REPRODUCTIVE BEHAVIOUR AND ECOLOGY OF SYMPHODUS (CRENILABRUS) OCELLATUS, A EUROPEAN WRASSE WITH FOUR TYPES OF MALE BEHAVIOUR

by

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(With 13 Figures)
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Introduction

Polymorphic mating tactics within species are receiving increasing attention in evolutionary theory (*e.g.* GADGIL, 1972; ALCOCK, 1979; CADE, 1980; DAWKINS, 1980; RUBENSTEIN, 1980; MAYNARD SMITH, 1982; WALTZ, 1982; GROSS, 1984; proceedings of a symposium on alternative mating tactics 1984, Amer. Zool. 24; p. 306-418). They are probably much more common under natural conditions than previously thought. For example, at least 64 species of fish are known to have at least two male reproductive modes (P. WIRTZ, unpublished review): (i) The "territorial type" is characterised by the defence of a female, nest, hole of spawning territory, the performance of courtship behaviour and sometimes by the preparation of a spawning site and broodcare. (ii) The "parasitic type" exploits the investment of territorials by attempting to fertilise eggs when the latter are spawning ("sneaked fertilisations").

Many tropical wrasses (family Labridae) are known to employ alternative mating tactics, mostly in combination with sequential her-

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maphroditism. Protogynous "secondary" males are territorial while "primary" males, which do not pass through the female stage, are kleptogamic (Reinboth, 1962; Robertson & Choat, 1974; Warner & Robertson, 1978; Warner, 1982). Spawning is pelagic. European wrasses differ from this tropical pattern in two principal ways: many are gonochoristic (Stefani, 1955; Quignard, 1966; Dipper & Pullin, 1979) and most species lay demersal eggs (Quignard, 1966; Robertson & Hoffman, 1977; Lejeune, 1984; Potts, 1984, 1985; see Bauchot & Quignard, 1973 for further literature), which mostly coincides with male broodcare. Territorial males in 8 of the 9 *Symphodus* species investigated (formerly *Crenilabrus*: Bauchot & Quignard, 1973) build nests from algae and/or sand and particles, and care for the eggs released into these nests by several females. Kleptogamic males were observed in 7 of these species (Soljan, 1930a, b; 1931; Fiedler, 1964; Dipper, 1981; Lejeune, 1984). Fiedler (1964) even documented three different types of reproductive males in *S. roisalli* (= *C. quinquemaculatus*) and *S. ocellatus*: "nest-builders" (*i.e.* the territorial type), "by-males" (*i.e.* sneakers) and "outsiders of fertilization", a second type of parasitic males first observed by Soljan (1930a, b, 1931). These "outsiders", henceforth called "satellites", were intermediate in size between females and nest-builders, defended the nest against smaller males and females (Fiedler, 1964) and were tolerated by the nest-builders (Soljan, 1930a). Satellites were subsequently found in a third species, *S. tinca*, by Lejeune (1984). These *Symphodus* species probably have the most complex fish mating systems yet reported, with the exception of that of the North American sunfish *Lepomis macrochirus* (Dominey, 1980; Gross & Charnov, 1980; Gross, 1982). Their reproductive behaviour could be of particular interest for an evolutionary perspective on the coexistence of different mating tactics within a population.

This paper is the first of a series concentrating on the reproductive biology of one of the above species, *Symphodus* (*Crenilabrus*) *ocellatus*. We aim to give a detailed account of its reproductive behaviour and ecology. The differences in behavioural tactics, time allocation and spacing of territorials and accessory males are described. We also report on a fourth type of male found in the same population and on the behaviour of females.

Subjects

S. ocellatus is a wrasse of max. 8.5 cm standard length (SL). It is widespread in the sublittoral zone along the rocky coast of the Mediterranean (Bauchot & Guignard, 1973; Voss, 1976). Histological studies of gonads have not revealed hermaphroditism in this species (see FIEDLER, 1964; R. R. WARNER, personal communication). 1 and 2 year old specimens are found during the reproductive season (SOLJAN, 1930b; FIEDLER, 1964). The species is temporarily dichromatic. The largest males in the population adopt a bright colour pattern shortly before the beginning of the reproductive season (description of colour patterns in LAHAYE, 1960; FIEDLER, 1964; LEJEUNE, 1984; colour plates in VOSS, 1976). Smaller males and all females retain their plain colouration (the female colour pattern is described by VOSS, 1976; the plate on p. 97 shows a male and not a female, however). None of the previous studies mention both of the differences between males and females. Only males have opercula lined with a bright red strip on the upper and lower edges and only females have a black semicircular dot at the frontal base of the genital papilla. The intensities of both patterns vary. The reproductive season lasts from April to August (depending on geographic location). Brightly coloured territorial males (T-males) build nests from algae (SOLJAN, 1930a) in which several females spawn. The eggs are protected and fanned by the nest-building male for about 80 hrs (at 21-22°C; LEJEUNE, 1984). The larvae then hatch and leave the nest to join the plankton. Nests are not colonial but aggregated in a favoured habitat (algae covered rocks). Further information on this, and other closely related species, is given by FIEDLER (1964), QUIGNARD (1966), LEJEUNE (1984) and references therein.

Study site

Our observations were made near the STARESO marine institute at Revellata Bay west of Calvi, Corsica. A map and a description of the habitat, annual temperature at 10 m depth and yearly photoperiod are given by LEJEUNE, 1984 (p. 104-105). An approximately 150 m stretch of the coast in front of the institute was surveyed occasionally for nests and marked individuals. The main study area comprised a huge boulder about 40 m south-east of the institute at the tip of a bay. This rock of about 300 m^2 horizontal surface descends perpendicularly from the coast to a depth of 8 m. Its sides are steep escarpments to the bottom, which is 5 to 10 m deep. The bottom is covered with sand or *Posidonia* grass beds. The total area in which most observations were made was about 500 m^2, in horizontal projection, on and around this rock. This includes a defined core area of 250 m^2 in horizontal projection (estimated surface 465 m^2) in which all nests were monitored. The observed nests occurred at depths of 1.1 to 7 m, mostly between 2.5 and 6 m. We occasionally found marked individuals up to 100 m from our study area. The 5 furthest sightings were 100, 100, 70, >40 and 30 m away from our study area. These fish were also seen in the study area that same day or up to 6 days later.

Density

The density of *C. ocellatus* was highest in our main study area. Six different transects across this area, each 15 m long and 2 m wide, were inspected twice between June 23rd and 26th, 1983 (between 12.30 and 20.30 hrs). The density was 0.94 ± 0.30 individuals per m^2 ($\bar{x} \pm s$). LEJEUNE (1984; p. 107-111) recorded a density of 0.34 indiv./m^2 over a wide range of rocky substrates around STARESO at depths of 3-6 m. The highest nest density (recorded 23 May, 1983) in our core study area (465 m^2 estimated surface) was 8 nests/100 m^2, half of which were in the active spawning period. (When a horizontal projection of the inspected area was used instead of an estimated surface measure including escarpments and fissures, the highest density rose to 15 nests/100 m^2). FIEDLER (1964) recorded a maximum of 2.4 nests/100 m^2 at his Jugoslavian study site (calculated from his data of the 1956 spawning season).

Reproductive season

The first nest of 1982 was built on 19 May, when the water temperature was 17.7°C. Temperature on the preceding 5 days was 16, 16, 16.5, 17.3 and 17.4°C, respectively.

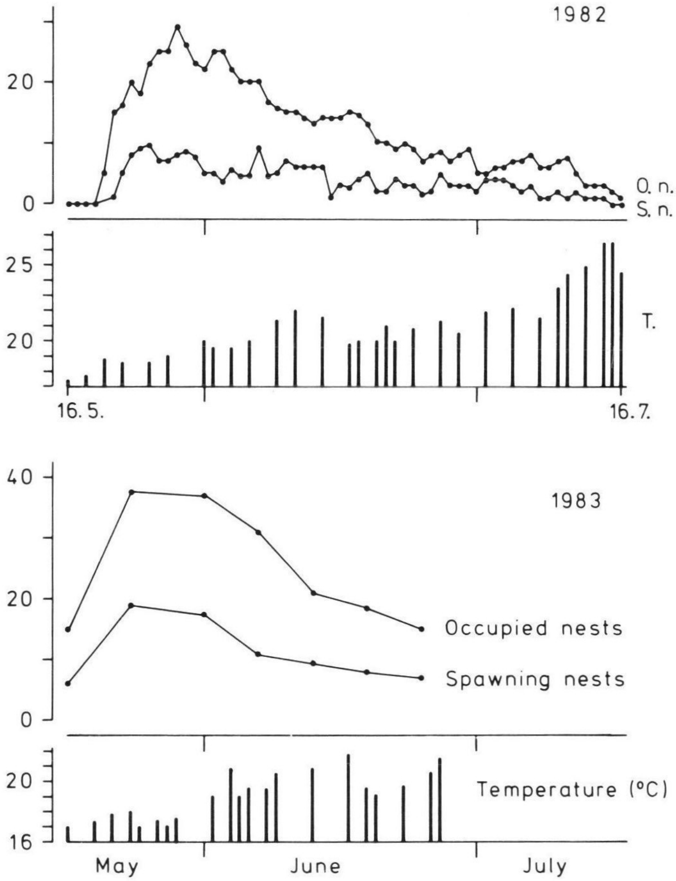

Fig. 1. The number of occupied nests and nests with spawning activity within our core study area (250 m^2 in horizontal projection) during the spawning seasons in 1982 and 1983. Water temperatures are also given.

The first spawnings occurred on 21 May, at a temperature of 19°C (Fig. 1). Six territorial males had already started to spawn (temperature 17°C), when the 1983 observations started on 16 May. This suggests that temperature at the time may not be the critical factor influencing the start of reproduction (compare also nest density and temperature in the course of the season, Fig. 1). Temperature rose above 22°C on 4 July, 1982, reaching 26.5°C on 14 July when the year's last nest with spawning activity was observed. The highest nest frequency for both years was recorded between 21 May and 6 June (Fig. 1). There was no second nest peak as presumed by LEJEUNE (1984). The first young of 1982 appeared in our observation area on 13 August, and were 1.5-2.5 cm long. This suggests that the planktonic phase lasts for less than 50 days, which agrees well with LEJEUNE's (1984) estimate of 46 days, based on otolith analysis of 6 juveniles.

