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Genetics of Body Color Inheritance in Thai and Egyptian Red Tilapia Strains

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Abstract

The Mendelian mode of red body color inheritance in Thai and Egyptian strains of red tilapia was studied. Breeding between red x red and red x wild parents resulted in mostly all red progenies; and in some red x wild crosses, progenies were also segregated into red and wild types. The F_1 red hybrids mated *inter se* and back-crossed to wild type, the progeny phenotype segre-gated closely into approximating the expected 3 red: 1 wild type and 1 red: 1 wild type ratios, re-spectively. These results demonstrate that red body color in the two mutant strains of tilapia is controlled by a single autosomal dominant "R" gene. But the red strains contain different propor-tions of heterozygotes (Rr). In order to produce pure breeding strains, it is important to identify heterozygotes so the "r" allele can be selected out. In light of the present study, the progeny test-ing technique has been proposed as a probable solution.

Introduction

Most commercially available red tilapia strains are hybrids crossbred with as many as four different species, predominantly *Oreochromis mossambicus* and *O. niloticus* (Brummet et al. 1988; McAndrew et al. 1988). There is much doubt and confusion about the origin of these mutant strains of tilapia as their overall history has not been properly documented. However, due to their characteristic body color, fast growth and high demand in the market, red strains have become increasingly popular among fish farmers in some regions, and have recently attracted considerable attention among fishery workers who studied their genetics of body color inheritance (Behrends et al. 1982, 1988; Behrends and Smitherman 1984; Kuo 1984, 1988; Kuo and Tsay 1984, 1988; Berger and Rothbard 1987; Pruginin 1987; Scott et al. 1987; Galman et al. 1988; Mires 1988; Avtalion and Reich 1989; Wohlfarth et al. 1990).

A common problem among red tilapia strains is that majority of them do not breed true. Another problem is that a number of individuals in each genera-

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tion appear blotchy. Neither of these types are as valuable as the pure red individuals (McAndrew et al. 1988). To date, the underlying genetic mechanism of body color traits is not fully understood. There have been few attempts to overcome the problems in developing a true-breeding population of commercially available red tilapia strains. There are a few published or unpublished reports available (for review see Wohlfarth et al. 1990; Hussain 1992) on these aspects of red tilapia strains (Behrends et al. 1982; Scott et al. 1987; Huang et al. 1988a, 1988b; McAndrew et al. 1988; Mires 1988; Tave et al. 1989; Hilsdorf 1990).

This study, therefore, sought to determine the genetic mechanisms that control red body color in Thai and Egyptian strains of red tilapia, as well as the development of pure-breeding populations of the fish.

Materials and Methods

Both the Thai and Egyptian red tilapia strains used in this study were obtained from the Tilapia Reference Collection maintained at the Institute of Aquaculture, University of Stirling, Scotland. The Thai red tilapia, presumably a hybrid of *O. niloticus* x *O. mossambicus*, was introduced in 1989 to the Tropical Aquarium of the above institute from the Asian Institute of Technology, Thailand. The red and wild type *O. niloticus* descended from pure stock originally obtained from a wild population in Lake Manzala, Egypt, in 1979 (McAndrew and Majumdar 1983). The broodstock of these strains were maintained in a recirculated water system and fed regularly with trout pellets.

Fish spawning, stripping, egg fertilization and incubation protocols used in this study were as described by Hussain et al. (1991). After stripping, the spent red or wild type female was individually tagged, returned to the broodstock tank and replaced with another rested, sexually mature individual to guarantee frequent spawning.

Red x red and red x wild parental groups had been bred beforehand. Subsequently, the F_1 hybrids were mated to their sibs to produce F_2 generations, and back-crossed to wild types. In most cases, eggs stripped from a female were divided into three to four equal batches (300-400 eggs) and fertilized with freshly collected milt of pre-selected males. In these crosses, some males and females were mated more than once but in different crosses (i.e., to avoid the chance of mating more than once with the same individual).

