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Sexual dimorphism in two pure cichlid species, *Oreochromis niloticus niloticus* (Linnaeus 1758) and *Sarotherodon melanotheron melanotheron* Rüppel 1852, and their intergeneric hybrids

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Growth performances and sexual growth dimorphism were compared in two pure species of tilapia, *Oreochromis niloticus niloticus* (OO) and *Sarotherodon melanotheron melanotheron* (SS), and their reciprocal intergeneric hybrids (male *O. n. niloticus* × female *S. m. melanotheron* [OS] and male *S. m. melanotheron* × female *O. n. niloticus* [SO]). Fish obtained from artificial reproduction were reared on artificial diets over 10 weeks at 25 ± 2 °C, under light regimes of 12 h light:12 h darkness. Growth was measured on a weekly basis. Social interactions were recorded with a video camera. Pure *O. n. niloticus* achieved the fastest growth rates (Mean Specific Growth Rate (SGR) of 2.7 ± 0.6% d^{-1} for males and 2.3 ± 0.4% d^{-1} for female) and *S. m. melanotheron* the slowest (1.3 ± 0.3% d^{-1} for males and 1.4 ± 0.3% d^{-1} for females). The SGR of the intergeneric hybrids fell between that of the two pure strains. OS females grew faster (1.7 ± 0.4% d^{-1}) than SO females (1.3 ± 0.2% d^{-1}), whereas no difference was observed between males. Aggressive behaviour emerged first among faster-growing fish (*O. niloticus* and SO). The role of parental components in behavioural and physiological traits of tilapia is discussed.

Keywords: sexual growth dimorphism, social interactions, thyroid hormones, 11-ketotestosterone

Introduction

Growth heterogeneity among fish might originate from a broad series of exogenous and endogenous factors (for a review see Kestemont et al. 2003). It is well documented that three families of hormones influence the somatic growth of fish: growth hormone, thyroid hormones and sex steroids (Donaldson et al. 1979, Le Bail 1988, Sumpter 1992). As regards cichlids, several experiments have demonstrated the growth-enhancing effects of androgens (Hanson et al. 1983, Ufodike and Madu 1996) and triiodothyronine (T3) (Toguyeni et al. 1996). Similarly, it is well known that food availability and dominance hierarchies strongly influence growth heterogeneity in fish (Koebele 1985, Jobling and Wandsvik 1983) but this issue has only rarely been addressed within the context of sexual growth dimorphism (Fauconneau et al. 1997, Toguyéni et al. 2002).

There is strong sexual growth dimorphism in the cichlid genus *Oreochromis*, with males growing faster and larger than females (Trewavas 1983, Hanson et al. 1983, Baroiller and Jalabert 1989, Mélard et al. 1994) from soon after the

end of the period when the phenotypic sex is determined (Baras and Mélard 1997). Recent studies provided evidence that the determinism of between-sex growth dimorphism in *Oreochromis niloticus* was multifactorial and that the faster growth of males had a genetic component, overcoming factors strictly related to the phenotypic sex (Toguyéni et al. 2002). These studies substantiated those of Hanson et al. (1983), who observed that genotypically female tilapia (XX genotype) still grew at a slower rate than genotypically male fish (XY genotype) when both were treated with 17α-methyltestosterone, an anabolic androgen. From these observations, it may be hypothesised that between-sex growth dimorphism in *O. niloticus* is governed by a factor associated with the Y chromosome and/or by autosomes involved in sex determination. However, Hanson et al. (1983) did not mention whether the different experimental groups were full siblings, half-siblings or unrelated, so these differences may also reflect some maternal influence.

Hybridisation between different tilapia species produces viable fertile fish, even when species with different sex determination mechanisms are hybridised (Hickling 1960, Chen 1969, Jabalert et al. 1971, Mires 1977). This feature provides an opportunity to experimentally test for the influence of a genetic component on sexual growth dimorphism by comparing the growth rates of two species with contrasting patterns of sexual growth dimorphisms with those of their reciprocal hybrids. For example, Chevassus (1982) used hybridisation to evaluate the role of genetic factors on growth heterogeneity among salmonids and cyprinids.