Behaviour patterns

FIEDLER (1964) compared the behaviour of 8 Mediterranean *Symphodus* (*Crenilabrus*) species. We modify and extend his classification of the behaviour patterns of *S. ocellatus*, with particular emphasis on reproductive activities.

Spawning.

The sequence of spawning usually includes 3 successive components. The female bumps her head vigorously against the nest, forming a little hollow. She then performs a curved and accelerated thrust, at the apex of which she pushes her belly (*i.e.* genital papilla) into the hollow. The male spawning follows immediately afterwards or sometimes occurs almost simultaneously. This looks very similar to the female's movement. The male comes very close above the female before spawning, often making direct body contact with her. The initiating head thrusts of the female may be omitted during the spawning series. Neither eggs nor spawn can be seen during spawning.

Courtship.

(i) ''nest showing'' consists of a quick, upward rush by the male, which stops up to *ca* 0.5 m away from the nest. It is followed by a U-turn and a very exaggerated return to the nest with the tail beating at a high amplitude. The nest is sometimes circled in this exaggerated fashion. Often nest showing ends with very intensive fanning (*i.e.* at high frequency and amplitude), which clearly differs from fanning performed as broodcare (''courtship-fanning''; see RIDLEY & RECHTEN (1981) for a possible function). Nes showing is sometimes followed by (ii) ''courtship spawning''. This is a quick series of exaggerated spawning movements performed in the nest, usually when conspecifics approach.

Non-aggressive interactions with females.

(i) ''approach to female'' is a direct motion of up to *ca* 1.5 m towards a female. It is made at a moderate speed, decelerating before the female is reached. If the female turns away she may be followed for a short distance, ignored or chased away; otherwise contact following succeeds. Occasionally a similar kind of approach may be directed against a male, but this is usually terminated prematurely and was not included in the quantitative recordings. (ii) ''Contact following'' consists of a male's winding movements, with head slightly upward, when it is above a female. One or two thirds of his body length overlap with her's (Fig. 2). Sometimes the male touches or pushes lightly against the female's back with his belly. Contact following occurs either when the female is at the nest or swims more or less towards it. It is often initiated by a frontal approach towards the female and a quick U-turn to attain the right position. It is terminated when the female swims away from the nest. She is then often driven away. Contact following is directed against males only occasionally. ''Approach to female'' and ''contact following'' occur during the spawning phase of a nest and only in its vicinity. A male may begin his approach when a female comes within about 2 m of the nest area.

Nest construction.

''Nest building'' includes collecting a piece of alga, transporting it by mouth to the nest (often several meters away, see SOLJAN, 1930) and pushing it into the nest. Material may often also be rearranged within the nest. Nests are about 20 cm in outer diameter and, in our population, consisted mainly of *Cystoseira balearica*, in combination with some other species of algae (see LEJEUNE, 1984). Further data on nests are given by SOLJAN (1930a), FIEDLER (1964) and LEJEUNE (1984).

Broodcare.

(i) ''fanning'' involves rhythmic pectoral oscillations of high amplitude with compensatory movements of the tip of the dorsal fin, (ii) ''feeding in the nest'', by which the T-male (*i.e.* territorial male) consumes tiny gastropods, eggs (presumably rotten, see

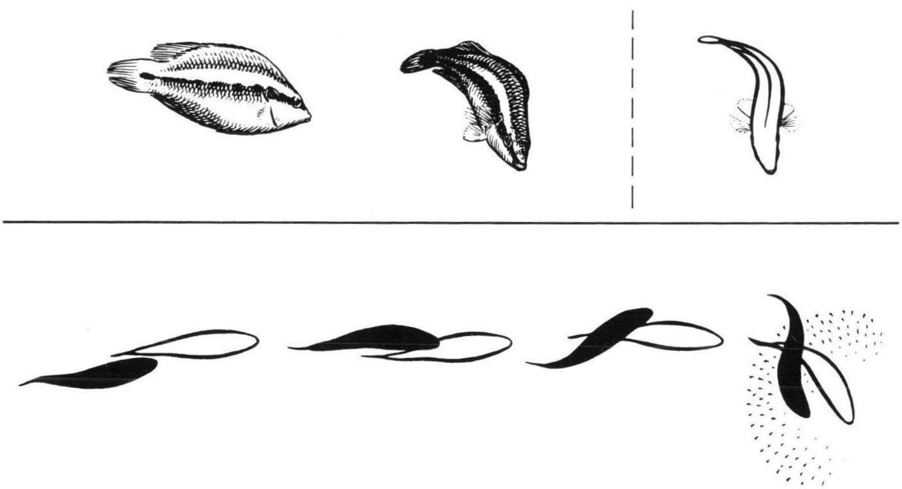

Fig. 2. Above, left: submissive S-bend display of an accessory male (right) in front of an approaching T-male (left); right: S-bend display seen from above. Below: male (black) contact following a female (white) which approaches a nest (stippled circle); seen from above. Drawings made from slides and film by H. Kacher.

below) and other items, (iii) "removing snails and particles": these are mainly conical snails and may be carried several metres away from the nest.

Defence of a territory, especially the nest.

(i) "fast attack", by which a male tries to hit an opponent (female or male) at the apex of an accelerated lunge, (ii) "restrained attack" usually consists of two components - a moderate to fast approach terminated in front of the opponent and spreading the opercula to a variable degree. Sometimes only one component occurs. The opponent is only rarely touched with the mouth, (iii) "fight", which involves parallel swimming, circling, ramming, biting, and mouth fighting. It is described in detail by Fiedler (1964). Fast and restrained attacks are performed against all kinds of opponents, but interspecific aggression mainly consists of the first type. Fights only occur between conspecifics of the same social category, *e.g.* between T-males.

Submissive behaviour of accessory males.

The submissive male bends its body along its longitudinal axis in an S-shape, in front of the dominant (see Fig. 2). It sometimes remains in this position for up to three seconds. Another S-bend in opposite direction often follows. This may lead to a series lasting for several seconds. The dorsal fin is erect at the front and rear, but folded in the middle (see Fiedler, 1964).

There are a few other very rare or highly variable and barely definable behaviour patterns which were not included in the quantitative recordings. These include fin-spreading, which is often combined with other behaviours; head-down display of T-males (see Fiedler, 1964) and an S-bend display of T-males to prevent others from entering the nest.

Methods

All observations were made by SCUBA diving from 16 May to 19 July, 1982 (with additional observations in August) and from 16 May to 28 June, 1983. Five observers spent a total of about 750 hrs in underwater observations. There was no indication of periodicity in reproductive activities during full daylight (see also LEJEUNE, 1984). Observations were therefore spread over the day. 365 specimens were caught, measured (SL, to the nearest mm) and most of them weighed (to the nearest 0.01 g) generally at the start of the spawning season. 354 of them were marked individually by injecting alcian blue into scale pouches and 297 (= 84%) were observed subsequently. They were easily recognizable until the end of each reproductive season, when 31% of the initially marked fish were recaptured. One marked fish, which was found in the next year, could still be easily recognised. All nests within the core area (250 m^2 in horizontal projection, with an estimated surface of 465 m^2) in 1982 were monitored throughout the spawning season ($N = 88$). This included a daily 2 min protocol of reproductive activities at each nest ($N = 572$ protocols). Inspections were made at about 6 day intervals in 1983 ($N = 122$ nests; see Fig. 1). Additional nests were observed daily in other areas outside the reproductive peak. Each nest was marked by a numbered stone and its location was mapped. The activity and location of marked fish were recorded whenever possible, with special attention paid to individuals participating in reproductive activities at and around nests. Temperature was measured on average once every 2.2 days between 10 and 12 a.m. about 40 m from the observation area at a depth of 0.5 m. The 1982 data were compared with continuous measurements made at a depth of 2 m in the middle of Revellata Bay. Since the daily means matched our own samples closely (mean deviation: 0.04 C $\pm$ 0.59; $\bar{x} \pm s$) the measurements were combined to give a temperature profile for the reproductive season (Fig. 1). The thermocline was almost always below 6 m, so daily temperatures were nearly the same at all observation sites.

Classification of accessory males.

Plainly coloured males often participate in reproduction. They occasionally rush quickly into a nest, turn sharply when the nest surface is reached and leave the nest area immediately. This behaviour was termed "sneaking". It starts at variable distances from the nest (up to *ca* 80 cm), usually either during or immediately after (*i.e.* often within half a second) female spawning. It can also happen when a female is not spawning but is near the nest or approaching it (= "sneaking into the empty nest"). Sneaking in *S. ocellatus* was previously viewed as a fertilisation attempt (SOLJAN, 1930a, b; FIEDLER, 1964; LEJEUNE, 1984) and we agree with this interpretation. Nevertheless, direct experimental evidence is lacking as naturally released sperm is not visible in this species. There are four pieces of evidence supporting the fertilisation hypothesis: (i) sneaking usually occurs immediately after a female has spawned. (ii) accessory males release sperm when the abdomen is pressed gently with the fingers. Artificial fertilization experiments have shown this sperm to be viable. (iii) accessory males have huge testes (unpublished data) which do not differ histologically from those of T-males (FIEDLER, 1964). (iv) the development of large testes and the behaviour of these males reduce growth and result in a considerable weight loss (unpublished data). The behaviour, which is performed frequently (see below), presumably involves an additional risk. We observed many attacks (including a successful one) by predators (*Dentex dentex*, *Serranus cabrilla*) against adult *S. ocellatus* at nests in spawning condition. There were none elsewhere. Sneaking is complex and skillful and only occurs in the context described above (spawning is different). At present the only reasonable explanation is that sneaking is an fertilization attempt and may often be successfull. This has been proven experimentally for salmon (*Salmo salar*: JONES & KING, 1952; *Oncorhynchus keta*: SCHRODER & DUKER, 1979; SCHRODER, 1981).

A plainly coloured male sneaking as described was termed sneaker. If a male, besides sneaking, defended the nest area against conspecifics, interacted with females and behaved submissively towards the T-male it was termed satellite. By definition a sneaker only occasionally showed one or the other element of these behaviours, if any. All marked and unmarked males around a nest were classified according to this criterion at each observation period, irrespective of their previous behaviour.

