

## ORIGINAL ARTICLES

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**Alternative male mating tactics in a cichlid, *Pelvicachromis pulcher*: a comparison of reproductive effort and success**

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**Abstract** *Pelvicachromis pulcher* is a small African cichlid which breeds in holes. Males may either reproduce monogamously (pair males), polygynously (harem males), or be tolerated as helpers in a harem territory (satellite males). These helpers share in defence of the territory against conspecifics, heterospecific competitors and predators. There are two male colour morphs that are fixed for life and are apparently genetically determined. These differ in their potential mating strategy. Red morph males may become harem owners, while yellow morph males may become satellite males, and males of both morphs may alternatively pair up monogamously. We compared the reproductive effort and success of these three male reproductive strategies. Effort was measured as attack rates, time expenditure and the risk of being injured or killed when attacking competitors or predators of three sympatric fish species. Reproductive success was measured by observing how many eggs were fertilized by each male when this was possible, and by using genetic markers. The number of fry surviving to independence of parental care was used as a criterion of success. The reproductive success of harem males was 3.3 times higher than that of pair males and 7 times higher than that of the average satellite male. Dominant satellite males, however, were as successful as monogamous pair males, using the measure of fertilized eggs. To our knowledge, this has not been found previously in any fish species. Both harem and pair males had lower parental defence costs per sired offspring, however, than males using the alternative satellite tactic. Defence effort was significantly related to the risk of injury.

**Key words** Alternative mating tactics · Cichlids · Reproductive effort/success · Genetic markers

**Introduction**

Mating tactics often vary between and within populations (Emlen and Oring 1977; Davies 1991; Taborsky 1994). This may be due to environmental variability or to alternative ways in which individuals maximize their inclusive fitness (Arak 1984). In many cichlid species, territorial males recruit females to their spawning sites while non-territorial males may adopt alternative mating strategies (e.g. McKaye 1983; Kuwamura 1987). These non-territorial males may try to steal fertilizations while the territory owners are spawning, by simultaneous parasitic spawning (SPS). This behaviour has been observed in 140 fish species of 28 families, including 15 cichlids (Taborsky, in press). In some species, these additional males not only steal fertilizations but also join in some of the activities of territory owners. Depending on circumstances, they are then called helpers or satellite males (see Taborsky 1994 for a discussion of terms).

Despite the numerous accounts of alternative male mating tactics in fish there is as yet very little information on their relative mating success, apart from observations of spawning rates. How many descendants do parasitic males sire? And what are their benefits and costs compared to those of territory owners? Another question which has been answered only very rarely is whether males only perform one tactic for life or whether they switch between different mating tactics (e.g. Constantz 1975). *Pelvicachromis pulcher* is ideally suited to study these and related questions. This species has polymorphic males and shows considerable brood care effort, with division of labour between the members of a social group. There are three alternative ways for males of this species to share in reproduction. Additionally, these fish are relatively easy to keep and breed under semi-natural conditions in tanks, which has invaluable practical advantages (see Taborsky 1984).

This paper deals with the different reproductive tactics of males which result in different costs and benefits for harem males, pair males and satellites. We compare

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defence behaviour associated with these options as index of reproductive effort and reproductive success.

## Materials and methods

### The species

#### Ecology

*Pelvicachromis* are small, sexually dimorphic cichlid fish with colour polymorphisms in some species (Thys van den Audenarde 1968; Heiligenberg 1965b), living in the freshwater zones of West African rainforest rivers (Nwadiaro 1985). The sex ratio was found to be 1 male: 2 females in the upper part of the Sombreiro River, at all other locations it was 1:1 (Nwadiaro 1985). Two dry and two rainy seasons per year determine the suitability of feeding and spawning conditions (Lowe-McConnell 1969, 1975), as well as the conditions for raising offspring. Young use flooded meadows for feeding and hiding from predators (Freyhof J., personal communication). *P. pulcher* breeds in holes which are intensely competed for by males. In the wild, only some *P. pulcher* own territories, while many live in aggregations (Sjölander 1972).

#### Sexual and colour polymorphism

Sexual and colour polymorphisms are characteristic for the entire genus *Pelvicachromis*. Male *P. pulcher* grow up to 12 cm total length (TL) and females up to 7 cm TL. Females have intensely coloured purple patches on their bellies. In the males, there are red and yellow colour morphs. The former are red from the mouth edges to the belly region and have dark red opercula, while the latter have red bellies but yellow opercula and lips. These characteristic colour patterns are first shown by animals before they become territorial, i.e. at an age of about 6 months, and from then on they are fixed for life. Heiligenberg (1965b) assumed that this colour polymorphism is genetically determined (red and yellow chested males of *P. spec. affin. pulcher*). The morph differences are not restricted to colour patterns only. Red morph males are more aggressive and patrol their territories more intensively than males of the yellow morph (E. Martin, unpublished work).

