

**INTERACTIONS BETWEEN GROWTH, SEX, REPRODUCTION, AND ACTIVITY  
LEVELS IN CONTROL AND FAST-GROWING STRAINS OF NILE TILAPIA  
(*Oreochromis niloticus*)**

**by**

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## Abstract

Cultured fish play an important role in meeting increasing demands of human consumption around the world. To meet consumer demand for larger-sized fish, fish culturist seek strains that possess a high growth rate and reach harvestable size before attaining sexual maturation. Given the importance for farmers of understanding growth phenomena and controlling sexual maturation in fish stocks, this thesis examined the relationship between growth, behavioural activity, and sexual maturation in control strains of Nile tilapia, *Oreochromis niloticus*, and in strains resulting from a project devoted to the Genetic Improvement of Farmed Tilapias (GIFT). Behavioural activity of fish groups was videorecorded each month of the three month study period.

Under laboratory conditions, the fast-growing GIFT fish performed less locomotory and agonistic activity than the slow-growing control fish. Mirror image stimulation tests performed on individual males supported the finding that controls are more aggressive than GIFT fish. In the comparison of females and males, the fast-growing male GIFT performed less locomotory, but more agonistic behaviour than the slow-growing female GIFT. In the controls, growth rates of males and females were relatively similar even though, the male controls performed more locomotory and agonistic behaviour than the female control fish. In all, low growth was associated with a high activity level; however, a few experimental observations appear to deviate from this relationship and are discussed.

Nesting behaviour, which is often the first indication of sexual maturity, was observed only in males. Male controls performed more nesting behaviour than male GIFT fish. Also, significantly more nests were built by the control than GIFT fish. This suggest, at least in males, that the slow-growing control fish became sexually mature sooner, and at a smaller size than the fast-growing GIFT fish. Furthermore, male GIFT fish required more time to complete their nest(s), and built fewer nests than male control fish.

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## CHAPTER I

### General Introduction and Background Information

#### Introduction to the Problem

Rearing of cultured fish in fish farms has become a fast growing industry. With the increase in demand for fish products on world markets and the reduction in wild fish stocks due to overexploitation of natural fish populations, cultured fish play an important role in meeting the increasing demand of fish for human consumption around the world.

One important production trait of farmed fish is its size at first sexual maturation. Fish strains that possess a high growth rate and reach harvestable size before attaining sexual maturation are sought by fish culturists because sexual maturation and spawning complicate production operations and/or affect product quality. This is especially important for the tilapias (mainly *Oreochromis* and *Tilapia*, Fam. Cichlidae), fish of African origin, which is now farmed for local and export markets in over 80 countries (e.g., Philippines, Taiwan, Israel, and United States). When tilapia are stocked in an unpopulated pond or another aquaculture facility, the fish often shift towards a more altricial life style, characterized by a shorter period of somatic growth, an earlier onset of reproductive maturity, and more numerous, smaller eggs (Fryer and Iles, 1972; Noakes and Balon, 1982). The fish become "stunted," in that they are smaller than other adults of the same species. The real phenomenon is that the fish are

not "small for their age," but "old for their size" (Noakes and Balon, 1982). These stunted individuals are unsuitable for the market, thus causing problems in the fish industry. This provides the overall background for the work presented here.

## Background

### *Wild vs. Hatchery-reared fish*

Growth rate comparisons have been made between wild and hatchery-reared fish. Vincent (1960), and Flick and Webster (1964) observed in the brook trout, *Salvelinus fontinalis*, that under hatchery conditions, farmed fish grew faster than wild stocks. Einum and Fleming (1997), and Fleming and Einum (1997) also observed, under hatchery conditions, faster growth in farmed Atlantic salmon, *Salmo salar*, than in wild stock. Even under natural conditions, wild stock had a lower growth rate than farmed fish (Einum and Fleming, 1997). Furthermore, Davis and Fenderson (1971) observed in Atlantic salmon that, even though hatchery and wild parr were matched for size when introduced to a divided outdoor stream aquarium, hatchery parr were on average larger in size than wild parr as the study progressed. Overall, hatchery-reared fish seem to have a growth advantage over wild fish stocks.

Wild and hatchery-reared fish differ not only in growth rates, but also in their behavioural activity. Bachman (1984) observed in the brown trout, *Salmo trutta*, that hatchery-reared fish fed less than wild fish. A similar feeding pattern was observed in Atlantic salmon (Fenderson *et al.*, 1968; Sosiak *et al.*, 1979). Davis and Fenderson (1971), and Sosiak (1978) also observed in Atlantic salmon that

hatchery parr were less shelter-oriented and more mobile than wild parr, and exhibited higher frequencies of agonistic behaviours. Norman (1987), in contrast, found Atlantic salmon fry of the hatchery stocks to be less aggressive.