Quantitative measurements of behaviour.

1) Time budgets of territorial males.

Durations of nest building, fanning and the presence of females in the nest were recorded with stop watches, as were feeding frequencies (number of bites) inside and outside the nest. The actual durations of the behaviours were recorded, unlike LEJEUNE's measurements which included pure locomotory and exploratory activities preceding and following the respective behaviours (see LEJEUNE, 1984). Discrepancies between his and our results are mainly due to this. Time per recording was 5 min, distributed over all phases of the nest cycle (N = 164 protocols).

2) Behavioural frequencies of reproductive males.

A marked territory holder or accessory male was selected at a nest in the spawning period and observed for 10 min. Behaviours were recorded with an underwater tape recorder. They included all clearly recognizable behaviours except nest building and fanning, which were included in the time budgets, and purely locomotory and comfort movements (*e.g.* chafing). All behaviours recorded as frequencies generally lasted for only up to one second per single event. Submissive behaviour of sneakers and satellites towards a territorial male or a satellite was recorded with a stopwatch. We recorded the number of males and females in a 2 m circle around the nest at the beginning and end of each protocol. These individuals probably had some relationship with the nest, *e.g.* satellites, sneakers, or females staying at, approaching or leaving it (N = 237 protocols of 10 min each).

3) Male distance from nest.

The territorial male, all satellites and up to 3 sneakers were watched for 5 min each at randomly chosen nests during their spawning period. The distance of these individuals from the nest was recorded at 30 sec intervals. A 1 m surveyor's rod was placed radially from the nest to aid distance estimation. The distance classes were: 0 (*i.e.* in the nest); >0-20 cm; >20-50 cm; >50-100 cm; >100-200 cm; >200 cm (N = 99 protocols).

4) Reactions of territorial males to sneakers and satellites.

During the first 5 min of a protocol the time satellites and sneakers spent in an imaginary sphere 20 cm in radius around a territorial male was measured with two stopwatches. In the second 5 min period each frontal encounter of the territorial male with a satellite or sneaker was recorded, provided it was within 20 cm of and an angle of about 10° to the territorial male's longitudinal axis. Additionally, the territorial male's reaction to the encountered male was classified (lunge, restrained attack or no behavioural reaction). The number of satellites and sneakers around the nest was noted before and after the protocols (N = 23 protocols).

All 4 protocol types described were preceded by a minimum timespan of 2 min during which the observer lay quietly in position without recording, allowing the subjects to habituate to his or her presence. *S. ocellatus* generally did not seem to be disturbed by observers. Observations were only made at nests in spawning condition in all protocol types except (1). All available nests in the core study area were used for the quantitative recordings when possible. Individually marked fish were preferred, for practical reasons, when available at a chosen nest.

5) Reproductive behaviour of females.

Individual females were followed for 30 min to record all nest approaches and spawnings as well as location (nest number), time of occurrence and interactions with males. Previous observations had shown that all recorded females were in spawning condition. Some protocols were terminated prematurely because the focal female was lost from sight. The mean recording time was 23.6 min (only protocols >10 min were analysed, N = 38 protocols of 35 females). The visited nests and all those nearby in spawning condition were noted for all but one of these recordings.

Medians and nonparametric statistics were used when data differed from a normal distribution ($p<0.1$). Probabilities given in the text are two-tailed, unless otherwise stated. s = standard deviation.

Results

1. Territorial males.

In 1982 all captured males >6.2 cm (size range: 6.9-8.0 cm; $\bar{x} \pm s$: $7.27 + 0.30$) and in 1983 all >6.8 cm, except two (size range: 6.8-8.15 cm; $\bar{x} \pm s$: $7.73 + 0.23$), displayed the bright T-male colour pattern (significance of the size difference between both years, $p<0.001$; T-test, N = 37 + 41; members of both sexes and all social categories were significant larger in 1983 than in 1982). T-males were also heavier than plainly coloured fish ($p<0.001$; T-tests, various sample sizes), with hardly any overlap (see Figs 3 and 4 for a size and weight comparison of the different types of fish).

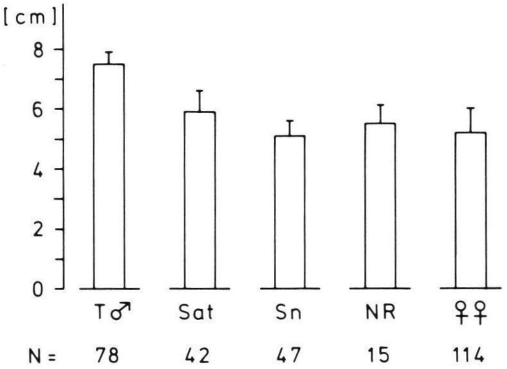

Fig. 3. Standard lengths ($\bar{x} \pm s$) of T-males, "satellite individuals", "sneaker individuals", non-reproductive males (NR) and females.

a) *Nest cycle.*

The nest cycle contains three phases: nest construction, spawning and broodcare. The limits of these phases are defined by the onset and end

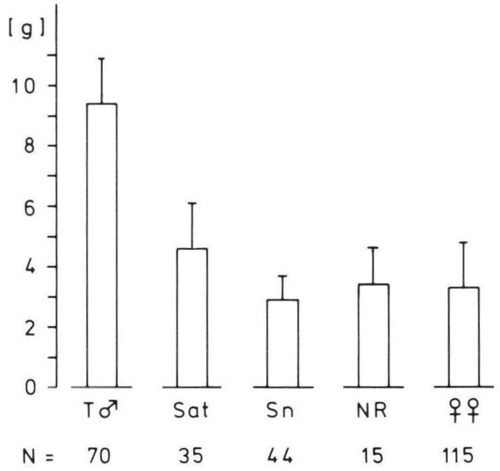

Fig. 4. Weights ($\bar{x} \pm s$) of T-males, "satellite individuals", "sneaker individuals", non-reproductive males (NR) and females.

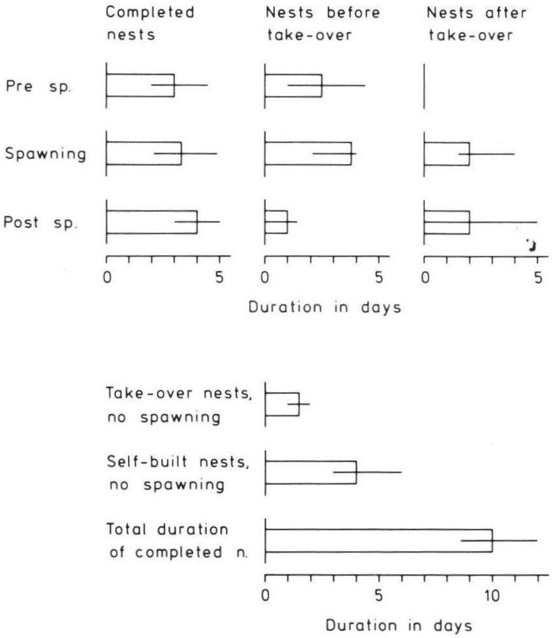

Fig. 5. Durations of nest phases. Medians and interquartile ranges are given. The number of T-males involved: above, from left to right: N = 27, 16, 7; below, from top: N = 16, 15, 27.

of spawning. Completed nests were occupied for a median total period of 10 days (Fig. 5; N = 27 T-males with an average of 1.7 nests/T-male). Nests in which we did not observe spawning, either because it did not occur at all or only very rarely, were left after a median period of 4 d (N = 15 T-males with an average of 1.2 nests/T-male). The mean nest duration in our total sample is thus 7.7 d. This is similar to FIEDLER's (1964) mean nest interval of 6.75 d for 20 individual T-males and LEJEUNE's (1984) result of 7.8 d for the population we studied. Non-spawning T-males with fully constructed nests remained in them for longer than the average duration of the prespawning phase ($p<0.05$; Mann-Whitney U-test, N = 15+43). This suggests that nests are left after a certain amount of time has been spent unsuccessfully attempting to attract females. The median time interval between the abandonment of one unspawned nest and the beginning of another was 1 day (quartiles: 0 and 1.3 d; N = 15 T-males with an average of 2.2 nest intervals/T-male).

26 marked T-males observed in 1982 had a median of 3 successive nests per season (quartiles: 1 and 5, range: 1-9). In 1983, 28 T-males observed until July 26th (*i.e.* not during the whole spawning season) had a mean of 2.57 nests. This matches the data of the previous year: The T-males then had a mean number of 2.64 nests before 26 July in 1982. Many males left the observation area after completing one or two nests. Some may have bred again elsewhere. This suggestion is supported by an increase in new (= unmarked) T-males building nests in the observation area towards the end of the season; from 29 July the ratio of unmarked/marked T-males increased ($p<0.05$; χ^2-test, N = 108 nests subdivided into 10 d periods, nest take-overs included). If only the T-males that spent most of their time in the observation area are analysed (>30 d, including the most active time of the season), then the median number of nests per T-male was 5 (quartiles 3 and 6.25; N = 10 T-males). On average, 3 of these were completed and 2 were unsuccessful. We suggest that 3 (estimate of the total sample) to 5 nests/season marks the limit between which the true mean of successive nests of a T-male lies.

b) *Time budgets.*

Time budget data of T-males throughout the nest cycle are given in Fig. 6. Nest building and fanning constitute a major effort by T-males (together they total an average of 33% to 62% of each day in a nest cycle). In the prespawning phase T-males spent about 22% of their time