The early and advanced fry rearing was carried out in 15-l perspex, 60-l circular and 500-l glass fiber tanks. The fish were fed routinely with the recommended dosage of various sizes of trout feeds (McAndrew and Majumdar 1989).

In the early stage (just after hatching or before yolk sac resorption) it was difficult to differentiate body color pattern, therefore, phenotype scoring of most of the progeny sub-samples was done just 1-2 weeks after the first feeding stage with an Olympus binocular dissecting microscope. The fish were anesthetized using ethyl 4-amiobenzoate (Sigma Ltd.) and killed, if necessary for handling, to score melanophores by observing body surface. In certain cases, if the body color pattern was confused, progenies were left to grow for up to 2 months, then rechecked for their phenotypes.

Progeny phenotypes in many of the crosses were categorized as "red" (including blotched type) and "wild" type (those normally pigmented and completely different from those of the red phenotype) of the same strains. Only F_1 progenies were categorized into full red (approximately <10% body surface with melanophores) and blotched types (approximately >10% body surface with melanophores), although both types together were designated as "red." To determine the observed ratio of color segregation, the proportion of progeny phenotypes were calculated as

$$\frac{\text{No. of progeny of a given phenotype}}{\text{Total no. of survivors}} \cdot 100$$

Observed body color segregation ratio data of all parental crosses (except red x red), sib and back-crosses were analyzed by the chi-square goodness-of-fit test.

Results

Parental Breeding Experiments

RED X RED PARENTAL CROSS

A total of six and eight different crosses were made independently for Thai and Egyptian red tilapia strains, respectively. The body color segregation of progenies was 100% red in all these crosses (tables are not shown, for details see Hussain 1992). Thus, it was roughly presumed that the parental stock of both strains are either "RR" or "Rr" genotypes or a combination of both (allele designation for both strains according to McAndrew et al. 1988).

RED X WILD TYPE PARENTAL CROSS

The results of parental crosses between wild type *O. niloticus* females x Thai red males, and between wild type *O. niloticus* females x Egyptian red males are presented in Tables 1 and 2, respectively. In wild type *O. niloticus* female x Thai red male crosses, a total of five females and six males were mated. The progenies segregated into 100% red and 0% wild type in seven crosses indicating that five red males were homozygotes (RR). In the remaining cross (no. 6), the progeny segregated into 41.8% red and 58.2% wild type, the male was presumably an "Rr" heterozygote, and the progeny ratio was not significantly different from the expected 1:1 ratio (Table 1). A total of five different wild type females used in these crossbreeding trials were assumed to be all recessive homozygotes (rr).

In wild *O. niloticus* female x Egyptian red male crosses, a total of 10 different crosses were carried out, progenies in seven crosses segregated into red and wild type individuals (Table 2). The proportion of red progenies in these seven crosses was 37.5-55.9% (mean = 48.1 ± 6.7 SD), of which only number 7 significantly deviated ($P<0.05$) from the expected 1:1 ratio. This indicated that

Table 1. Body color segregation in F_1 progenies derived from parental crosses between wild type *O. niloticus* females and Thai red tilapia males.

Cross no.	Parent's tag: Wild female (presumed genotype)	Parent's tag: Red male (presumed genotype)	Progeny no.	F_1 progeny phenotype: Red: Full (no.)	Red: Blotch (no.)	Wild type (no.)	Proportion* of red (%)	Chi-square
1	1320 (rr)	0931 (RR)	49	20	29	0	100	0.000
2	0977 (rr)	0978 (RR)	154	52	102	0	100	0.000
3	0425 (rr)	0411 (RR)	337	23	314	0	100	0.000
4	0930 (rr)	0416 (RR)	129	71	58	0	100	0.000
5	0425 (rr)	0416 (RR)	143	89	54	0	100	0.000
6	0472 (rr)	0471 (Rr)	146	0	61	85	41.8	3.945
7	0472 (rr)	0411 (RR)	116	50	66	0	100	0.000
8	0425 (rr)	0547 (RR)	90	78	12	0	100	0.000

*Expected proportion of red in parental crosses RR x rr = 100%, and Rr x rr = 50%.

all red males involved in the seven crosses were presumably heterozygotes (Rr), and when crossed with wild type (rr) females, gave a phenotypic ratio of red:wild close to 1:1. In the remaining three crosses, all progenies segregated into 100% red and 0% wild type.