The present study aimed to analyse (1) the role of genetic and social factors on the dynamics of sexual growth dimorphism and (2) the correlation between plasma levels of sex steroid and thyroid hormones and somatic growth in two tilapiine species, the Nile tilapia *Oreochromis niloticus niloticus* (Linnaeus 1758) and the blackchin tilapia *Sarotherodon melanotheron melanotheron* Rüppel 1852 and their hybrids.

Materials and methods

Materials

Fish used in this experiment were produced from hatchery-reared breeders from Bouaké, Ivory Coast, and raised in the GAMET experimental facilities at Montpellier France. Intergeneric hybridisation between *Sarotherodon* and *Oreochromis* can only be achieved by *in vitro* fertilisation, because *Sarotherodon* is a male mouthbrooding genus and *Oreochromis* is a female mouthbrooding genus (Trewavas 1983). In order to limit genetic variability, a single female and a single male of each species were selected for artificial reproduction. The broods of each female were randomly subdivided into two batches, which were artificially fertilised with the milt of the two species, thereby producing four batches: two pure species and two reciprocal intergeneric hybrids. Here the abbreviations OO and SS are used to designate the two pure species (*Oreochromis niloticus niloticus* and *Sarotherodon melanotheron melanotheron*, respectively) whilst OS designates hybrids from a male *Oreochromis* and a female *Sarotherodon*, and SO is used for the reciprocal cross. Fertilised eggs and embryos were incubated over 11 days at 27 °C in McDonald jars until the onset of exogenous feeding (Rana 1986). Juveniles were raised in 100 l aquariums in Montpellier until they attained a body mass of 4 g, and were then transferred to the Aquaculture Research Station of the University of Liège, Tihange, Belgium.

Hatching rates of artificially-fertilised tilapia eggs were much lower than those from spontaneous reproduction and no more than 18 juveniles attained the 4 g mark in one of the hybrid groups (OS). For the sake of consistency, no more than 18 fish were used in each of the four crosses. Such low fish numbers prevented the use of replications, because tilapia become overaggressive when raised at low densities and because the gender of the fish was unknown at the start of the experiment (see below).

Methods

After twenty days of acclimatisation at 28 °C, the fish averaged 9 g and were tagged with surgically implanted passive integrated transponders, following the procedure evaluated by Baras et al. (1999). Individual tagging was necessary for investigating the growth trajectories of males and females in the four crosses. The phenotypic sex of live tilapia cannot be determined with confidence by examining the urogenital papilla until the fish attain 30–50 g (Huet 1972) and neither of the two species possesses heteromorphic sex chromosomes that can be identified from karyotype analysis (Harvey et al. 2002). Therefore, the phenotypic sex of fish under study and the sex ratios of the groups were unknown until the end of the study, when they were dissected and their gonads examined.

The four groups of fish were raised over 74 days at 25 ± 2 °C (mean and range) in four 250 l (1 × 0.5 × 0.5 m) aquaria in an indoor recirculating system where day length was set at 12L:12D. Aquaria sides were covered with dark plastic sheets to isolate the fish from external influences. The fish were fed formulated feed (50% proteins and 11% lipids for the first three weeks, then 45% proteins and 8% lipids until the end of the experiment), which were distributed via automatic feeders during daylight hours. The daily food ration was intermediate between the optimum (R_{opt}) and maximum (R_{max}) food rations determined by Mélard (1986) for *O. niloticus*. This ration was supposed to cover the needs of *S. melanotheron*, which reputedly grows slower than *O. niloticus* (Legendre 1992). Every week, all fish were anaesthetised with 2-phenoxy-ethanol, 0.4 ml l^{-1}, and their mass was measured to the nearest 0.01 g. Food rations were adjusted on a weekly basis. The specific growth rate (SGR, % d^{-1}) was calculated as:

$$SGR = 100\ [(\log M_2 - \log M_1)\ (t_2 - t_1)]$$

where M_2 and M_1 are the body masses at times t_2 and t_1, respectively.

In order to provide an insight into their behaviours, each group of fish was filmed three times on the 56th day of the experiment (15-minute sequences, morning, midday, afternoon). During each period, social interactions were counted and ranked as simple attacks, attacks and pursuits, frontal display (with or without jaw locking). The proportion

of time spent in the upper and lower halves of the water column was also determined.