#### Reproductive behaviour

Non-reproductive males and females live in common aggregations. Territorial males defend multi-purpose territories of about 0.25 m<sup>2</sup> around shelters which are holes under leaves, stones or pieces of wood (Sjölander 1972). After pair formation, territory defence and sand or debris removal by digging are performed by both partners. At spawning, the partners take turns with only one fish being in the cave at a time while the other one guards the cave entrance and wards off intruders (i.e. sequential spawning). Females stick lines of about 10 eggs each to the roofs and sides of their caves, producing a total clutch of approximately 40–80 eggs. Then they take care of the eggs and wrigglers while their partner guards the area around the shelter. Free-swimming fry are closely guarded by the female while the male defends the surrounding area. Intruding congeners are attacked by the same-sex guarders. Both parents chase predators, dig holes, collect and transport larvae and scattered fry in their mouths, and feed fry. For the latter purpose they carry pieces of plants or snails (and commercial dry food in the laboratory) to the shoal of fry, break the material up by chewing and spit it towards the young.

Territorial pair males (TPMs) defend their territories continuously. They stay in the territory together with their partners and young until the latter are independent of parental care. For subsequent broods the same shelter is used or the territory owners (male, or male and female) dig a new shelter within the same ter-

ritory. Other males give up their breeding territories as soon as their young are free-swimming, and migrate with their families. They are referred to as non-territorial pair males (NTPMs).

### Study population and laboratory conditions

In this study we used fish imported from Lagos and Port Harcourt (Nigeria), and their F1 and F2 descendants. The fish were kept and bred in tanks of 50–150 l. Observations were made in two 6000-l tanks (400 cm × 250 cm × 60 cm water level), under semi-natural conditions. The artificial habitat resembled a little creek with a waterfall at one end. Two-shallow-water zones with slow-flowing water and sandy bottom were separated by a central zone with fast flowing water with patches of *Vallisneria* sp. and rocks covered by *Anubias* sp. Wooden roots and three big rocks structured the central part of the tank. *P. pulcher* sheltered and spawned between those rocks or dug shelters under sloping stone slabs and wooden roots, or they stayed between the leaves and roots of *Anubias* sp. All three zones of the tanks were used by the *P. pulcher* males, which either swam and fed in aggregations of 10–15 individuals in the central part of the tank, or were territory owners (at any point in time, 12–17 males were unpaired, while the remaining 15–20 were already mated), using mainly the shallower water zones of the tanks. Sympatric fish species observed (Sjölander 1972) and caught in the same part of the river from which the study fish originated were included in these observation tanks. These included *Hemichromis fasciatus*, *Chromidotilapia guentheri*, *Alestes (Brycinus)* sp., *Pelvicachromis taeniatus* and some small, unidentified *Aphyosemion* and catfish species. Three of these species (*Alestes* sp., *P. taeniatus* and *H. fasciatus*) are predators and competitors of *P. pulcher* posing different levels of risk. *Alestes* sp. are fry predators, congeners are competitors for breeding sites and conspecifics additionally for reproduction, and *H. fasciatus* are predators of all sizes of *P. pulcher*. The fish were fed a diet of frozen vegetables and meat, live *Daphnia* and *Cyclops*, algae or dry food (Tetra Tabimin), each day at 0800 hours. Artificial daylight was provided for 12 h/day. *P. pulcher* were individually distinguished by the observer by means of their body and fin colouration, especially by the pattern of spots on dorsal and caudal fins. These individual patterns are visible in fish larger than about 1.3 cm TL, before young become independent of parental care.

### Behavioural records

Eggs and fry were counted daily and the distribution, status and territorial behaviour of all cichlids was observed for 30 min. On 5 days per week one of us (E.M.) recorded the behaviour of *P. pulcher* between 0830 and 1030 hours and between 1400 and 1600 hours, and on a 6th day she made observations for 12 h continuously in one of the 6000-l tanks. Pairs, harems and aggregations of non-territorial individuals were observed simultaneously (which resulted in an observation period of about 20 min per individual per day, spread over the whole 4-h observation period). These records were used for measuring the sizes and borders of territories and for an indication of the state within the breeding cycle. Records of focal individuals were used for measuring time budgets and attack rates.

### Measures of reproductive effort

The numbers of courtship displays and spawning events were counted when spawning was observed. Attacks [i.e. orientation against, and attacking: for a description of agonistic behaviour of *Pelvicachromis* see Heiligenberg (1963, 1964, 1965a) and Danthinne and Voss (1972)] were recorded when they were either shown against *Alestes*, *Pelvicachromis* or *Hemichromis* ( $n = 10$  harems with three satellite males each, 10 territorial pairs, and 11 non-territorial pairs). We recorded attack rates and durations (males outside their shelters: recording started from orientation against the intruder, included attack and chasing and ended with the male's

