that all young males start as sneakers, and later become territorial. The relationship between age and reproductive strategy in *T. tripteronotus* is not as clear as supposed by Wirtz (1977). He assumed that sneakers are 1 yr old and territorial males 2 yr old. The distinction of only two year-classes is based on the interpretation by Gordina et al. (1972) of the bimodal pattern in male body-length distribution. In contrast, our results show that several small males were sneakers for two years and that large males may be territorials also for several years. We assume that behavioural and morphological polymorphism is sequential and probably age-dependent. This is markedly different from the situation in, for example, bluegill sunfish, where males have alternative life-history pathways leading to either a parental life style or a life as cuckolder (Gross 1984).

Comparison between ecological and ethological aspects of both species show, without exception, that in addition to the participation in reproduction of non-territorial males, the reproductive system of *Tripterygion tripteronotus* is more intense than that of *T. delaisi*: the density of nest sites of *T. tripteronotus* is higher; breeding territories are in greater demand; fewer territorial males are unsuccessful in attracting females to spawn. Moreover, during spawning, female *T. tripteronotus* lay more eggs in a shorter time and the fertilization frequency of the male is higher. The breeding season lasts 5 mo, two months more than that of *T. delaisi*.

These results led to the following hypothesis about the development of an alternative male mating strategy in *Tripterygion tripteronotus*. For reasons that will be discussed later, *T. tripteronotus* is confined to a restricted area in shallow water. This restricted habitat range, combined, however, with a good food supply, results in increased population density. The number of territorial sites then becomes the limiting factor, resulting in increased competition. Competitive displacement of small males constitutes a selective pressure which favours the development of an alternative mating strategy in these males. This hypothesis agrees well with Gross's theory (1984) that a primary requisite for the development of alternative reproductive strategies is individual competition for access to mates; in our case, competition for nest sites. We expect the reproductive fitness of sneakers to be lower than that of territorial males. Sneakers must, however, achieve a certain level of reproductive success, otherwise the evolution of such an alternative strategy would have been improbable. Subordinate reproductive strategies at the individual level (called "tactics" by Gross) are regarded as an evolutionarily stable "best of a bad situation" (BBS) strategy.

For *Tripterygion delaisi*, nest sites are not in short supply, an alternative male strategy is not necessary, and did not evolve. Males invest in growth first and reproduce as territorials later. Possibly all non-territorial *T. delaisi* males become territorial in their second year, as suggested by their fast growth rate and low territorial:non-territorial male ratio. Female *T. delaisi* are larger than female *T. tripteronotus*; the former convert less energy to eggs and are relatively slow spawners.

An important assumption in our hypothesis is that the distribution of *Tripterygion tripteronotus* is restricted to the narrow range upper water layers. Why did this species not extend into deeper waters instead of developing an alternative strategy? The key to the answer is probably the striking colour of the territorial males, the conspicuousness of which supposedly contributes to courtship success. In the upper water layers of the Mediterranean Sea, red-coloured males are more conspicuous than yellow males, the latter being less discernible because of the reflection of sunlight onto small waves, which causes intermittant flashes of light on the rocks in the shallow part of the littoral. However, a serious disadvantage of the colour red is the restricted area wherein this colour dominates. Red light is very quickly absorbed in water; the colour red is striking within the first few metres of water, but takes on a dull blackish hue with increasing depth.

*Tripterygion tripteronotus* does not occur in the East-Atlantic Ocean, where the tides render the upper few metres unsuitable for nest-breeding fishes.

We assume that the evolution of *Tripterygion tripteronotus* began in the Mediterranean Sea with the appearance of a red morph of *T. delaisi*. Red territorial males proved to be more successful breeders in shallow waters than yellow morphs. This differentiation may have arisen from allopatric, i.e., *T. delaisi* individuals temporarily isolated in a shallow pool in the Mediterranean Sea, or sympatric conditions by the development of polymorphism for resource use (Coyne and Barton 1988). Our hypothesis makes a multiple invasion by a common ancestor, as suggested by Zander (1973) and Wirtz (1980), less plausible.

In conclusion, the red colour of territorial male *Tripterygion tripteronotus* is probably the key to questions regarding the evolution of these two closely related fish species and the development of the alternative mating strategy in *T. tripteronotus*.

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