At the end of the experiment, fish were anaesthetised and blood samples were collected from each group. The plasma was used for radio-immunological determination of 11-ketotestosterone (11-KT, Fostier et al. 1983), thyroxin (T4) and triiodothyronine (T3, Byamungu et al. 1990). Thereafter, fish were sacrificed (using an excessive dose of 2-phenoxy-ethanol, i.e. 3.0 g l^{-1}), dissected and their gonads examined to ascertain their sex.

Statistics

Considering the relatively small sample size, the body weights and mean concentrations of hormone in the different groups were compared with one-way ANOVA. Bonferroni multiple comparison tests were used to compare initial and final body weight differences between groups. ANCOVA was used to compare the slopes of the growth parameters of the different groups. Chi-square test was used to compare the distribution of the fish in the water column.

Results

Growth

No fish died and no reproduction was observed during the 74-day experiment. Sex ratios varied between crosses, but were never significantly unbalanced (χ^2 tests, $p > 0.05$; Table 1). At the start of the experiment the sizes of males and females did not differ significantly in any of the four crosses. Pure *Sarotherodon m. melanotheron* (SS) were slightly smaller than pure *O. n. niloticus* (OO) and their hybrids (OS and SO), but the difference was not significant.

At the end of the experiment (Day 74), pure *S. m. melanotheron* were the smallest of all the crosses and exhibited no sexual growth dimorphism, whereas pure *O. n. niloticus* were the largest fish, with a significant between-sex dimorphism, females being smaller (Table 1). Hybrid sizes fell in between those of the two pure species. The OS and SO males were almost identical in size, which was intermediate between those of the two pure species. Amongst the females, OS and OO were not significantly different, but were significantly larger than SO females, which were not significantly larger than SS females. In other words, there was no significant between-sex difference among OS hybrids, whereas for the reciprocal cross the difference was significant.

SGR-to-size models were produced for males and females of the four crosses (Table 2). All fits were best when linear, with highly significant probabilities for both the intercept and slope. The intercepts of the growth models

Table 1: Initial and final mean body mass (BM) in males (M) and females (F) of pure *O. n. niloticus*, *S. m. melanotheron* and their reciprocal hybrids. Crosses designated by two letters ('O' or 'S') that refer to the genera of (firstly) the father and (secondly) the mother. Comparisons of body masses at the start (Day 0) and end (Day 74) of the experiment with one-way ANOVA. Within each column, values sharing a common superscript do not differ, other comparisons differ at $p < 0.05$ (Bonferroni tests) (SGR = specific growth rate, O = *Oreochromis,* S = *Sarotherodon, N* = number of fish)

Cross	Sex	*N*	Mean BM (SD) Day 0	Mean BM (SD) Day 74	SGR (% BM d^{-1})
OO	M	5	10.98 (2.03)	74.49 (2.89)^{a}	2.60 (0.26)^{a}
OO	F	13	9.87 (2.13)	51.81 (11.53)^{b}	2.24 (0.33)^{ab}
OS	M	12	11.02 (1.54)	44.89 (11.43)^{b}	1.86 (0.29)^{bc}
OS	F	6	10.86 (1.61)	37.50 (12.19)^{b}	1.62 (0.35)^{cd}
SO	M	7	10.73 (1.84)	45.11 (14.53)^{b}	1.88 (0.38)^{bc}
SO	F	11	10.75 (1.09)	27.71 (8.52)^{c}	1.23 (0.37)^{d}
SS	M	10	9.37 (1.77)	24.57 (5.24)^{c}	1.29 (0.32)^{d}
SS	F	8	9.05 (1.16)	24.92 (3.50)^{c}	1.37 (0.17)^{d}
			$F = 1.92$, df = 71 $p = 0.0815$	$F = 21.07$, df = 71 $p < 0.0001$	