return to the territory or shelter. If a male started his attack from the shelter, recording ended when he was back in his shelter again). Data were collected between the 3rd day before spawning (i.e. when the territory had already reached its final size) and ended when either young left the territory/parents at the size of approximately 2 cm TL or on the day a second clutch was laid if the young had not already left. Recording ended when more than 95% of the young had left the parents' territory. Dominance hierarchies among male harem members were established between 10 and 7 days before spawning starts. Usually, yellow males began to chase away intruders from near the harem territory border and show submissive behaviour when attacked by the red harem male. When more than one yellow male joined the harem, a linear dominance hierarchy was established among the future satellites by chasing, frontal and lateral displays, circling and sometimes escalated fights during the first day after arrival of the newcomer(s). Cooperative harem defence, i.e. when harem male and satellite male(s) simultaneously attacked an intruder, were counted as one attack for every fish separately. The risk resulting from territory and brood defence was estimated by recording the damage a defender suffered from the intruder that it attacked. *P. pulcher* males attacking *Alestes* sp. received in return only (1) few injuries to fins or scales, which regenerated within a few days. Attacks on *Pelvicachromis* sp. sometimes resulted in (2) injuries to body and fins; wounds on lips and loss of scales; this occurred regularly in escalated fights. When *H. fasciatus* was attacked and struck back, (3) heavy injuries to flanks and tail could result; four satellite males were even killed when they attacked these predators.

#### Measures of reproductive success

The reproductive success of all males was measured during their second and third reproductive periods. We disregarded the first reproductive period as many of the first clutches were eaten by the pair members or pairs "divorced" after the first spawning. Each spawning was recorded and all eggs and free-swimming young were counted daily, until they became independent of brood care. During spawning, we tried to count the eggs after each individual spawning act (i.e. when female and male changed places). As the fish spawned under the roof or at the sides of a cave, which was either a half-flowerpot or a self-dug shelter under sloping stone slabs or roots, it was usually possible to observe spawning without disturbing the fish. The numbers of eggs spawned immediately before a male entered the shelter and spawned there were attributed to this male.

When egg numbers could not be unequivocally attributed to the participating males in the way described, male reproductive success was determined by using the following procedure:

1. During spawning, the number of changes between female and male was recorded to determine the number of female spawning acts.
2. The total number of eggs laid, i.e. total clutch size, was divided by the number of female spawning acts, to estimate the number of eggs per spawning act.
3. The number of spawning acts by a particular male was multiplied by the estimated number of eggs laid at each spawning act. In addition, two different genetic markers of male colour patterns were additionally used to estimate paternity. Firstly, when paternity was unequivocal, i.e. when only one male had spawned with a female, 20–25% of sons sired by red morph males also belonged to the red morph (Lagos population:  $\bar{x} = 20\%$ , Q1 = 12%, Q3 = 23%; Port Harcourt population:  $\bar{x} = 25\%$ , Q1 = 18%, Q3 = 25%). None of the sons sired by yellow morph males ever belonged to the red morph. Secondly, while all females (except two) had dotted dorsal fins, only about 65% of the males of the Lagos population and about 82% of the males derived from the Port Harcourt population showed this colour pattern. When paternity was unequivocal (i.e. in monogamous pairs), 98.2% of the sons sired by fathers with dotted dorsals also showed this pattern ( $\bar{x} = 98.2\%$ , Q1 = 95%, Q3 = 100%,  $n = 21$ ), while fathers without dotted dorsals sired no (0%) sons with this pattern. This allowed us

to estimate parentage when one male with and one without a dotted dorsal fin participated in a spawning. The dotted dorsal fin pattern was clearly visible from a size of about 1.3 cm TL.

We found a significant correlation between the estimates based on direct spawning observations and those based on the described genetic markers on dorsal fins (checked when young were > than 2 cm) when two or more males sired a clutch ( $n = 15$  satellite males, 7 cases in 6 different harems; Spearman rank correlation analysis,  $r_s = 0.67$ ;  $P < 0.01$ ). For the estimates that were based on the described genetic markers we assumed that the sex ratios and mortality rates of offspring did not differ during early ontogeny between males with different colour patterns. Survival rates of offspring were estimated by measuring the proportion of free-swimming young that reached the size of 2 cm, at which time they became independent of parental care. "Dotted" individuals could additionally be checked by individual colour patterns until adulthood and information was collected about their life histories (membership in aggregations, settling, territoriality, mating tactics and reproductive success).

#### Data analyses

Medians ( $\bar{x}$ ) and quartiles (Q1, Q3) were calculated and non-parametric statistics were used throughout as most of the data distributions differed significantly from normality (Cramer-van Mises Test). We tested for differences between male types with Mann-Whitney *U*-tests and Kruskal-Wallis *H*-tests. Spearman rank correlation coefficients ( $r_s$ ) were calculated between (1) attack rates and injury risk, (2) time expenditure for attacks and injury risk and (3) spawning rates and the number of satellite male offspring. All tests used were two-tailed.

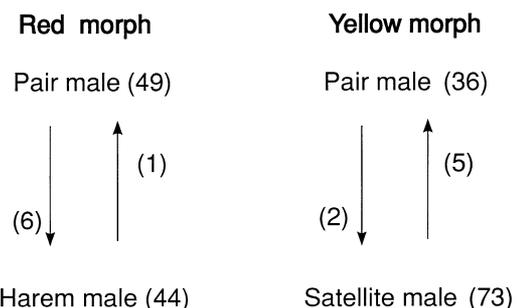
## Results

### Reproductive options

Figure 1 shows the mating options and the plasticity of *P. pulcher* males of the two colour morphs.