An attempt was made to differentiate between full red (Fig. 1) and blotched type progenies (Fig. 2) as described by McAndrew et al. (1988). But no clear-cut pattern of segregation of blotching was observed in F_1 progenies derived from wild type *O. niloticus* female x Thai red male crosses. Some crosses (no. 4 and 5) involving both homozygous red males (RR) and wild type females (rr) in wild vs Egyptian red strain breeding trials produced a higher percentage of blotch pattern in F_1 progenies (Rr) compared to most of the crosses between heterozygous red males (Rr) and homozygous wild females (rr). But the results from crosses no. 3 and 6 were not consistent with this trend (Table 2).

Sib Cross Breeding Experiments

To determine and confirm more precisely the Mendelian mode of inheritance of the dominant red gene (R) action over recessive wild type (r), a series

Table 2. Body color segregation in F_1 progenies derived from parental crosses between wild type *O. niloticus* females and Egyptian red tilapia males.

Cross no.	Parent's tag		Progeny no.	F_1 progeny phenotype			Proportion* of red (%)	Chi-square
	Wild female (presumed genotype)	Red male		Red		Wild type (no.)		
				Full (no.)	Blotch (no.)			
1	0924 (rr)	1397 (Rr)	343	92	91	160	53.4	1.542
2	0924 (rr)	1361 (Rr)	136	41	35	60	55.9	1.882
3	0511 (rr)	0468 (Rr)	144	3	70	71	50.9	0.028
4	0512 (rr)	0516 (RR)	96	10	86	0	100	0.000
5	0474 (rr)	0473 (RR)	78	7	71	0	100	0.000
6	0415 (rr)	0516 (RR)	72	67	3	0	100	0.000
7	0415 (rr)	0515 (Rr)	80	20	10	50	37.5	5.000*
8	0425 (rr)	0478 (Rr)	89	23	16	50	43.8	1.360
9	0415 (rr)	0414 (Rr)	92	13	35	44	52.2	0.677
10	0477 (rr)	0476 (Rr)	104	14	31	59	43.3	1.188

*Expected proportion of red in parental crosses RR x rr = 100%, and Rr x rr = 50%; *P<0.05.

of breeding trials involving F_1 sib crosses were carried out. In nine crosses between F_1 red sibs (wild type *O. niloticus* ♀ x Thai red tilapia ♂), F_2 progenies were segregated into red and wild phenotypes (Table 3). The observed proportion was 67-76% (mean = 74.7 ± 3.1 SD) red progenies and 22.6-33.0% (mean = 25.3 ± 3.1 SD) wild progenies. The observed segregation of the progeny phenotypes was significantly different (P<0.001) only in cross no. 6 from the expected 3 red:1 wild ratio.

The results of 10 crosses among F_1 red sibs (wild type *O. niloticus* ♀ x Egyptian red strain ♂) shown in Table 4 are 68-75.6% (mean = 73.3 ± 2.4 SD) F_2 red progenies and 24.4-32% (mean = 26.7 ± 2.4 SD) wild progenies. Analysis of these observed phenotypic ratios revealed that they were not significantly different (P>0.05) from the expected 3 red:1 wild type ratio.