Holm and Fernö (1978) went a step further in their study, by examining the connection between aggressive activity and growth rate. They observed that aggressive Atlantic salmon parr grew less rapidly, while parr with the most rapid growth performed aggressive actions less often (Holm and Fernö, 1978). These results imply a negative relationship between aggressive activity and growth. Furthermore, Robinson and Doyle (1990) found a negative correlation between aggression and growth in the tilapia hybrid, *Oreochromis mossambicus* x *O. hornorum*. Unfortunately, there is little information on the relationship between activity and growth in farmed-reared and wild fish stocks. Thus, more research is needed to examine these relationships to see to what extent growth differences between farmed-reared and wild fish can be attributed to differences in locomotory and/or aggressive activity levels of fish stocks.

#### *Sexual dimorphism in size*

As information has accumulated on growth rates of various fish species, it has become apparent that either a) the males and females of a given species grow at the same rate and have similar maximum sizes (e.g., herrings), b) the females have faster growth rates and reach larger size than the males (e.g., codfishes), or c) the males have faster growth rates and become larger than the females (e.g., cichlids) (Fryer and Iles, 1972). The sex-related growth differences in cichlids,

including Nile tilapia, are well established (van Someren and Whitehead, 1959; Mabaye, 1971; Fryer and Iles, 1972; Lowe-McConnell, 1975, 1982; Balarin and Hatton, 1979; Palada-de Vera and Eknath, 1993; Toguyéni *et al.*, 1996, 1997).

The causes of male growth superiority in cichlids have been examined; however, no single explanation of sexual dimorphism in size has been widely accepted. One hypothesis is that tilapia females put so much more energy into egg production, producing eggs at very frequent intervals, which may result in costs to growth; also the females almost cease to feed while mouthbrooding their eggs and young (Lowe-McConnell, 1975). Another is that male sex hormones have an anabolic or growth promoting effect, and thus could result in the higher growth of males (Donaldson *et al.*, 1979; Ufodike and Madu, 1986). In addition, thyroid hormones ( $T_3$  and  $T_4$ ) also participate in regulating growth and development. Toguyéni *et al.* (1996, 1997) observed, in Nile tilapia, that plasma  $T_3$  levels were higher in males than females, which could account for the males' growth advantage. It was also suggested that the difference in growth may be related to a sex-linked genetic characteristic which gives the male an advantage either through efficiency of food conversion, or through aggressive feeding behaviour (Mabaye, 1971). Behavioural activity and its association with larger-sized males compared to females is an area that remains to be explored. Toguyéni *et al.* (1997) observed, in mixed sex groups of Nile tilapia, an increase in activity and a decrease in growth; however, no connection was made between the higher growth of males and their activity level. Therefore, more experimentation is needed to study the relationship between growth and activity level in both sexes.

*Nile tilapia (Oreochromis niloticus)*

*Oreochromis niloticus* originates from the upper Nile in Uganda. It has moved southwards, colonizing all the western Rift lakes down to Lake Tanganyika, and has colonized central and western Africa, by the Chad and Niger basins. Its expansion is still taking place; it has not yet reached some of the tributaries of the upper Niger and it is rare in the coastal rivers of western Africa (Philippart and Ruwet, 1982). It is found not only in several of the great lakes of Africa but even outside Africa in at least one coastal river of Israel (Fryer and Iles, 1972).

*Oreochromis niloticus*, a maternal mouthbrooding cichlid, has a lek-based breeding system analogous to those seen in lekking birds (Fryer and Iles, 1972; McKaye, 1984). Males congregate in shallow waters where they excavate a shallow, saucer-like depression, to which they attract a succession of females. In the study of McKaye (1986), the term 'bower' was given to this bowl-shaped depression instead of 'nest' because it is used only as a site for courting females, and mating (Borgia, 1985); it is constructed independently of the need to care for eggs and young (McKaye, 1986). However, both terms (i.e., nest and bower) have been used to describe the depression in the sand, and thus both terms are used here. As eggs are being deposited in the bower, the female quickly takes eggs and sperm into her mouth, where fertilization takes place, and then leaves for brooding grounds. The embryos and fry are brooded in the female's mouth for approximately 20-30 days and then released (Fryer and Iles, 1972).