#### Red morph males

Of the 100 red morph males used in this study 50 became monogamously paired to one female, while the other 50 red morph males obtained two or more females and hence became harem owners. Males of this morph never



**Fig. 1** Plasticity of males with regard to mating tactics. Numbers given in parentheses are numbers of males either remaining with one or changing between two tactics (note that there are no transitions between satellite and harem male tactics)

used other mating tactics, but individual males changed between pair and harem status (Fig. 1).

*Yellow morph males*

Males of this morph obtained either pair or satellite status. Of the 38 yellow morph pair males 2 became satellites when they lost their partner or territory, and 5 of 78 yellow morph satellite males took over part of the harem territories in which they had been tolerated and paired up with a former harem female. Yellow morph males never obtained harems, even when the harem male died (8 cases) or when they were the only male in one of the smaller holding and breeding tanks (27 cases). Of the 73 satellite males 20 changed between harems.

The behaviour of yellow morph males was size-dependent. All of them tried to defend a territory but when they were small most were expelled and became satellite males in their first reproductive season. In the subsequent season nearly all satellite males again tried to defend a territory and pair up with a female. Of 73 satellites 20 remained in a harem, however, even when they had the chance to obtain their own territory (e.g. when a territorial neighbour male died).

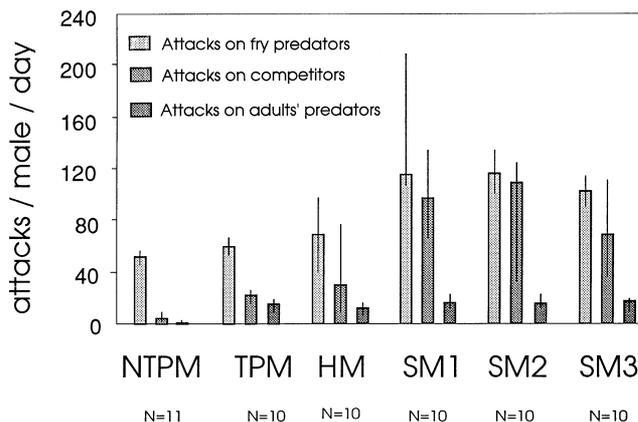
The costs of territory defence

*Attack rates*

*Pair males.* Attack rates of territorial pair males were significantly higher than those of non-territorial pair males, against all three classes of intruders (*U*-tests,  $n = 10$  territorial pair males + 11 non-territorial pair males; against *Alestes* sp.  $P < 0.02$ , against *P. pulcher* and *P. taeniatus*  $P < 0.001$ , against *H. fasciatus*  $P < 0.001$ ; Table 1). The breeding cycles of territorial pair males were significantly shorter than those of non-territorial pair males (territorial pair males  $\bar{x} = 30.5$  days,  $Q1 = 30, Q3 = 32$ ; non-territorial pair males  $\bar{x} = 39$  days,  $Q1 = 33, Q3 = 45$ ; *U*-test,  $P < 0.05$ ). The total number of attacks of monogamous *P. pulcher* males during an entire breeding cycle, i.e. between sub-

sequent spawnings, did not differ significantly between territorial and non-territorial breeding males for attacks against *Alestes* sp. (*U*-test,  $P > 0.1, n = 10 + 11$ ), but it was higher for territorial than for non-territorial males against *Pelvicachromis* sp. and against *H. fasciatus* (*U*-tests,  $P < 0.001, n = 10 + 11$  for both tests).

*Harem and satellite males.* Harem territories were defended by their owners and by tolerated satellite males. Some of the harem territories were defended for more than one consecutive spawning cycle of the female harem members. Then, harem males and satellites shared the territory defence also between reproductive periods. These non-reproductive periods are not included, however, in the data sets presented here. We recorded attack rates of all members of ten harems which all had three satellites. Between the satellite males a clear, linear rank order was established. Harem males attacked intruders less often than their satellite males (Fig. 2) and per-



**Fig. 2** Attack rates of pair males, harem males and satellite males against three types of intruders. Medians and quartiles of the attacks/male/day during the breeding cycle. Fry predators = *Alestes*, competitors = *Pelvicachromis*, predators = *Hemichromis*. (Abbreviations: non-territorial pair males (NTPMs) leave their territory with their families as soon as the young are free-swimming and will have to establish a new territory for the next breeding attempt, while territorial pair males (TPMs) defend their territory during the whole breeding cycle, HM harem males, SM1–SM3 satellite males, separated by dominance position within the harem’s dominance hierarchy)

**Table 1** Attack rates of territorial and non-territorial pair males. Ranges, medians ( $\bar{x}$ ) and quartiles (Q1 and Q3) of attacks against *Alestes* sp. (fry predator), *Pelvicachromis pulcher* and *P. taeniatus* (competitors), and *Hemichromis fasciatus* (predator) are given