Table 2: Relationships between mean growth (SGR, % *M* d^{-1}) and mean body mass in males and females of pure *O. niloticus*, *S. melanotheron* and their reciprocal hybrids. Crosses designated by two letters ('O' or 'S') that refer to the genera of (firstly) the father and (secondly) the mother. All models are constructed from nine data points, which correspond to the last nine rearing weeks. The growth during the first week was markedly slower than normal in all groups, probably due to acclimation to new rearing conditions, and was not retained for calculation. Values between brackets are the standard errors of coefficients. Slopes that share a common superscript do not differ, other comparisons differ at $p < 0.05$ (ANCOVA, tests of parallelism) (O = *Oreochromis,* S = *Sarotherodon*)

Cross	Sex	Intercept	Slope	r^2	*F*	*p* intercept	*p* slope
OO	M	5.286 (0.320)	–0.068 (0.007)^{a}	0.923	84.37	<0.0001	0.0001
OO	F	5.639 (0.370)	–0.110 (0.011)^{bc}	0.932	95.66	<0.0001	<0.0001
OS	M	5.522 (0.366)	–0.124 (0.012)^{bc}	0.949	111.13	<0.0001	<0.0001
OS	F	4.972 (0.503)	–0.132 (0.019)^{bc}	0.890	48.46	<0.0001	0.0004
SO	M	3.662 (0.381)	–0.070 (0.014)^{a}	0.790	26.36	<0.0001	0.0013
SO	F	2.837 (0.391)	–0.088 (0.020)^{ab}	0.735	19.46	0.0002	0.0031
SS	M	4.435 (0.583)	–0.182 (0.034)^{c}	0.807	29.24	<0.0001	0.0010
SS	F	3.735 (0.733)	–0.143 (0.044)^{bc}	0.606	10.75	0.0014	0.0135

were greater in fish sired by a male *O. niloticus* (from 5.0% to 5.6% d^{-1} in OO and OS crosses) than in those sired by a male *S. melanotheron* (from 2.8% to 4.4% d^{-1} in SS and SO crosses). In contrast, the slopes of the models appeared to be influenced more by the female than by the male parent: the slope was steeper in fish sired by a female *S. melanotheron* (from –0.12% to –0.18% d^{-1} g^{-1} in SS and OS crosses) than in fish sired by a female *O. niloticus* (from –0.07% to –0.11% d^{-1} g^{-1} in OO and SO crosses).

Endocrinology

At the end of the experiment males had higher plasma levels of 11-KT than females in all groups, with the exception of *S. melanotheron* (Figure 1a). Male and female *S. melanotheron* respectively showed the lowest and highest levels of androgen in comparison to their counterparts in the other groups. Among males, 11-KT levels were significantly higher in *O. niloticus* (31.6 ± 8.1 ng ml^{-1}) than in *S. melanotheron (*4.1 ± 0.2 ng ml^{-1}); hybrid males showed levels that were similar and intermediate between those of the pure species.

Levels of T4 were significantly higher in males than in females in the two hybrid groups (Figure 1b). The highest T4 levels among males were observed in *S. melanotheron* (16.9 ± 3.7 ng ml^{-1}), and the lowest ones in *O. niloticus* (5.4 ± 0.8 ng ml^{-1}). Levels of T4 in hybrid females from both crosses were similar to those of female *O. niloticus*, but significantly ($p < 0.05$) lower than those of female *S. melanotheron*. In all four crosses, T3 levels were significantly higher in male than in female fish (Figure 1c). There was no significant difference between males from different groups. Among females, T3 levels were significantly higher in the two pure species than in OS hybrids, but were not higher than in the SO hybrids.

The T3:T4 ratio, deduced from the data shown in Figure 1b and 1c, was significantly correlated to the growth rate over the 74-day experiment:

$$SGR = 0.757 + 3.09\ T3{:}T4$$

$F = 56.84$, $r^2 = 0.905$, df = 7, $p = 0.0010$ and $p = 0.0003$, for the intercept and slope, respectively.