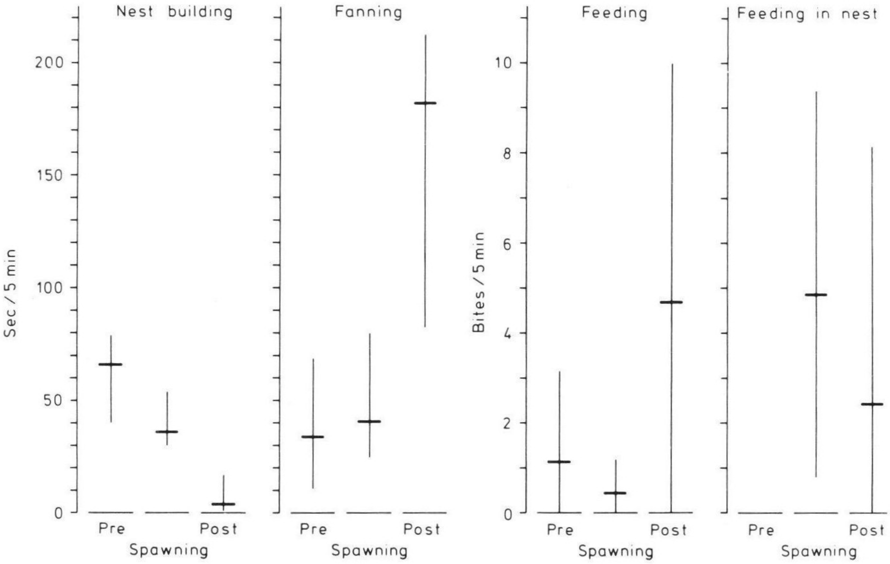

Fig. 6. Durations of nest building and fanning behaviour and frequencies of feeding in the nest and feeding elsewhere (= "feeding") over the nest cycle. Number of T-males involved in the three phases: 10, 28, 15 for nest building and fanning; 10, 26, 15, for feeding and 7, 17, 10 for feeding in the nest.

with nest building behaviour. They rarely fed or fanned. In the spawning phase nest building and fanning counterbalanced each other and most feeding took place in the nest (comparison of feeding inside and outside the nest: $p<0.01$; Wilcoxon matched-pairs signed-ranks test, $N=16$). Nest building declined between spawning and postspawning ($p<0.001$; U-test, $N=28+15$), while fanning greatly increased ($p<0.001$; U-test, $N=28+15$). T-males fanned on average for over 60% of the postspawning phase. Feeding outside the nest was more frequent during this time than in the spawning phase ($p<0.05$; U-test, $N=26+15$). There were no trends within the phases, except for a tendency to increase fanning on the last day of spawning.

Four T-males had two nests simultaneously, one in the post- and one in the prespawning phase. All nest building activity was performed in the new nest and all fanning in the old. This contradicts FIEDLER's (1964) suggestion that T-males cannot start a new nest during the broodcare or spawning phases. Another T-male spawned on one day and built another nest the next day, where it spawned again a day later.

Courtship behaviour was only measured quantitatively during the spawning phase. It declined during this period (Table 1). The number of nests in which nest showing and courtship spawning occurred and the duration of these behaviours per recording correlated negatively with the course of the spawning phase ($rs = -1.0$, $p = 0.01$ and $rs = -0.9$, $p = 0.05$, Spearman rank correlation tests, one-tailed, $N = 5$ days).

TABLE 1. The occurrence (in percent of the number of sampled nests) and frequency of courtship behaviour at nests in the spawning phase

	Days with spawning activity				
	1	2	3	4	≥5
% nests with nest showing	61.5	26.9	21.4	20	0
% nests with courtship spawning	53.8	26.9	21.4	20	11.1
Frequencies ($\bar{x}$ per 10 min) of nest showing	5.3	6.9	4.4	2	0
Frequencies ($\bar{x}$ per 10 min) of courtship spawning	3.9	6.9	1.7	1.5	1
Sample size	13	26	14	10	9

Nests lacking courtship were excluded from the frequency figures.

c. *Spacing*.

T-males were involved in nesting during most of their time in the main study area (on average 13.6 d compared to 3.1 d without nests; $N = 38$ T-males). The number of T-males recorded there without a nest was low, particularly during the peak of reproduction (in 1982 21 May-29 July). T-males' home ranges measured up to *ca* 140 m^2 (in horizontal projection) while they were in the study area. However the area encompassing successive nests of a T-male was much smaller (see Fig. 7 for average distances between successive nests). There were no fixed territory borders (see also FIEDLER, 1964) and no indication of a preference for certain nest sites.

Different types of conspecifics and fish of other species are attacked at different distances from the nest. Habitat geography and the phase of the spawning cycle also influence attack distance. A radius of 1 to 4 m around the nest is defended against strange T-males. Short fights between neighbouring T-males and displays including fin-spreading, parallel swimming and restrained attacks occur very rarely. All other conspecifics are attacked up to 2 m from the nest; the closer they come the more often they are attacked, especially during the spawning phase.

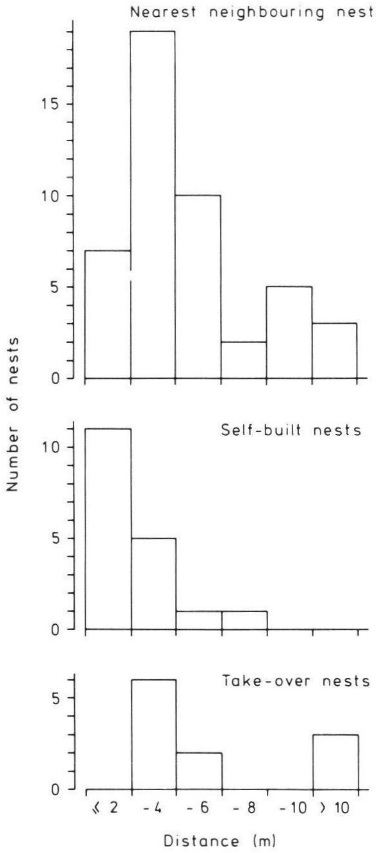

Fig. 7. Frequency distributions of distances between nearest neighbouring nests, successive self-built nests and between self-built and subsequent take-over nests.

Most interspecific attacks occur within 2 m from the nest and are directed against congeneric species. 79.1% of lunge and 65.2% of restrained attacks were on *Symphodus tinca*, *S. mediterraneus* and *S. quinquemaculatus* (N = 107 10-min recordings of 28 different T-males at 38 nests, during which 117 aggressive and 35 restrained attacks occurred; median frequency/10 min = 0.5, quartiles 0.12 and 1.92, for pooled attack rates). This can not be solely attributed to fish densities (cf. LEJEUNE, 1984 for a comparison of *Symphodus* spp. with *Coris julis*, as counted in and around our study area). Two further species, *Chromis chromis* and *Labrus bergylta*, each received more than 5% of all interspecific attacks. Fights with *S. quinquemaculatus*, *S. tinca*, *Coris julis* and *Chromis chromis* were observed. Most of the attacked species are nest predators; one *Chromis chromis* male was a space competitor of a T-male.

The median distance between neighbouring nests in spawning condition was 4 m (see Fig. 7; quartiles 2.5 and 5.55, range = 1-13 m; N = 46 distances between 63 nests, each distance was included once only in the analysis). Sometimes neighbouring nests were as little as one or two metres apart and in full sight of each other. This contrasts with FIEDLER's suggestion (1964) that this would never happen. Successive nests were built by an individual at a median distance of 1.95 m from the previous nests (quartiles 1.2 and 3.12, range = 2-7 m; N = 18 T-males, with a mean of 2.33 nests each).

d) *Nest take-overs.*

All nests in the main study area were observed daily in 1982. A change of ownership was recorded in 24 out of 88 cases (= 27.3%). 20.8% of nest acquisitions occurred before spawning was observed, 29.2% during spawning and 50% in the postspawning phases. At least some of these acquisitions were aggressive replacements: In 3 cases the previous owners approached their former nests repeatedly and were repelled by the new owners for up to three days after the take-over. In two additional instances the previous owners finally regained their nests after 1 and 6 days. In one of these, the original take-over male later regained the nest. One escalated fight lasted >35 min. The previous owner expelled its opponent after more than 280 mouth rammings and 30 body rammings. However, the winner was badly wounded and disappeared three days later. 12 out of 13 individually marked replacement males also built their own nests. They were on average slightly larger and heavier than other T-males but the differences were not statistically significant (U-tests, N = 9+28 and 9+24). Four out of five new owners were larger and heavier than their predecessors. The durations of the prespawning and spawning phases of subsequently acquired nests did not differ from those of the rest of the population (U-tests, N = 16+27 and 16+28; see Fig. 5), nor did the spawning rates before take-over (U-test, N = 8+54 nests) or the sizes and weights of the nest owners (U-tests, N = 9+28 and 9+24). These results suggest that neither the size nor the success of a T-male predict whether its nest will be acquired by a competitor.

The median distance between a taken-over nest and the preceding self-built nest of the usurper was 4 m (quartiles 3 and 10.7, range 2.5-13 m; N = 11), which is further than the distance between two successive self-built nests ($p<0.001$; U-test, N = 11+18, see Fig. 7). The time interval between two successive nests was shorter when the second one was a take-over (medians 0 and 1 d; $p<0.02$; U-test, $N = 11+15$).

There are two functions of nest take-overs: either the successors spawned (7 T-males) or at least courted (1 T-male) in the acquired nest (33.3%), or only fed there (16 T-males, 66.7%). In the latter, the T-males kept their acquired nests for a median period of only 1.5 days. This is significantly shorter than the prespawning phases in self-built nests (median = 3; $p<0.01$; U-test, $N = 16+43$; see Fig. 5). This suggests that the purpose of these take-overs was merely nutritional and not for reproduction. However, the new owners fanned in 11 out of 16 of these nests. This fanning did not differ from ordinary fanning in any obvious way. We measured the amount of fanning of one T-male on two different days. It was within the interquartile range of postspawning phase fanning in self-built nests. Four of the nests acquired for feeding were in the spawning phase at the point of take-over, 10 in the postspawning phase and in 2 we had not observed any spawning.