Intruder	All pair males ( $n = 21$ )	Range	$\bar{x}$	Q1	Q3
Fry predator		36–72	56	52	64
Competitor		2–31	14	4.5	21
Predator		0–22	2	1	14
	Territorial pair males ( $n = 10$ )				
Fry predator		56–72	60	56	68
Competitor		16–31	22	18	24
Predator		6–22	15.5	11	18
	Non-territorial pair males ( $n = 11$ )				
Fry predator		36–66	52	48	59
Competitor		2–14	5	4	9
Predator		0–2	1	1	2

formed 17.1% of the entire defence of all male harem members against *Alestes* sp. ( $\bar{x} = 69$ ,  $Q1 = 42$ ,  $Q3 = 97$  attacks per day of the spawning period), 9.8% against *Pelvicachromis* sp. ( $\bar{x} = 30$ ,  $Q1 = 12$ ,  $Q3 = 78$ ) and 19.7% against *Hemichromis fasciatus* ( $\bar{x} = 12$ ,  $Q1 = 9$ ,  $Q3 = 18$ ). Satellite males showed significantly more attacks against *Alestes* sp. and *Pelvicachromis* sp. on an individual basis (*Alestes*:  $P < 0.005$ , *Pelvicachromis* sp.:  $P < 0.02$ , Kruskal-Wallis one-way ANOVAs). Attack rates did not differ significantly between satellite males of different ranks against all types of intruders (Kruskal-Wallis one-way ANOVA).

The average duration of a single attack against the different types of competitors and predators was 12 s. ( $\bar{x}$ ,  $Q1 = 8$  s,  $Q3 = 15$  s). This did not differ between the different male reproductive types (harem owners, satellites of three different dominance ranks, territorial and non-territorial pair males; Kruskal-Wallis one-way ANOVA,  $n = 61$ ,  $P > 0.1$ ). However, the total amount of time spent with attacks on predators of adults (*Hemichromis fasciatus*) differed significantly between the harem members; satellites spent more than twice as much time as harem owners (Kruskal-Wallis one-way ANOVA,  $n = 40$ ,  $P < 0.05$ ).

### Risk

We investigated whether the risk of being injured was related to attack frequencies on each of the three types of intruders. When all types of males were combined, damage correlated positively with the attack rates against *Alestes* sp. ( $r_s = 0.7$ ,  $n = 40$ ,  $P < 0.001$ ) and *Pelvicachromis* sp. ( $r_s = 0.44$ ,  $n = 40$ ,  $P < 0.002$ ), but not against *H. fasciatus* ( $r_s = 0.28$ ,  $n = 40$ ,  $P > 0.1$ ). This relationship held also when satellite males were tested separately. The attack rates of harem males did not correlate positively with injury risks against all types of intruders. The fight durations against intruding *Alestes* sp. and *Pelvicachromis* sp. were positively correlated with the risk of being injured ( $r_s = 0.59$ ,  $P < 0.001$  and  $r_s = 0.49$ ,  $P < 0.02$ , respectively) when all types of males were combined.

### Benefits

#### Net reproductive success

**Pairs.** We never observed parasitic males participate in pair spawnings. A pair male was always the genetic father of all young it guarded.

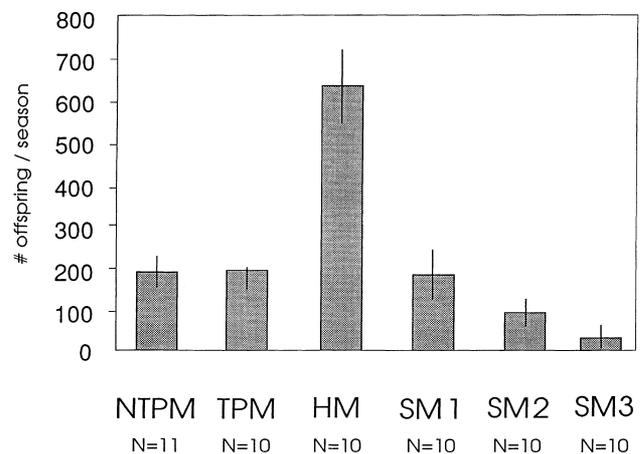
**Harems.** Harem and satellite males compete for spawning with the female harem members. Satellite males were only observed to spawn when harems contained three or more females. In smaller harems satellite males helped in territory defence as they did in larger harems, but without a share in reproduction ( $n = 27$  spawning ob-

servations, 12 different harems). When reproductive success was compared between male types, harem males exceeded monogamous males more than threefold (offspring production 3.3 times higher than by territorial pair males and 3.4 times higher than by non-territorial pair males) and the average of satellite males sevenfold (Fig. 3). Satellite males had an average success of about half (48%) that of monogamous males. When separated for rank, the dominant satellite males had 29% of harem males' success, the second satellites 14% and the submissive satellites only 5%. Dominant satellites were nearly as successful as pair males.