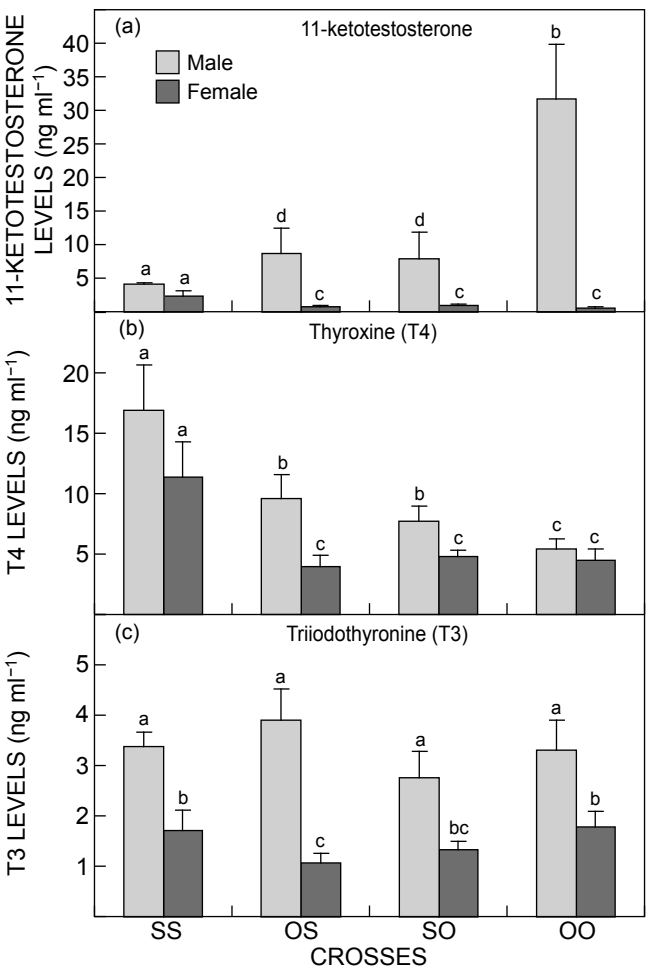

Figure 1: Plasma concentrations of (a) 11-ketotestosterone, (b) thyroxine T4 and (c) triiodothyronine T3 in pure *O. n. niloticus*, *S. m. melanotheron* and their reciprocal hybrids on Day 74. Crosses are designated by two letters ('O' or 'S') which refer to the genera of (firstly) the father and (secondly) the mother. Bars and whiskers = means ± 1 SEM. Categories sharing at least one common superscript are not significantly different at $p < 0.05$ (O = *Oreochromis*, S = *Sarotherodon*)

Behaviour

The four groups of fish exhibited contrasting patterns of space utilisation (Table 3). Fish sired by male *S. melanotheron*, (SS and SO) occupied predominantly the upper part of the water column, whereas those sired by male *O. niloticus*, (OO and OS) occupied both the lower and upper parts of the water column equally. Since the fish were tagged internally it was impossible to determine whether differences between the behaviours of individual fish were sex-related.

The analysis of aggressive interactions on Day 56 revealed several differences between crosses (Figure 2). Over one hour all groups of fish exhibited similar mean numbers of aggressive interactions, except for the OS hybrids that were almost twice as aggressive as the others. All groups exhibited simple attacks and pursuits, while frontal displays were observed exclusively among fish sired by female *S. melanotheron* (i.e. SS and OS crosses). The total percentage of prolonged attacks (either pursuit or frontal display) was lower among groups sired by male *S. melanotheron* than among those sired by male *O. niloticus*.

Table 3: Water column utilisation in pure *O. niloticus*, *S. melanotheron* and their reciprocal hybrids. Crosses designated by two letters ('O' or 'S') which refer to the genera of (firstly) the father and (secondly) the mother. Data originate from video sequences from 09:00 to 15:00 on the Day 56 of the experiment. Statistics: χ^2 = 129.08; $p < 0.0001$. All pairwise comparisons differ at $p < 0.001$ (O = *Oreochromis,* S = *Sarotherodon*)

Cross	*N* observations	Proportion in upper water column (%)
OO	270	59.5
OS	252	42.2
SO	270	89.4
SS	198	75.2

Discussion

Growth performances and between-sex growth dimorphism

These results were consistent with those of McAndrew and Majumdar (1989) who observed, over a shorter (40 day) growing period, that hybrids between several *Oreochromis* species had growth patterns that were intermediate between those of the pure species. However, we obtained hybrids from a cross between two genera with different parental mouth-brooding strategies for the first time. With regard to the two pure species, our results confirm that *S. melanotheron* grows more slowly than *O. niloticus*. Starting from equivalent bodyweights, over 74 days *S. melanotheron* reached only 33% and 50%, respectively, of the weights of male and female *O. niloticus*.