The lengths of the spawning and postspawning phases in nests acquired for reproduction did not differ from those of self-built nests (U-test, $N = 7+28$ and $7+30$; see Fig. 5). However, there was no prespawning period in these nests; spawning always occurred on the day of the take-over. Thus acquiring a nest reduced the interval between the completion of one nest and the first spawning in the next (medians 0.25 and 3.95 d; $p<0.02$; U-test, $N = 4+12$). The spawning rate did not differ from that at self-built nests (U-test, $N = 5+54$ nests). One of the nests acquired for spawning was taken over in the prespawning phase, 4 during spawning and 1 in the postspawning phase. The phases in the remaining two cases could not be identified.

e) *The nest-presence of accessory males.*

We recorded the number of sneakers in a radius of about 2 m around each of 59 nests of 45 different T-males in the spawning phase. Several measurements were frequently taken at the same nest on successive days, but only the mean per nest was used for further analyses. The number of sneakers simultaneously present at a nest ranged from 1 to 14 (excluding times when nests were without sneakers), with a median of 3 (quartiles: 1 and 5.7). Sneakers were found in the vicinity of only 3 out of 58 nests (= 5.2%) in the period before the first spawning was observed at that nest. On the first day of spawning there were sneakers at 25 out of 59 nests (= 43.1%; 12 times ≤ 3 individuals, 13 times >3). We noted the numbers of sneakers around a nest at the start of 115 10 min observations. In all but 11 instances this number had changed after 10 min, by a median of 30% of the initial number (quartiles: 14.3 and 60%). In 70 instances we checked whether an individual sneaker was present at the same nest on successive days (*i.e.* 14 individuals, and a mean of 5 nests/indiv.). The median duration of a sneaker's presence at a given nest was 1.58 days (quartiles: 1.15 and 1.87; 14 individuals).

Satellite males were present at 57 out of 67 nests (= 85.1%) for some time during the nest's spawning phase in 1982. The proportion was 77.4% (n = 84 nests) in the following year. We made a total of 104 inspections at 53 nests of 40 different T-males where satellites were present. Three satellites were simultaneously present on one occasion (= 1%), two on seven (= 6.7%) and one in each of the remaining cases (64 individual satellites were involved). 26 out of 58 nests (44.8%) checked for satellites and for spawning, had a satellite before the first spawning was observed (2 satellites in 4 cases, 1 in 22). This was usually on the day before spawning was observed (20 out of 26 instances). Satellites were present at 39 out of 59 nests (= 66.1%) on the first day of spawning. This is a higher proportion than that for sneakers ($p < 0.02$; χ^2-test, N = 118). The presence and number of satellites at nests in spawning condition differed only 3 times between the start and end of 109 10 min observations. We noted how long an individual satellite stayed at a nest in spawning phase on 75 occasions over successive days (*i.e.* 15 individuals, with a mean of 5 nests/indiv.). This was 2.92 days (= median, quartiles: 2 and 3.18; N = 15 indiv.). As these males occasionally behaved like sneakers (see below), the median time for which they showed all the features of a satellite at a given nest was 2.5 days (quartiles: 1.86 and 2.82; 15 individuals). Both are significantly longer than the average time a sneaker remained at the nest ($p < 0.001$ and $p < 0.01$; U-test, N = 14 + 15 for both comparisons).

12 T-males in spawning phase were experimentally removed from their nests. A satellite was present in three of these instances. They continued to defend the nests against conspecifics other than T-males; once also against specimens of *S. tinca* and *S. roissali*. The satellites started feeding extensively in the nest within 15 min. They occasionally tried to spawn with females. In no instance of artificial or natural T-male replacement did a satellite take over the nest, defend it against T-males, court, fan or perform nest building behaviour. However, other T-males frequently did. None of the individually marked kleptogamic males changed to T-male colouration within a reproductive season.

2) A quantitative comparison of the behaviour of reproductive males.

Fig. 8 compares attack rates of reproductively active males at or near a nest in spawning condition. An average was taken of all of an individual's protocols at one particular nest ($\bar{x} = 1.6$). This yielded 32 means from 20 sneakers, 64 from 40 satellites and 53 from 40 T-males. Only nests with a satellite at the time of measurement were included. This coincided with the presence of sneakers in all but one protocol. Differences were analysed using the U-test.

Sneakers attack males and females less frequently than do satellites or T-males ($p<0.001$ for all categories). Satellites attack females (lunge attacks $p<0.02$, restrained attacks $p<0.05$) and sneakers ($p<0.001$ for lunge and restrained attacks) more often than do T-males. There is no significant difference between the total attack frequencies on accessory males by T-males and satellites (see Fig. 8). Strange T-males are attacked exclusively by the nest owner. We observed a satellite displaying against

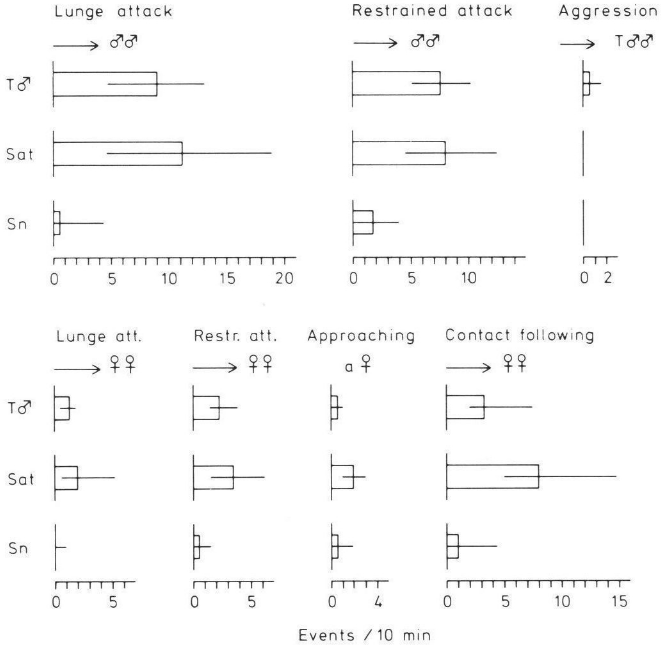

Fig. 8. Attack rates of T-males, satellites and sneakers (ordinate) on conspecific males other than T-males, on T-males and on females (see heading of each graph for receiver of the behaviour). Non-aggressive interactions with females are also given. Sample sizes are in the text.

a strange T-male on only one occasion. Satellites approach and follow females more often than do T-males ($p<0.001$ for both categories), who contact follow females more often than do sneakers ($p<0.001$).

Fig. 9 compares the feeding, submissive and reproductive behaviour of the different male types. Sneakers feed more than T-males or satellites when all three kinds are reproductively active ($p<0.01$ for both comparisons). Sneakers and satellites feed almost exclusively outside the nest, but T-males make more than 95% of their bites inside it (Fig. 6). Two T-males with high nest-feeding rates in the spawning phase had 27 and 38 eggs in their guts, a few of which were developed. We found 3 eggs in the gut of a third nest-feeding T-male in postspawning phase. Satellites spent an average of 2.33% of their time at a nest with displaying submissively towards the T-male. This is very different from the minute amount of submissive behaviour exhibited by sneakers ($p<0.001$). The latter show more S-bending in front of satellites than of T-males ($P<0.001$; Wilcoxon test, $N = 17$). The number of T-male spawnings far exceeds the sum of individual satellite and sneaker's spawnings and

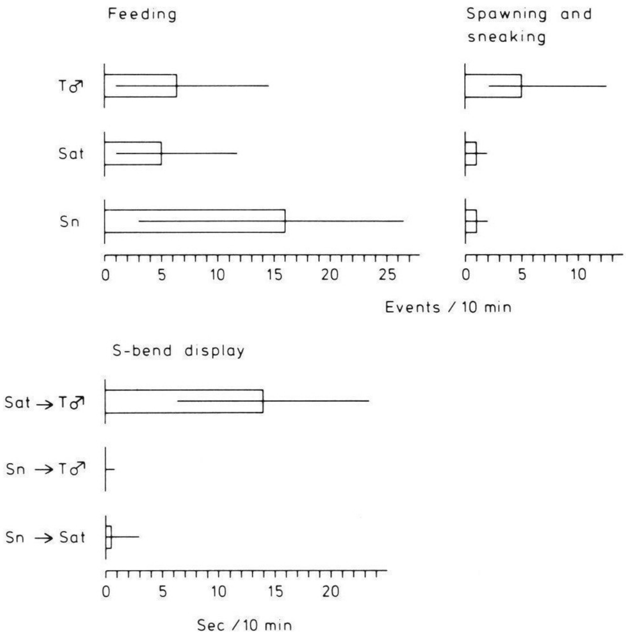

Fig. 9. Frequencies of feeding and fertilisation attempts of T-males, satellites and sneakers; durations of submissive behaviour of satellites and sneakers. Same sample sizes as in Fig. 8.

sneakings ($p<0.001$ for both comparisons). These totals do not differ between satellites and sneakers, nor does the number of sneakings alone. However, the frequencies of spawnings and of sneaks into the empty nest (*i.e.* without immediate female spawning) were higher for satellites ($p<0.05$ for both comparisons).

3) Distance from nest during reproductive activity.

The median distances from nests of 22 T-males, 17 satellites and 16 sneakers present at 26 nests in spawning phase were analysed. Protocol medians were combined for each individual (mean number of protocols per individual = 1.8). Fig. 10 reveals that T-males were on average closer to their nest (median = 5 cm) than were satellites (median = 35 cm; $p<0.001$; U-test, $N = 22+17$), which in turn were closer than sneakers (median = 75 cm; $p<0.005$; U-test, $N = 17+16$). 11 T-males, 11

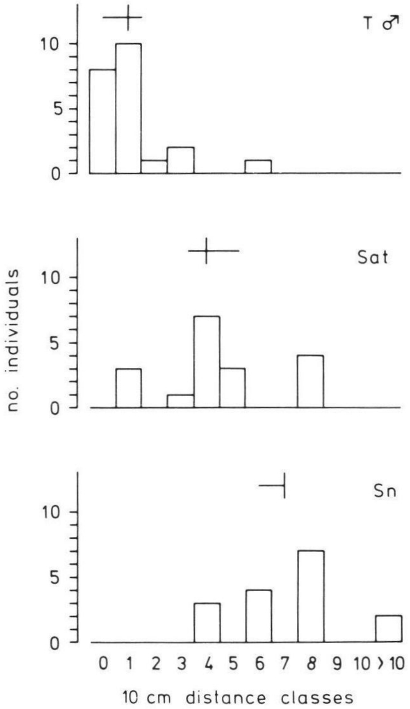

Fig. 10. Frequency distributions of median distances of T-males, satellites and sneakers from the nest. Ordinate: number of individuals. Abscissa: 10 cm distance classes (*e.g.* all distances between 1 and 10 cm belong to class "1"). Medians (= vertical lines) and interquartile ranges (= horizontal lines) are marked above the frequency histograms.

satellites and 2 sneakers observed during the pre- and postspawning phases at unsuccessful nests (N = 12 different nests) showed a similar result (the respective medians were 2.5, 45 and 112.5 cm for T-males, satellites and sneakers). No correlation was found between the simultaneously measured distances of T-males and either satellites or sneakers from the nest.