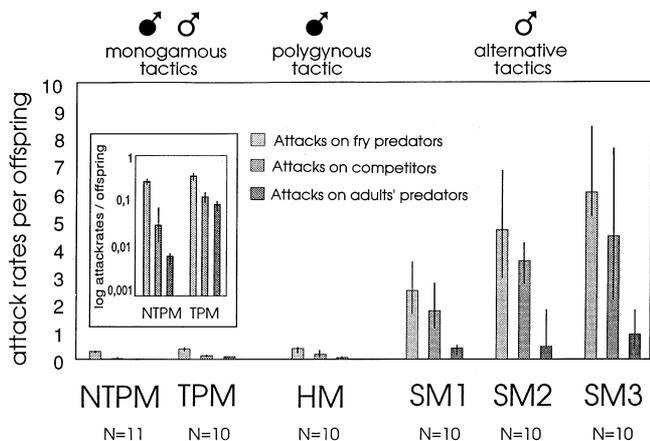
The difference between harem male and all other male types was significant, as was that between monogamous males and subdominant satellite males (Kruskal-Wallis one-way ANOVA,  $n = 61$ ,  $P < 0.001$ ). Dominant satellite males differed from satellite males in the second rank position ( $U$ -test,  $P < 0.01$ ) and from non-territorial pair males ( $U$ -test,  $P < 0.02$ ). Offspring production also differed between the two monogamous tactics ( $U$ -test,  $P < 0.05$ ), but not between territorial pair males and dominant satellites or between subdominant satellite males ( $U$ -tests,  $P > 0.05$ ).

### Reproductive effort per success

For a comparison of costs of offspring production between the different types of males, defence rates were related to the number of offspring produced (counted at independence; i.e. approximately 2 cm TL). Satellite males performed on average between 13 and 36 times as many attacks on predators and competitors per produced offspring than pair males did (Fig. 4) (Kruskal-Wallis one-way ANOVA,  $n = 51$ ,  $P < 0.001$ ). Pair males had only between 22 and 80% of the attacks per



**Fig. 3** Male reproductive success. Medians and quartiles are given of the reproductive success (number of fertilized eggs) of the six different male tactics during a breeding cycle. See text for results of statistical comparisons. Abbreviations as in Fig. 2



**Fig. 4** Defence effort per produced offspring. The reproductive effort per success is compared for monogamous (*NTPM*, *TPM*), polygynous (*HM*) and alternative (*SM1*, *SM2*, *SM3*) male tactics. Attack rates (medians and quartiles) against the three different intruder types were calculated per produced offspring (number of fertilized eggs) per day, for one entire breeding cycle. Abbreviations and intruder species as in Fig. 2 (filled male symbols red morph males, open male symbols yellow morph males)

produced offspring of harem males (Kruskal-Wallis one-way ANOVA,  $n = 31$ ,  $P < 0.01$ ). These ratios depended on the type of predator or competitor.

#### Survival of males and their offspring

Under semi-natural conditions, red and yellow morph males had significantly different lifespans, depending on their reproductive tactics. Most harem males died at approximately 3 years of age with apparently age-related symptoms, while pair males had an average lifespan of 5–6 years and satellite males even reached 7–9 years old (harem males:  $\bar{x} = 3$ ,  $Q1 = 2.5$ ,  $Q3 = 4$  years; pair males:  $\bar{x} = 5.5$ ,  $Q1 = 4.5$ ,  $Q3 = 6.5$  years, satellite males:  $\bar{x} = 7.5$ ,  $Q1 = 5.5$ ,  $Q3 = 8$  years, Kruskal-Wallis one-way ANOVA,  $n = 36$  harem males, 72 pair males and 32 satellite males,  $P < 0.05$ ).

Complete data sets of offspring survival were available from all broods of pair males. The average survival rate was 85.7% ( $\bar{x}$ ,  $Q1 = 73.2$ ,  $Q3 = 93.5$ ; territorial pair males:  $\bar{x} = 87.9$ ,  $Q1 = 83.33$ ,  $Q3 = 90.77$ ; non-territorial pair males:  $\bar{x} = 78.4$ ,  $Q1 = 70.67$ ,  $Q3 = 88.97$ ). In harems, fry were often adopted by other female harem members which confused the calculation of offspring survival rates. Therefore, only cases in which no adoptions occurred were included in the survival data for harem and satellite male offspring. Survival rates of harem male offspring were on average 84.7% ( $\bar{x}$ ,  $Q1 = 83.6$ ,  $Q3 = 88.88$ ), which did not differ significantly from pair males ( $U$ -test,  $n = 3277$ ,  $P > 0.1$ ). The offspring of satellite males (pooled data) had survival rates of only 44% ( $\bar{x}$ ,  $Q1 = 21.6\%$ ,  $Q3 = 66\%$ ), which was significantly lower than survival rates of monogamous males' young ( $U$ -test,  $P < 0.001$ ,  $n = 24 + 21$ ).