Hybrids showed contrasting growth patterns during the experiment. Whilst OS and SO males had almost similar growth rates, females started differing significantly after five weeks of rearing. The OS females grew significantly faster than SS females, whereas there was no difference between SO and SS females. This was surprising, since they are presumed to share a similar XX pair of sex chromosomes, if the genetic sex determination in *S. melanotheron* is an XX-XY system. The finding that hybrid sex ratios were close to 1:1 supports this hypothesis. The between-hybrids growth difference could be linked to an overall advantage due to the *O. niloticus* autosomes, to a strong positive effect linked to the *O. niloticus* male sex-determining gene(s), and/or to a strong negative effect linked to the *O. niloticus* X chromosome. Thus, sexual growth dimorphism in tilapia could be the result of a combination between the positive determinant of the Y and the negative determinant of the X chromosome.

In addition, differences of growth between the reciprocal hybrids could also result from maternal effects, since male SO showed slower growth in the earlier stages of the experiment (according to the slope) than OS males, whereas we did not observe any difference in older fish (at 74 days). Consequently, *O. niloticus* oocytes could be less favourable for growth than those of *S. melanotheron*. In that case, the OS females grew faster than the SO because they originated from a female *S. melanotheron*. However, in view of the small sample size and of the difference between sex ratios in the two hybrid groups, this hypothesis needs further validation since we found previously that the growth of male and female tilapia was influenced by sex ratio and the resulting social interactions (Toguyéni 1996, Toguyéni et al. 1997).

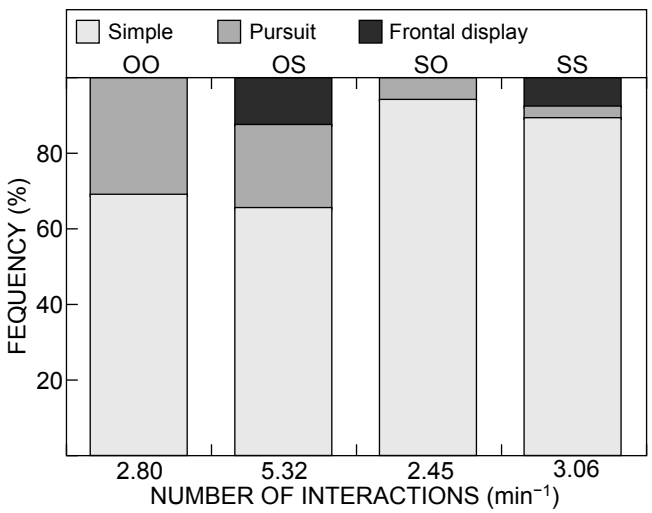

Figure 2: Frequency of three types of dominance behaviour in pure *O. n. niloticus*, *S. m. melanotheron* and their reciprocal hybrids. Crosses are designated by two letters ('O' or 'S') which refer to the genera of (firstly) the father and (secondly) the mother. Data originate from three sequences of 15 min each on Day 56 of the experiment (O = *Oreochromis*, S = *Sarotherodon*)

Two contrasting sexual growth dimorphism traits were observed in this study. In fish originating from an *O. niloticus* female (pure species and SO hybrid), sexual dimorphism emerged at an early age (after 7 and 14 days of rearing, respectively). The between-sex difference increased progressively in both groups, but proportionally faster in the hybrids (difference of 63% vs 44% of female body weight), despite the fact that they grew at a slower rate than did the pure species. Notably, when male *O. niloticus* started growing faster than females, our fish were slightly larger than those of Baras and Mélard (1997), who worked with a strain from Lake Manzala (Egypt). These differences may reflect genuine differences between strains, but they may also originate from different environmental constraints, since our 250 l aquaria were larger than theirs (50 l). In the two groups originating from a female *S. melanotheron*, the between-sex growth dimorphism tended to emerge at a much older age (age 120 days post-fertilisation in hybrid OS and even later in the pure species: Trewavas 1983). However, the weights of male and female fish did not differ significantly at the end of the experiment. Once again, this difference between the two categories of hybrid fish suggests that sexual growth dimorphism is influenced by the direction of the cross.