We recorded the amount of time satellites and sneakers spent within 20 cm of a T-male at 23 nests in spawning condition (N = 20 T-males; mean number of satellites and sneakers per nest = 1.13 and 4.1, respectively; individuals may have been recorded more often than once as many were unmarked). On average a satellite male spent twice as long within 20 cm of a T-male as did a sneaker (Fig. 11). Satellites at 22 nests spent more time than sneakers inside this radius; the opposite occurred at 1 nest ($p < 0.001$, sign test). One would expect that sneakers do not mutually influence their distance from the nest. This was supported by a positive relationship between the number of sneakers present at a nest and the time some sneaker was within 20 cm of the T-male ($r_s = 0.78$; $p < 0.005$, Spearman rank correlation analysis, one-tailed; N = 11).

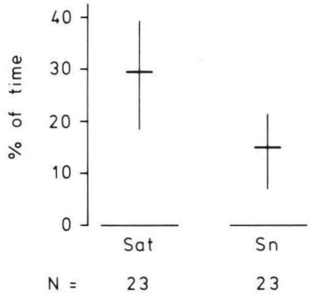

Fig. 11. Proportions of time some satellite or sneaker was within 20 cm of a T-male. Medians and interquartile ranges are given.

4) The behaviour of T-males towards satellites and sneakers.

T-male aggression against conspecific males other than T-males (see Fig. 8, upper left) was classified as attacks on satellites or sneakers for all nests where both types were present (N = 51 nests of 40 T-males, each nest mean is derived from an average of 2 protocols). Most T-male attacks were against sneakers ($p < 0.001$ for combined attack frequencies; Wilcoxon test, N = 51). This is despite satellites spending an average of twice as long a short distance away from T-males (see above) and having markedly more frontal encounters with them. The T-male encountered satellites more often than sneakers in 19 out of 22 recordings at different nests ($p<0.005$, sign test). Additionally, the ratio of T-male lunges to restrained attacks was lower against satellites than sneakers (median attack ratio = 0.74 for satellites and 1.44 for sneakers; $p<0.001$; Wilcoxon test, $N = 44$).

We recorded T-males' reactions to frontal encounters with satellites and sneakers at 22 nests ($N = 20$ T-males). Fig. 12 shows that in nearly 70% of cases a T-male did not react at all to a frontal encounter with a satellite 20 cm or less away. This figure was 37% for sneakers ($p<0.001$; U-test, $N = 22+21$). On the other hand a sneaker was more than 4 times more likely to receive a lunge attack when encountered by a T-male than was a satellite ($p<0.001$; U-test, $N = 22+21$). There was no difference in restrained attacks. These results suggest that satellites are more tolerated by T-males than are sneakers.

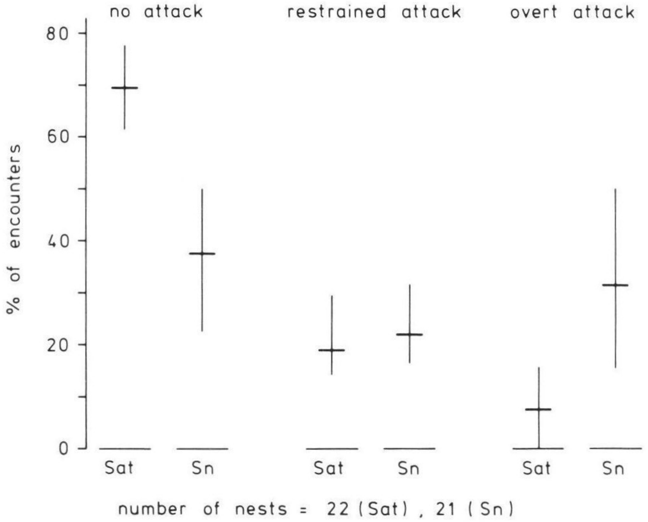

Fig. 12. Reactions of T-males to frontal encounters with satellites and sneakers. Median proportions with interquartile ranges of three different types of reactions are given.

5) "Sneaker individuals".

Many of the kleptogamic males never displayed satellite behaviour. These fish are defined here as "sneaker individuals". They were 4.1 to 6 cm long (Fig. 3) and weighed 1.55 to 4.85 g (Fig. 4). "Sneaker individuals'' participated in reproduction at an average of 6 nests in a season (= median; quartiles: 4.5 and 7.75; N = 8 individuals observed for >20 days each, mean observation period = 39 days). The nests visited by one ''sneaker individual'' were situated within an estimated 98 m^2 in horizontal projection (= median; quartiles = 80 and 146 m^2; N = 8 individuals, mean number of sightings = 22). This is perhaps close to the total area regularly patrolled by these males. Marked individuals were not often found in areas adjacent to our main study site, where nests were relatively scarce and further apart.

6) ''Satellite individuals''.

Males which at least sometimes behaved like satellites are termed ''satellite individuals''. They were larger than ''sneaker individuals'' ($p<0.001$; T-test, N = 42 + 47; Fig. 3) but nearly always smaller than T-males (40 out of 42 satellites). Their weights were also intermediate ($p<0.001$ and $p<0.001$; T-test, N = 35 + 70 and 35 + 44; Fig. 4). ''Satellite individuals'' often appear more reddish with pronounced contrasts between dark and light parts of the body, which may be partly a sudden colour adjustment: their colouration was seen to fade when they had lost a fight for a satellite position or when they were foraging away from a nest. THRESHER (1979) described a similar conditional colour change in a wrasse. ''Satellite individuals'' stayed at a median of 10.5 nests in spawning condition during a reproductive season (quartiles: 7 and 13.25; N = 10 individuals observed for >20 days each, mean observation period 45.8 days), but behaved like satellites at a median of only 6 nests (quartiles 4 and 10.25). ''Satellite individuals'' visited nests within 155 m^2 in horizontal projection (= median; quartiles: 90 and 205 m^2; N = 10 individuals observed for >20 days, mean number of sightings = 27). This is not significantly different from the respective measure for ''sneaker individuals''.

The proportion of time the satellite role is performed depends on body size. The larger a ''satellite individual'', the more often it adopted the satellite rather than the sneaker role ($p<0.001$; Fig. 13). This is perhaps mainly due to position in the size hierarchy of accessory males around a nest: Five ''satellite individuals'', each of which was the largest accessory male at a nest, were each observed on an average of 20 occasions. They behaved like a satellite in 80, 90.9, 95.8, 100 and 100% of the cases in which they were observed. The comparable percentages for 6 ''satellite individuals'' which were not the largest accessory males at a nest, observed on an average of 10 occasions, were 0, 25, 33.3, 37.5, 38.5

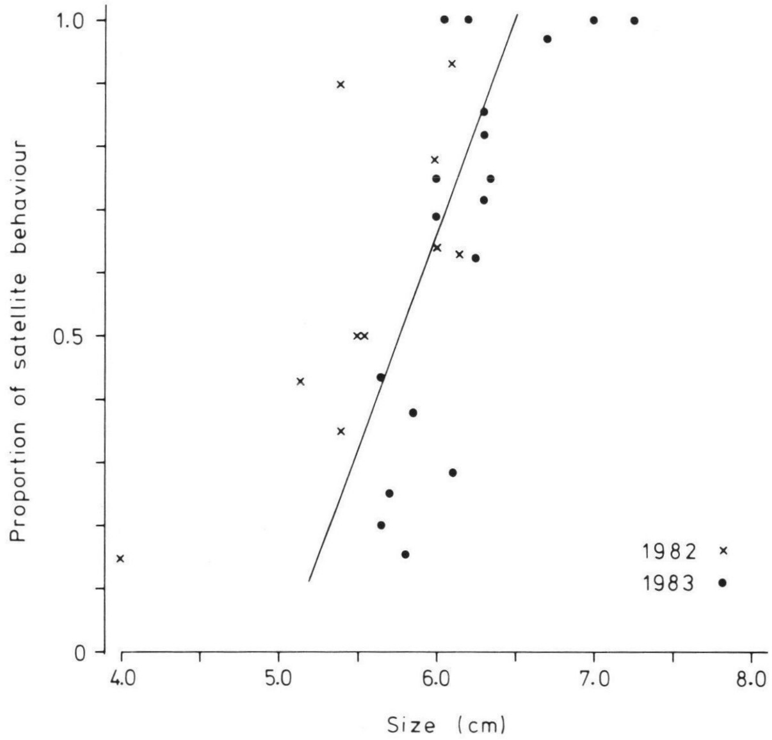

Fig. 13. Proportions of observations during which satellite individuals of different sizes performed satellite instead of sneaker behaviour. Values of individuals and the linear regression are given (r = 0.67).

and 52.9%. The differences between these two sets of proportions is highly significant ($p<0.005$; U-test, N = 5+6). The absolute size of males in these two groups overlapped completely; two individuals are contained in both groups.

7) Non-reproductive males.

Not all marked males engaged in reproduction during a specific year. Some, observed repeatedly in the study area, never stayed at a nest or displayed any reproductive activity. 15 males were classified as non-reproductive by their behaviour. They were observed on an average of 4 different days over a mean timespan of 17 days. They fed for most of the time. The testes of 13 of them were examined. All had very small testes (<0.05% of body weight, except one with 0.69%), in contrast to those of reproductive males (unpublished data).

The sizes and weights of non-reproductives overlap with those of sneakers and satellites (Figs 3, 4). Preliminary otolith analyses suggest that these males have equal ages (unpublished data). Colouration is also similar, though the non-reproductive males often appear paler and more greenish than the kleptogamic ones. This may reflect a temporary pattern, as in satellites. Reproductive males sometimes turn much paler when they join a foraging group. The sizes and memberships of these foraging groups of females and different types of males change frequently. Feeding schools were large towards the end of both reproductive seasons (up to 28 individuals, on 10 July, 1982), but rather small before *ca* 20th June, *i.e.* animals then fed less and/or more solitarily. Feeding aggregations are sometimes heterospecific. The species which mingle most frequently with *S. occelatus* are *S. tinca*, *S. quinquemaculatus*, *S. rostratus* and *Coris julis*. Often several *S. occelatus* follow a large *S. tinca* and feed on the remnants spreading from its mouth when it scrunches large pieces of algae.