## Discussion

*P. pulcher* males use different reproductive tactics. Intrasexual competition for breeding territories requires a minimum body size to become a successful territory owner. Moreover, we found that the morphology of a male predetermines his reproductive options. Because a male's morphology (i.e. colour morph) is heritable, the potential reproductive status of males appears to be highly genetically determined. The two male morphs of *P. pulcher* proved to be irreversible after expression at an early stage in ontogeny, which occurs before the onset of territoriality and before the first spawning. Therefore, the types of *P. pulcher* males have different reproductive options right from the beginning, which includes their chances of maintaining a territory, obtaining a mate and breeding successfully.

A similar predetermination of male reproductive tactics in fish is known from coho salmon (*Oncorhynchus kisutch*), in which eggs fertilized by parasitic male offspring than did those sired by males of the large and aggressive "hooknose" morph (Iwamoto et al. 1983). There is also evidence for a genetic predisposition of the reproductive tactic in two poeciliids (see Taborsky 1994 for a review). In other cases, in which alternative reproductive pathways appear to be fixed for life such as in bluegill sunfish (*Lepomis macrochirus*; Dominey 1980; Gross 1982), it is unclear whether those pathways are genetically determined or dependent on an ontogenetic switch (Taborsky M., in press).

#### A comparison of costs of different male reproductive tactics

Behavioural effort was measured mainly in the form of territory and fry defence. When competition increases at the onset of spawning, a male appears to be unable to defend a territory on his own. In monogamous pairs females then share the duties of territory defence, while harem owners form coalitions with satellites to defend the territory.

Of all male types, satellite males attacked intruders and potential competitors most often, followed by the harem owners and by pair males. The fewest but most risky attacks were against *H. fasciatus*, with similar rates shown by harem males, territorial pair males and satellite males. Satellite males invested twice as much time in defence and incurred therefore a greater risk than males of the other two types, as they chased predators further away from the harem territory.

In contrast to pair males, harem owners do not have the option of leaving the territory after spawning, because harems are site-dependent. The only harem male that left his territory had to establish a new territory and paired monogamously thereafter (see Fig. 1.). Harem

males may, however, save effort by accepting the help of satellite males with territory defence.

#### Why do harem males tolerate satellite males?

The presence of satellite males in a territory causes competition for fertilizations between the latter and the territory owner (Kodric-Brown 1977; Ross 1983; Yanagisawa 1987; Taborsky 1994). Do the benefits of accepting one or several satellite males in a territory outweigh the costs of reproductive competition to the harem owners in *P. pulcher*?

The defence effort of satellite males surpassed that of harem males considerably, which helped to keep defence costs of harem males against fry-predators and hole competitors low. The highest attack rates of satellite males shown against congeners were attacks against conspecific males of the yellow morph, probably in order to reduce reproductive parasitism by these males and to prevent them from taking over their own satellite position in the harem. This resembles behaviour shown by satellite males of some Mediterranean wrasses (Fiedler 1964; Warner and Lejeune 1985; Taborsky et al. 1987) which defend a nest male's territory only against their own reproductive competitors (see Taborsky 1994 for review and discussion). In *P. pulcher*, apparently this "selfish" behaviour of satellite males benefits harem owners as well, as it excludes males that may try to split off part of the harem territory or take over a female, or that may cannibalize eggs and fry or parasitize the harem male's own fertilization attempts. With the help of genetic markers we found that harem males lost only a relatively small proportion of potential offspring to the reproductive parasitism of satellite males, in total never exceeding one-third of the number of young produced in a harem.

We conclude that in general harem males benefit from the presence of satellite males, and suggest that this is the ultimate reason why the latter are tolerated. This reciprocal association between territory owners and satellites is similar to that in the Mediterranean ocellated wrasse (Taborsky et al. 1987; Taborsky 1994) and differs from a situation in which territory owners are either not able to expel satellite males (Yanagisawa 1987) or where expulsion would be more costly than tolerance (Kodric-Brown 1977).

#### The reproductive success of different male types

##### *Fertilization success at spawning*

It is difficult to estimate male success when more than one male participates in spawning. The most widely used estimate simply counts male spawning, movements, and if more than one male participated in a spawning the resulting number is often divided by the number of participating males ("pair spawning equivalents", Warner et al. 1975). However, sperm competition and posi-

tion effects may cause substantial mistakes when the spawning success of "bourgeois" and parasitic males is estimated in this way (Ross and Reed 1978; Schroder and Duker 1979; Schroder 1981; Taborsky 1994). The term bourgeois refers to males investing in primary access to females. The term parasitic refers to males exploiting this investment of bourgeois males. See a discussion of terms in the FORUM section of this issue). If pair spawning equivalents had been used for *P. pulcher*, the success of harem males would have been greatly underestimated and, conversely, the estimates of satellite male success, especially, that of the lowest-ranking satellite males would have been substantially overestimated.

Usually, when a low-ranking harem female spawned, both the harem owner and satellite males participated. This resulted in a clutch fathered by two or more males. Using observational methods and genetic markers we confirmed that satellite males did produce offspring, and we found that the dominance rank of satellite males greatly influenced their reproductive success. The success of the highest ranking satellite males was similar to that of bourgeois monogamous males, while subdominant satellites had only very little fertilization success.