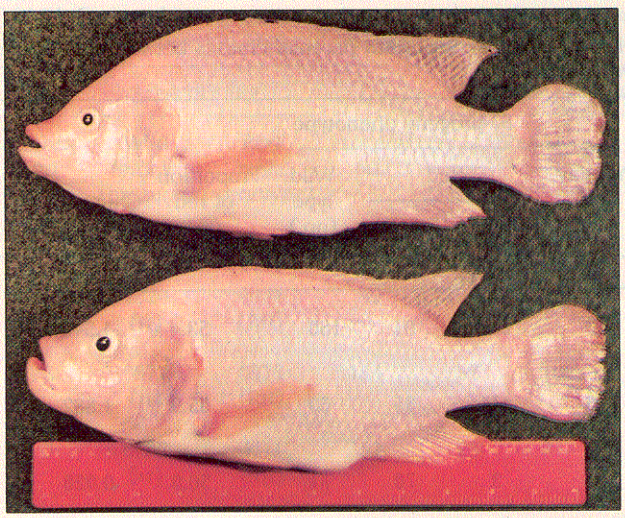

Fig. 1. Pure red (unblotched) phenotype of Thai red tilapia strain.

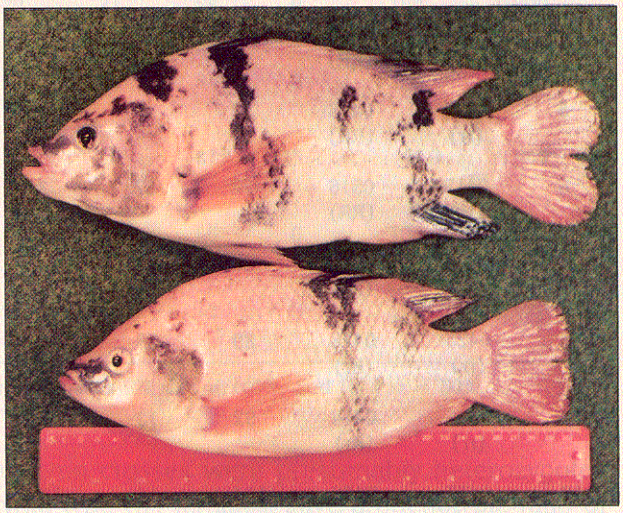

Fig. 2. Blotched phenotype of Thai red tilapia strain.

Table 3. Body color segregation in F_2 progenies derived from sib-crosses between F_1 (wild type *O. niloticus* ♀ x Thai red tilapia ♂) red females and F_1 (wild type *O. niloticus* ♀ x Thai red tilapia ♂) red males. Observed proportion of F_2 progeny phenotypes is shown in parentheses.

Cross no.	Parent's tag: Red female (Rr)	Parent's tag: Red male (Rr)	Progeny no.	F_2 progeny phenotype#: Red no.	Red (%)	Wild no.	Wild (%)	Chi-square
1	0701	0705	243	188	(77.4)	55	(22.6)	0.726
2	0702	0706	132	97	(73.5)	35	(26.5)	0.162
3	0703	0705	164	125	(76.0)	39	(24.0)	0.053
4	0704	0707	325	247	(76.0)	78	(24.0)	0.053
5	0712	0709	416	310	(74.5)	106	(25.5)	0.013
6	0712	0711	336	225	(67.0)	111	(33.0)	11.571***
7	0716	0707	254	192	(75.6)	62	(24.4)	0.047
8	0716	0709	100	77	(77.0)	23	(23.0)	0.213
9	0716	0714	201	151	(75.1)	50	(24.9)	0.001

#Expected proportion of red and wild in sib crosses Rr x Rr is 75% and 25%, respectively; *P<0.05; **P<0.01; ***P<0.001.

Table 4. Body color segregation in F_2 progenies derived from sib-crosses between F_1 (wild type *O. niloticus* ♀ x Egyptian red tilapia ♂) red females and F_1 (wild type *O. niloticus* ♀ x Egyptian red tilapia ♂) red males. Observed proportion of F_2 progeny phenotypes are shown in parentheses.