The median estimate of the areas visited by marked non-reproductive males was 83 m^2 in horizontal projection (quartiles: 65 and 118 m^2; N = 8 individuals, all except 1 observed for >20 days; mean number of sightings = 7). The males hardly ever approached nests, although they sometimes fed near-by. Social interactions were very rarely observed. We saw a non-reproductive male feeding in a nest on four occasions (N = 3 different males), in two of which the nest was defended by a T-male in the spawning phase.

8) Females.

Females range from 3.7 to 6.8 cm, overlapping in size and weight with sneakers and non-reproductive males (Figs 3, 4). They are smaller and lighter than T-males and satellite individuals ($p<0.001$ for all comparisons; T-test, N = 114+78, 115+70, 114+42 and 115+35). 50 females were observed on >4 different days and the mean number of sightings was 5.25. Only 4 of the females caught for a gonadal check were never seen before at or in a nest in its spawning period. There were no undeveloped gonads in 38 dissected females. The minimum gonad weight, 0.17% of body weight, came from a female which had been observed spawning (cf. the minute gonads of non-reproductive males). We conclude that all females on the study site participate in reproduction every year.

FIEDLER (1964) reported rhythmic oogenesis. He and SOLJAN (1930b) remarked that female scales alone had 3-4 growth interruptions within a given spawning season. They concluded that this might result from different spawning intervals. Our data from marked females observed either when spawning or at least in or at nests in spawning condition are compatible with this hypothesis. 29 females were observed spawning or visiting spawning nests on more than one day within 6 days, 9 even within 3 or 4 days. 6 days seems to be the maximum length of a female spawning cycle, although our data do not permit a conclusive statistical analysis. Assuming this maximum cycle length of 6 days, we observed 29 females with two, 7 with three and one female with 4 successive spawning cycles. The interval between first and last observed spawning was, on average, 34.6 d for the 8 females with ≥3 observed spawning cycles. 27 females in spawning condition, followed for an average of 25 min, visited a nest every 2 min ($\bar{x} \pm s$: 120 ± 44 sec). The average timespan between two successive spawnings was *ca* 5.5 min (median 332 sec; quartiles: 228 and 550).

"Available" nests were defined as those with spawning activity which were either entered by an individually observed female or situated within 3 m of these nests. 3 m is a conservative estimate, as females often directly approached a nest from much larger distances. More than one nest was available to the observed female in 24 out of 37 protocols but all of them were visited in only 4 instances. Only one nest was entered in recordings of 25 females. 11 of the remaining 13 females, which all visited more than one nest, did not spawn in all of them. Only two out of 35 females spawned in 2 nests and one in 3. All others spawned repeatedly only in one nest when we followed them for nearly half an hour. This female conservatism is perhaps not due to their choice of individual T-males. 4 out of 12 females observed when spawning on successive days did not spawn with the same T-male, although the latter was still in spawning condition. 17 females observed on successive spawning cycles (*i.e.* >6 days apart) spawned in a total of 35 nests after the first observed cycle. A female spawned again with the same T-male on only one of these occasions.

The area in which all sightings of an individual female were made was estimated for each of 18 females. They were observed on an average of 9 occasions over a mean timespan of 42 days (minimum: 4 sightings within 24 days). The median estimate of a female's visited area was 138 m^2 (quartiles: 77 and 200). 11 females, each observed spawning in ≥3 different nests, distributed their eggs in nests located within an area of 68 m^2 (= median; quartiles: 51 and 88).

Discussion

1) A comparison of reproductive males.

a) *Spacing and nourishment.*

T-males build several successive nests within a defended area. Attack distances from the nest and intensities of aggression vary according to the intruder. They include vigorous attacks on even remote conspecific T-males, interspecific defence against congeneric species at medium distances and lunges and threats against small conspecifics close to the nest. This is perhaps best described as "serial territoriality" (MYRBERG & THRESHER, 1974; THRESHER, 1976). Attack readiness varies not only with the intruding species but also with the type of conspecific and the reproductive phase of the T-male. The take-over of neighbouring nests results in a shift of the defended area. The latter is abandoned when no more nests are built or taken over.

T-males feed about as much inside the nest as outside. There are several explanations for foraging inside. They may be forced to do so by their increasing hunger and/or because they cannot leave the nest area to forage. They may consume eggs and/or egg predators (*e.g.* snails). These explanations are not mutually exclusive. They may be tested by looking at the distribution of feeding inside and outside the nest during the nest cycle (Fig. 6) and by carrying out gut analyses. (i) Increasing hunger is probably not a prime reason for feeding in the nest, which declines from the spawning to the postspawning phases. Feeding outside the nest greatly increases between these phases. (ii) Feeding inside instead of outside the nest cannot be explained by the need to stay at the nest. The proportion of nest-feeding is much higher in the spawning than in the postspawning phase. However, time spent in the nest increases towards the postspawning period, when T-males spend on average 3/5 of their time fanning. (iii) T-males very likely consume egg predators in the nest. There was a higher density of predatory snails in *S. ocellatus* nests than in nearby comparable algae (C. MICHEL, pers. comm.). This difference was high during the night, when T-males are inactive, but more or less negligible during the day. Additionally, many small molluscs and worms were found in the guts of 3 T-males after nest feeding. (iv) T-males feed on eggs in their nests. We conclude that feeding in the nest serves both functions, *i.e.* reduction of egg predators and ingestion of eggs. It is at present unclear whether fertilised, developing, healthy eggs constitute a large part of those consumed or whether most or all are dead.

Most nests in the spawning phase are attended by sneakers and satellites. There is a high variability in the number of accessory males behaving as sneakers but usually only one or sometimes two as satellites. The latter often visit a nest before spawning takes place, which sneakers rarely do. Satellites usually behave very submissively in front of the T-male during these temporary visits. We often observed them remaining in the vicinity of the nest between successive visits. This may improve their chances of becoming accepted as a satellite at the nest and being present from the onset of spawning. There are, in fact, more nests with satellites than with sneakers on the first day of spawning. Males showing satellite behaviour stay almost twice as long at a single nest in spawning phase as do sneakers, *i.e.* often for most of its duration. In contrast, the sneaker tactic consists of roaming about and staying temporarily at nests with high spawning activity. Sneakers feed more than twice as much as T-males or satellites, which both stay at the nest most of the time. Sneakers usually stay some distance away from a nest, and often they alternate between reproductive behaviour and feeding. T-male defence prevents accessory males feeding in a nest, except on rare occasions. They may feed there voraciously when the nest owner is absent. Accessory males do not take over vacated nests or change to the T-male colour pattern within a season.

b) *Male effort.*

Only T-males invest in the building of a nest, courtship, direct brood-cate, interspecific defence and defence against other T-males. A nest cycle takes about 10 days to complete, but time expenditure can be reduced by taking over another nest (see below). Successful T-males are cuckolded by sneakers and satellites. Satellites also defend the nest against conspecifics during the spawning phase, but their resources are nests of successful T-males. They make more attacks on other kleptogamic males than do T-males. An experimental analysis showing that this may reduce the sneaking rate of sneakers will be reported elsewhere. Attacks on females, also more often performed by satellites than by T-males, are harder to understand. It has been suggested that females prey heavily upon eggs in the nest (SOLJAN, 1930a, b). This may have resulted in part from a misinterpretation of the head pushing behaviour by which females prepare the spawning ground. By contrast, nest-feeding fish remove pieces of algae and chew on them. The two behaviours can be distinguished by close observation. We also observed "real" nest predation by females, but it was relatively rare. The expulsion of females may have another ultimate function. Several females are often simultaneously present at nests with high spawning activity. Only one female can spawn at a time; the others wait at the rim of the nest. A female is frequently forced to leave the nest prematurely because the others prevent it from spawning. The expulsion of females which are not ready to spawn or which have already finished may accelerate the spawning sequence.

Satellites approach and follow females approximately twice as often as do T-males. However, a functional analysis of these behaviours revealed that they are not courtship patterns when performed by accessory males, but are rather to obtain a good spawning position. True courtship, *i.e.* nest showing and courtship spawning, are not performed by satellites or sneakers. Thus FIEDLER's (1964) claim that accessory males "can perform all courtship patterns" is not true - they never show such patterns.

2) The choice of tactic.

The options for a given season are roughly predetermined by sex and size: only the largest males in the population change colour and set up territories. The smallest males cannot usually behave like satellites as they are unable to compete with bigger ones. Perhaps there is another factor, as yet unknown, which determines whether a male participates in reproduction at all. An otolith analysis is currently underway to investigate whether the non-reproductive individuals become the T-males of the subsequent year. We shall discuss more minor decisions here, *i.e.* when different behavioural options exist within a social class.

(i) *T-males.*

If a nest owner does not succeed in attracting females it must decide whether and when to abandon the nest. In nearly a third of all nests we never observed a female spawning. T-males relinguish these nests when the average duration of unsuccessful attempts to gain female spawnings exceeds the average prespawning period by one day (*i.e.* 25%). It may pay to start anew instead of continuing to wait if the male learns that females cannot be attracted to the nest.

T-males may also decide whether to build a nest of their own or to take one over. A successful take-over saves T-males an average of 4 days: the rest day usually interposed between two self-built nests and the complete prespawning period. This is about 36% of the length of a nest cycle (including the one day break). T-males also save the energy required to construct a nest. Similar nest take-overs have been described in bluegill sunfish (DOMINEY, 1981), lingcod (JEWELL, 1968) and in nesting megachilid bee females (*e.g.* EICKWORT, 1975). Although there are obvious benefits, nest acquisitions for spawning are relatively rare in *S. ocellatus*. This is probably due to the limited availability of suitable nests. Analysis of inter-nest distances revealed that virtually all take-overs occurred near the previous nest. Whatever the reason for this spatial restriction, neighbouring nests which are in the right phase at the right time and whose owners can be expelled seem to be rare. The other, more common type of take-over is carried out to obtain nourishment and is therefore not restricted to nests in the spawning phase. It is puzzling that 69% of the males which only fed in the acquired nest fanned. DANIELS (1979) hypothesized that fanning by take-over males of an antarctic fish species was true altruism. We have found a somewhat comparable situation but suggest that fanning may possibly provide a net benefit to the new nest owner. It might, for example, be a signal, which attracts further females for additional spawning or displays nest ownership. Alternatively, the T-male may prevent egg decay. Eggs are widely scattered in the nest and T-males spend up to 3 days feeding in a taken-over nest. Perhaps fanning enhances the distribution of egg odour. Attracted egg predators (*e.g.* predatory snails) may be a welcome additional food source. We will not speculate further before a quantitative analysis of the costs and benefits of fanning in acquired nests is made.