There are few data available for a comparison with other fish species. The relative success of parasitic and nesting males has been estimated in four salmonid species. In *Salmo salar*, 10.8% of eggs had been fertilized by an unknown number of stream-resident, parasitic males (Jordan and Youngson 1992), while an experimental study found that single parasitic males fertilized on average 5% of the eggs when spawning simultaneously with a bourgeois male (Hutchings and Myers 1988). This proportion declined to about 1% per parasitic male if 20 of these were simultaneously involved in a spawning. In *Salvelinus malma miyabei*, 7% of eggs were on average fertilized by single parasitic males (Taborsky 1994, recalculated from data of Maekawa and Onozato 1986). In *Oncorhynchus keta*, the figure was 25% (Schroder 1981). In *O. nerka* two parasitic males together fertilized 10% of the eggs when simultaneously spawning with a dominant male (Chebanov et al. 1983). In stickleback nests (*Gasterosteus aculeatus*) Rico et al. (1992) found an estimate of 3.5% of parasitically fertilized eggs. All these studies suggested that the reproductive success of parasitic reproductive tactics is inferior to that of bourgeois or dominant tactics. Dominant satellite males of *P. pulcher* are the only example we know of in fish in which a parasitic tactic results in a similar production of offspring to its bourgeois alternative, the monogamous pair male tactic, even on the level of single reproductive events or reproductive seasons, i.e. disregarding potential differences in survival probabilities (note that satellite males belong to the yellow morph which was never found to hold harems).

### *An estimate of lifetime reproductive success*

When calculated on a seasonal basis, the reproductive success of *P. pulcher* harem males was more than 3 times higher than that of monogamous pair males and dominant satellite males, while satellite males of second and third ranks had still lower success. On a longer time scale, however, additional benefits for dominant as well as for submissive satellite males may result from their potential to pair up with a female monogamously, either by splitting off part of the harem area or by leaving the harem territory with a female that was attracted to the harem site but not tolerated by the resident females.

When considering lifetime reproductive success, the lifespan of harem owners was only about half that of pair males and only about one-third that of satellite males. This result must be interpreted with caution, however, even though the data were obtained under semi-natural conditions including natural predators and competitors. As the conditions were similar for all males involved, these data may still suggest that the reproductive tactics of *P. pulcher* are balanced, equally successful alternatives between a short, but very productive reproductive lifetime (harem males), and a relatively low offspring production that is distributed over a longer reproductive lifespan (pair males and satellite males). Additionally, differences in survival rates of young which are mostly due to high predation risks (1) after leaving the harem area and (2) during the first territorial phase, when yellow morph males were expelled from their shelters more often than red morph males, influence the reproductive lifetime success of the three different male tactics. Similarly, Gross (1985) estimated a balanced lifetime reproductive success for bourgeois and parasitic males in coho salmon, *Oncorhynchus kisutch*, by using measures of the distance between males and the female during spawning, mortality rates during the ocean phase and of the time period that males stayed on the breeding grounds. Gross and Charnov (1980) and Gross (1982) also assumed an equilibrium between bourgeois and parasitic reproductive tactics in bluegill sunfish, *Lepomis macrochirus*, estimating that all parasitic males together fertilized as many eggs as all parental males did, based on intrusion frequencies and the proportional numbers of parasitic males. For this estimate all eggs spawned during "successful" intrusions were ascribed to the parasitic males, however, which may have substantially overestimated the success of parasitic males (see Gross 1996 for a discussion of the evolutionary stability of alternative reproductive phenotypes with unequal fitnesses).

### *Success estimates when defence costs per offspring are considered*

All bourgeois males engaged in similar total defence levels for the production of each offspring. In contrast, satellite males showed a much higher defence effort per

offspring produced. In another cichlid fish of similar size, *Neolamprologus pulcher*, agonistic behaviour has been shown to increase the basal metabolic rate 3–4 times (Grantner 1995). Apart from potential energy costs in *P. pulcher*, defence effort correlated positively with the risk of being injured by retaliation of the attacked fish. By this criterion, offspring were especially expensive for males in the second or third satellite positions. The low reproductive payoff of these males may suggest that they are primarily in a waiting position, i.e. their main benefit is the potential to gain the first position among satellites or take over a harem female to pair up with monogamously. This resembles conditions in a certain cooperatively breeding bird species in which broodcare helpers mainly gain by an improvement of their future reproductive potential (e.g. Reyer 1986)

### A hypothesis to explain the existence of two male morphs

Male polymorphism in *P. pulcher* may be partly stabilized by a seasonal variation in payoffs for red and yellow males. When water levels are high, red morph harem males probably produce great numbers of offspring that may spread into various niches. In the dry season, however, space is highly limited because many temporarily flooded areas will dry out. At the resulting high population densities of *P. pulcher* the more flexible and less aggressive yellow males may be at an advantage and consequently increase in proportion to red males. Highly productive wet seasons with increasing proportions of red males may alternate with dry seasons in which the proportions of yellow males are restored due to the latter's less demanding and more flexible reproductive tactics. This seasonal effect may be augmented by a higher life expectancy of the less productive yellow morph.

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