Cross no.	F_1 parent's tag		Progeny no.	F_2 progeny phenotype*				Chi-square
	Red female (Rr)	Red male (Rr)		Red no.	(%)	Wild no.	(%)	
1	0745	0743	128	87	(68.0)	41	(32.0)	3.375
2	0745	0744	162	122	(75.3)	40	(24.7)	0.006
3	0746	0749	109	80	(73.4)	29	(26.6)	0.149
4	0747	0749	180	132	(73.3)	48	(26.7)	0.267
5	0748	0749	114	86	(75.4)	28	(24.6)	0.012
6	0746	0750	172	130	(75.6)	42	(24.4)	0.031
7	0748	0750	198	149	(75.3)	49	(24.7)	0.006
8	0747	0750	187	137	(73.3)	50	(26.7)	0.271
9	0746	0751	183	133	(72.7)	50	(27.3)	0.526
10	0747	0751	110	78	(70.9)	32	(29.1)	0.982

*Expected proportion of red and wild in sib crosses Rr x Rr is 75% and 25%, respectively.

Back Cross Breeding Experiments

The progenies of 11 back-crosses between F_1 red (wild type *O. niloticus* ♀ x Thai red tilapia ♂) males and recessive wild type *O. niloticus* females were segregated into red and wild type individuals (Table 5). The proportion was 37.4-52.5% (mean = 46.5 ± 4.0 SD) red phenotypic individuals, and 47.5-62.6% (53.5 ± 4.0 SD) wild type individuals. Only in cross no. 4 was the distribution of color pattern significantly different ($P<0.05$) from the expected 1:1 ratio.

Table 5. Body color segregation in progenies derived from back-crosses between wild type *O. niloticus* females and F_1 red (wild type *O. niloticus* ♀ x Thai red tilapia ♂) males[1]. Observed proportion of progeny phenotypes is shown in parentheses.

Cross no.	Parent's tag		Progeny no.	Progeny phenotype*				Chi-square
	Red female (Rr)	Red male (Rr)		Red no.	(%)	Wild no.	(%)	
1	0506	0397	280	124	(44.3)	156	(55.7)	3.657
2	0596	0390	144	67	(46.5)	77	(53.5)	0.694
3	0596	0391	141	74	(52.5)	67	(47.5)	0.347
4	0596	0392	107	40	(37.4)	67	(62.6)	6.813**
5	0930	0707	308	157	(51.0)	151	(49.0)	0.117
6	0930	0708	457	210	(46.0)	247	(54.0)	2.996
7	0930	0709	267	118	(44.2)	149	(55.8)	3.599
8	0930	0710	345	164	(47.5)	181	(52.5)	0.838
9	0715	0707	126	61	(48.4)	65	(51.6)	0.127
10	0715	0713	235	105	(44.7)	130	(55.3)	2.659
11	0715	0714	201	98	(48.8)	103	(51.2)	0.124

*Expected proportion of red and wild in back crosses Rr x rr is 50% and 50%, respectively;
**$P<0.05$.

Table 6. Body color segregation in progenies derived from back-crosses between wild type *O. niloticus* females and F_1 red (wild type *O. niloticus* ♀ x Egyptian red tilapia ♂) males[1]. Observed proportion of progeny phenotypes is shown in parentheses.

Cross no.	Parent's tag		Progeny no.	Progeny phenotype*				Chi-square
	Wild female (Rr)	F_1 red male (Rr)		Red no.	(%)	Wild no.	(%)	
1	0506	1390	213	107	(50.2)	106	(49.8)	0.004
2	0502	0706	240	119	(49.6)	121	(50.4)	0.016
3	0502	0367	168	85	(50.6)	83	(49.4)	0.024
4	0502	1390	758	368	(48.5)	390	(51.5)	0.638
5	0580	1394	291	155	(53.3)	136	(46.7)	1.240
6	0580	0370	301	161	(53.5)	140	(46.5)	1.465
7	0580	1392	261	136	(52.1)	125	(47.9)	0.464
8	0580	1390	309	134	(43.4)	175	(56.6)	5.440**
9	0580	0752	377	181	(48.0)	196	(52.0)	0.597
10	0569	0747	434	211	(48.6)	223	(51.4)	0.332

*Expected proportion of red and wild in back crosses Rr x rr is 50% and 50%, respectively; **$P<0.05$.