Our results provide some evidence that the sexual growth dimorphism in the two hybrid categories is essentially dependent on the growth of female fish, as hybrid males showed similar growth performances. This agrees with the conclusion of Baras and Mélard (1997) who found, from the growth patterns of *Oreochromis niloticus* before and after the emergence of between-sex growth dimorphism, that tilapia growth initially followed a 'female' growth-curve.

Given the general trends based on a population average, the considerable variability of individual growth rates recorded in this study demonstrated that early size differences are not the prime factor in Nile tilapia, as shown in other studies (Palada de Vera and Eknath 1993, Baras and Mélard 1997), or in *S. melanotheron.*

Relationships between growth and endocrine status

After 74 days of rearing the levels of 11-KT were much higher in males of the fast growing group (*O. niloticus*) than in the slow-growing *S. melanotheron*. We observed that hybrid males, which had similar growth patterns intermediate to the two species, also had similar and intermediate levels of 11-KT. Similarly, there was a difference between the levels of 11-KT in male and female fish in all groups, except in *S. melanotheron* for which there was no marked

sexual growth dimorphism. All these data are in agreement with the hypothesis that androgens stimulate the growth of tilapia species. However, 11KT levels were similar in males and females, respectively, of both types of hybrids, whereas they had different growth and between-sex dimorphism. The latter observation, when considered together with previous experiments (Toguyéni 1996, Toguyéni et al. 1996) strongly support the idea that factors other than androgens may be involved in the between-sex growth dimorphism in *O. niloticus*. A balance between androgens (potential growth stimulators) and estrogens (potential growth inhibitors) could be more relevant than the androgen effect alone.

Thyroid hormones T3 and T4 have been found to influence fish growth through the stimulation of appetite and the improvement of feed-conversion ratios (Donaldson et al. 1979, Higgs et al. 1982, Jalabert et al. 1982). We observed that the levels of T4 were higher in males than in females in the hybrid groups. Furthermore, the levels of T3 did not differ significantly between males showing different growth rates. This suggests that thyroid hormones may also have some influence on the growth of tilapia, but are not the major factor. The residual variability may originate from the availability of hormone-binding receptors or from a decrease in receptivity to these hormones, which may be a limiting factor, as documented for other hormones, especially growth hormones (Markett et al. 1977). Further experiments that aim at documenting this point in pure species and hybrids may be worth considering.

Social interactions

The nature of social interactions within a group of tilapias varies substantially, depending on whether or not a dominance hierarchy is established. Prior to the establishment of dominance, face-to-face interactions are the first observed behaviour, which progressively turn to jaw-to-jaw confrontations. Later on, after the hierarchy is established, these two types of agonistic interactions are replaced by attacks, including sequences of pursuit in which the dominant fish starts defending a territory. When the behaviour of the four groups of tilapias was examined at mid-experiment (56 days) the social hierarchy was already well established in the two groups originating from a female *O. niloticus* breeder (pure species and hybrid SO), whereas it was not yet established in the two groups originating from a female *S. melanotheron* breeder. This suggests that social interaction patterns are related to sexual maturation.

In addition, in the groups where the social interactions were more violent, the majority of individuals occupied the upper part of the water column. This indicates the emergence or presence of dominant individuals. Inferior individuals occupied the upper waters of the aquaria, particularly the higher corners, and dominant individuals the bottom, which enabled them to build their territories and to nest. The fact that we were not able to distinguish the sex of the aggressive individuals does not enable us to draw conclusions on the relation between growth and space occupation.

The observation that the dynamics of social hierarchy apparently depend on the genetic origin of the female may look paradoxical in a group of species in which dominant and territorial behaviours are essentially displayed by male fish. However, in this study the two groups in which the hierarchy settled quite early on were also those in which sexual growth dimorphism emerged at an early age, and so these two factors could be linked.

Conclusion

Our comparison of sexual growth dimorphism in *O. n. niloticus* × *S. m. melanotheron* hybrids shows that, besides genetic factors, a maternal effect is probably involved. Furthermore, differences in androgens and thyroidal hormone levels are only partially correlated with growth dimorphism, and thus complementary physiological factors could be involved.

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