A third decision which T-males frequently encounter is whether to expel or tolerate an accessory male close to the nest. Satellites are bigger than sneakers and probably more serious competitors for T-males. They also spawn more often in the T-males' nests than do sneakers. Nevertheless, sneakers are much more often and more intensely attacked than satellites, even though the latter are more frequently encountered by the nest owners. The submissive "S-bending", which obviously has an appeasing effect (see also LEJEUNE, 1984), is probably an important proximate mechanism modulating the interactions between reproductive males. Satellites, unlike sneakers, perform it very frequently in front of the nest owner. There are several potential ultimate causes for the T-male's tolerance of a satellite. They include high costs/low benefits for the expulsion and reciprocal altruism between both cooperatively defending types of males. We shall report an experimental investigation of this aspect in a subsequent paper.

(ii) *Accessory males.*

Plainly coloured medium or large reproductive males have two options: adopting an opportunistic tactic of roaming about and staying wherever the chances of sneaking are good or a bourgeouis tactic of remaining at a nest, defending a superior position and behaving submissively towards the nest owner. The fact that the satellite tactic is primarily adopted by kleptogamic males in alpha position suggests an advantage of this behaviour over its alternative. Individual males usually behaved like satellites when they were the largest accessory male at the nest but rather adopted sneaker-like behaviour when larger satellites were present. This may be a conditional strategy, whereby the choice of tactic depends on relative sizes and what the others are doing (*e.g.* DAWKINS, 1980).

There are two possible reasons for only the largest accessory male adopting satellite behaviour. It may aggressively prevent others from displaying the behaviour or satellite behaviour may not be rewarding if already performed by another. Some observations suggest intense competition for a satellite position at a nest. We observed three intense fights for this position between males of the same size. Occasionally, satellites were attacked by a larger fish approaching the nest and left. A male, previously sneaker, took over the satellite position in 10 out of 33 25 min experimental removals of the original satellite. Small males often showed some elements of the behaviour during this time. When more than one satellite is present usually only the largest is close to the nest. A small male often follows a female from the territory periphery. The large satellite eventually takes over contact with her until she reaches the nest or is taken by the T-male.

(iii) *Females.*

Females spawn repeatedly with the same T-male over a day. One third of the recorded females spawned with different T-males on successive days, although the previous males were still available. A female hardly ever spawns with the same T-male on two successive cycles although some of its previous mates are still available in her home range. These results suggest that females do not choose individual T-males but rather specific nests or situations on each day. The high nest fidelity of spawning females over a day is presumably due to differences in the probability of premature abandonment of a nest. The clustering of eggs in a nest may improve the probability of the nest owner completing broodcare (see also VAN DEN ASSEM, 1967).

3) Characteristics of alternative reproductive tactics and a confusion of semantics.

Various forms of alternative male tactics have been described (see recent reviews in BLUM & BLUM (eds) 1979, and in the Symposium Proceedings 1984, American Zoologist 24; p. 306-418). ''Primary'' tactics, involve aggressive competition for and monopolization of mates and/or reproductive sites. ''Alternative'' tactics dispense with this investment. They usually result in lower reproductive success during each breeding episode than does the respective primary tactic (RUBENSTEIN, 1980; but see PERRILL *et al.*, 1978). They have been described within different frameworks and given various names (see WIRTZ, 1982). The same terms are often used for very divergent phenomena. The term ''satellite males'', for example, was initially used for accessory males in the ruff. They join and stay with resident males who tolerate them to various degrees (HOGAN-WARBURG, 1966; VAN RHIJN, 1973). This term was subsequently sometimes used for males employing any non-agonistic tactic to gain access to females (*e.g.* WALTZ, 1982), irrespective of their spacial and behavioural relationships with the males performing the primary (or ''typical'') tactic. ''Sneakers'' or ''sneaks'' have more often been used for parasitic males which do not stay near and interact with a dominant or territorial male. Rather, they emerge opportunistically and are expelled by the monopolizing males (*e.g.* CONSTANTZ, 1975; RUBENSTEIN, 1980; GROSS, 1982). We would strongly suggest a general application of this distinction between ''sneakers'' (*i.e.* purely opportunistic, floating, kleptogamic males) and ''satellites'' (*i.e.* kleptogamic males remaining within a defended range of monopolizing males). The necessity for this differentiation may be especially obvious in a species like *S. ocellatus* in which both behavioural types occur. Perhaps it would be convenient to distinguish ''non-tolerated satellites'' from ''tolerated satellites''. The former behave furtively or evasively when approached and hence are not detected and/or expelled by the monopolizing male from its defended domain (*e.g.* WELLS, 1977; HOWARD, 1978; PERRILL *et al.*, 1978, female mimics of DOMINEY, 1980; *i.e.* satellites of GROSS, 1982). The latter are allowed to stay within a defended range of a dominant male (*e.g.* HOGAN-WARBURG, 1966; BARLOW, 1967; CAMPANELLA & WOLF, 1974; DUNBAR & DUNBAR, 1975; KODRIC-BROWN, 1977; ROSS & REED, 1978; THRESHER, 1979; WIRTZ, 1982). Tolerance of dominant males often coincides with submissive behaviour by the satellite (*e.g.* HOGAN-WARBURG, 1966; CAMPANELLA & WOLF, 1974; DUNBAR & DUNBAR, 1975; THRESHER, 1979; WIRTZ, 1982).

4) The coincidence of satellites and sneakers in other species.

There are a few other examples from very diverse taxa where both sneak and satellite behaviours occur within a single species. These are a solitary bee (*Anthidium maculatum*, ALCOCK *et al.*, 1977), the bluegill sunfish (*e.g.* GROSS, 1982) and two frogs with a rather different opportunistic (sneaker) tactic (*Rana catesbeiana*, HOWARD, 1978; *Hyla regilla*, PERRILL, 1984). The choice of tactics in all but one of these species, as in *S. ocellatus*, depends on the size of the males (exception: *Hyla regilla*). Satellite bees, which occasionally attack intruders, seem to be ignored; territorial frog males often attempt to expel their satellites if these are detected. The mating behaviour of the bluegill sunfish is strikingly similar to *S. ocellatus* (DOMINEY, 1981; GROSS, 1982). Small males sneak (KEENLEYSIDE, 1972) and medium sized males spawn with nesting males and females (DOMINEY, 1980). Medium sized bluegill males adopt female colouration (hence ''female mimics''), whereas the small sneakers are conspicuously different from females. The reverse is true in *S. ocellatus*, where sneakers have a colour pattern very similar to that of the females. They may be sometimes mistaken for females by satellites and T-males, as can be inferred from the incidences of ''approach to female'' and ''female following'' directed towards sneakers. Satellites, on the other hand, often have a somewhat distinct colour pattern and behave in a conspicuous way. Female bluegill mimics seem to be ignored because they are not perceived as males (DOMINEY, 1980, 1981; GROSS, 1982). This is an important difference from *S. ocellatus* satellites which invest considerably in nest defence behaviour. They are tolerated although T-males lose fertilizations to them. However, the latter may also profit from a satellite's presence. This aspect will be treated elsewhere.

Summary

The temperate, gonochoristic wrasse *Symphodus ocellatus* was studied in the field (Corsica). The largest males defend an area within which an average of 3-5 successive nests are built from algae. These brightly coloured, paternal, territorial males (T-males) spend between one and two thirds of their time during the 10-day nest cycle building the nest and fanning. They eat very little at this time, although they consume eggs and invertebrates in the nest, including egg predators. T-males occasionally take over neighbouring nests. Nest acquisition has two functions: nourishment (2/3 of all take-overs) and reproduction (1/3). T-males practising the latter save over 1/3 of the time of a complete nest cycle. Most take-over males that acquire nests solely for nourishment fan it, as do their reproducing counterparts.

Small males with inconspicuous female colouration roam about and try to fertilize eggs parasitically when females spawn in T-males' nests. There are usually several of these ''sneakers'' around successful nests. Medium sized males (smaller than T-males and differently coloured) also cuckold T-males, but often display submissively to them. They participate in nest defence against conspecifics and in interactions with females, with an average effort that even exceeds that of the nest owners. Males displaying this ''satellite behaviour'' feed much less than sneakers and remain at one nest during most of its spawning phase. They are more tolerated by T-males than are sneakers, although they are on average only half as far away from the nest and thus much more frequently encountered by the T-male. The proportion of time a male spends as a satellite depends on its size. Usually only the largest accessory male at a nest behaves in this manner, though smaller males occasionally perform elements of satellite behaviour. Satellites never participate in nest building, courtship, direct broodcare or interspecific defence, nor do they take over abandoned nests.

A fourth type of male, similar in size and appearance to sneakers and satellites, refrains from reproduction in a specific year. These males are perhaps future T-males. All females seem to participate in reproduction every year. They spawn repeatedly in the same nest over one day, but often change nests and T-males on successive days.

Male tactics are roughly determined by size, but there are still choices to be made, such as when to give up a nest which has little spawning success, whether to build a nest or to attempt a take-over, or when to reproduce and whether to adopt the sneaker or satellite roles. The simultaneous occurrence of T-males, satellites and sneakers within a species is compared to a few other examples of diverse taxa.

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Zusammenfassung

Fortpflanzungsverhalten und -ökologie des gonochoren Lippfisches *Symphodus ocellatus* wurden vor der korsischen Küste untersucht. Die grössten Männchen verteidigen ein Gebiet innerhalb dessen im Mittel 3-5 aufeinanderfolgende Nester gebaut werden. Diese Prachtmännchen verbringen zwischen einem und zwei Drittel ihrer Zeit während der 10-