The progenies derived from 10 different back-crosses between seven F_1 red (wild type *O. niloticus* ♀ x Egyptian red strain ♂) males and four recessive wild type *O. niloticus* females were segregated into red (43-4-53.5%, mean = 49.8 ± 2.9 SD) and wild types (46.5-56.6%, mean = 50.2 ± 2.9 SD) (Table 6). The only significant deviation ($P<0.05$) from the expected 1:1 ratio was in cross no. 8.

Discussion

In this study, the results of all parental, sib and back-crosses indicate that red body color in Thai and Egyptian red tilapia strains is a simple autosomal, dominant trait controlled by a single gene with two alleles, "R" dominant for red color over "r" recessive for wild type. The present study also revealed that the dominant mode of color gene inheritance, particularly in the Thai strain, is complementary to that in the Egyptian strain described by McAndrew et al. (1988). This dominant red trait controlled by a single gene has been previously observed in the same strains (McAndrew et al. 1988; Hilsdorf 1990) and other tilapia strains (Behrends et al. 1982; Behrends and Smitherman 1984; Huang et al. 1988b; Avtalion and Reich 1989). On the other hand, blond body color of *O. niloticus* (Scott et al. 1987; McAndrew et al. 1988; Mires 1988) and red or gold color of *O. mossambicus* (Pruginin 1987; Tave et al. 1989; Wohlfarth et al. 1990) were explained as simple Mendelian recessive. The majority of color variants in fish are recessive traits in their mode of inheritance, particularly those reported in carp (Kirpichnikov 1981). Incomplete dominance was also observed in Taiwanese red tilapia by Huang et al. (1988a) and Wohlfarth et al. (1990).

In both Thai and Egyptian strains, the dominant nature of red body color has important implications for genetic research and for the development of

their pure breeding populations. The existing broodstock populations of these strains are a mixture of both homozygous "RR" individuals that breed true, and heterozygous "Rr" individuals that do not. Like other red strains, the origin of Thai red tilapia is less certain. Its origins were discussed for the first time in a workshop on "Tilapia Genetic Resources for Aquaculture" held in 1987 in Bangkok, Thailand. A Thai government official informed the meeting that red tilapia *O. mossambicus*, found in a pond in northeastern Thailand, was introduced from Malaysia in 1949 (according to Welcomme 1981). Thus, the fish was assumed to be a hybrid between *O. mossambicus* and *O. niloticus*. According to Pullin (1988) electrophoretic analysis of Thai red tilapia samples from the Asian Institute of Technology, Thailand, examined at the University of the Philippines' Marine Science Institute Laboratory, showed that both *O. mossambicus* and *O. niloticus* alleles were present. Recently Dr. B.J. McAndrew and Mrs. P. Sodsook (pers. comm.) came to the same conclusion after their electrophoretic analysis of the same Thai strain held at the Institute of Aquaculture, University of Stirling. In the case of Egyptian red tilapia, this problem arose because the single ancestor fish was reported to be a heterozygote (Rr, a spontaneous mutant), and successive generations were mostly or entirely derived from crosses between red x wild type at the Institute of Aquaculture, University of Stirling (McAndrew et al. 1988). Thus, the founder stock is represented by a mixture of homozygous (RR) and heterozygous (Rr) genotypes, as no attempts at progeny testing have been made.

Present data on the blotched phenotype in the two mutant strains are not enough to assess the mode of its inheritance, but it seems likely that this trait might be controlled by a single autosomal gene. And frequency of the blotchy pattern in these strains further indicates that the blotched phenotype might be epistatic to the "R" gene. McAndrew et al. (1988) stated that the blotched phenotype is hypostatic to the red gene and can be expressed only in its presence. The blotched phenotype cannot be eliminated from a population unless a clear-cut description of the level of blotching can be determined as a viable trait. This will require further detailed study.

The results of the present study suggest that if all red mutant brooders are to be true breeders in a population, they should be fixed as homozygous at the "R" allele, to allow the undesirable "r" allele to be selected out. In this case, progeny testing is a viable method for maintaining the production of all pure red progenies of Thai and Egyptian red tilapia strains.

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