In mouthbrooding cichlids, body size does not appear to be a major consideration in mate choice, as observed in substratum-spawning cichlids (McKaye, 1986). Males appear to court all females indiscriminately, while females choose males on the basis of the character and/or location of the bower (McKaye, 1984). It was observed that a large bower is preferred by females (McKaye *et al.*, 1990), and thus males who build large bowers should experience a higher mating success. Due to the importance of nest characters on mating success of males, more information on nest building by mouthbrooding cichlids, such as Nile tilapia, would be of interest.

Nile tilapia has dominated global tilapia culture since the 1980's, and its share of total tilapia production has increased dramatically from 33% or 66,000 mt in 1984 to 72% or 474,000 mt in 1995 (Rana, 1997). However, Pullin and Capili (1988) found that little attention had been given to the genetic improvement of farmed populations of Nile tilapia (see also Pullin, 1998). In 1988, an international workshop confirmed the findings of Pullin and Capili that tilapia broodstocks used for aquaculture outside Africa were limited in genetic diversity (Pullin, 1988; as cited in Pullin, 1998). It was concluded that more investment in research for the genetic improvement of tilapias was needed. Based upon these findings, the International Center for Living Aquatic Resources Management (ICLARM) and its collaborators initiated the Genetic Improvement of Farmed Tilapias (GIFT) project in the Philippines. Four new wild founder populations of Nile tilapia (from Egypt, Ghana, Kenya, and Senegal) and populations of four strains of Nile tilapia in current use by farmers in Asia ('Israel', Singapore, Taiwan, and

Thailand) were assembled. The genetic material from the best families of all strains were incorporated, according to their performance rankings, in a synthetic strain termed 'GIFT' strain. This synthetic strain has since been subjected to selective breeding for good growth (Pullin, 1998). A recent project found the estimated yield potential of the GIFT strain to be significantly higher than that of some of the existing farmed strains in Asia (ICLARM-ADB, 1998; as cited in Pullin, 1998).

### **Objectives of the present study**

It was with the initial aim of examining the relationship that exist between growth rate and activity level of fish from two strains of Nile tilapia (control and GIFT) that I commenced my preliminary observations in March, 1997. During the following 12 months, three experiments were undertaken. The first experiment examined a) the differences in the growth rates of the control and GIFT fish under controlled laboratory conditions, b) the relationship between growth rate and activity level, and c) the onset of sexual maturity as it relates to the differences in growth rates. The second experiment examined, in more detail, the differences in the offensive aggression between male fish of both strains. Lastly, the third experiment examined nest building in male fish from the control and GIFT strains of Nile tilapia.



## CHAPTER II

### General Materials and Methods

#### Experimental Animals

The two strains of Nile tilapia (*Oreochromis niloticus*), a fish of African origin, were imported into Vancouver, Canada from the International Center for Living Aquatic Resources Management (ICLARM), Bureau of Fisheries and Aquatic Resources (BFAR)/National Freshwater Fisheries Technology Research Center (NFFTRC), Muñoz, Nueva Ecija, Philippines. The two strains are: 4th generation of GIFT fish (see Background on Nile tilapia) and 'control' Nile tilapia from Bulacan Province, Philippines, typical of those fish farmed in Asian countries where selective breeding has not yet been widely applied.

#### Holding and Experimental Facilities

On arrival at the University of British Columbia (January 30th), the fish were placed in 55 and 102 L stock tanks with similar fish densities (approximately 5.5 L of water per fish) for a five week period to acclimatize the fish to the laboratory conditions; the fish were then transferred to the experimental aquaria. All experimental aquaria were maintained at  $24.0 \pm 0.5^{\circ}\text{C}$ ; the water temperature was similar to both pond sources in the Philippines (i.e., 24-25°C). The temperature of the water in the experimental tanks was maintained by the use of a room heater which kept the room temperature at approximately 27°C. Each experimental tank, with dimensions of 61.0 cm x 30.5 cm x 30.5 cm, was provided

with a layer of gravel (depth of 2.5 cm), and a box charcoal filter. All four sides of the tanks were covered with beige paper to prevent visual interaction between neighbouring fish. Illumination was provided, over a 12-h photoperiod, by fluorescent lights mounted 2 m above each row of tanks. The light strips were positioned upwards to minimize light reflection from the water surface from entering the camera lens during videorecording. During behavioural recording, two extra light strips, housed in a wooden frame, were placed on either side of the row of aquaria to allow the fish to be seen clearly. These two extra light strips were turned on 30 min prior to the observation sessions to acclimatize the fish to the higher light intensity. The fish were fed commercially prepared catfish feed (Otter Co-op, Aldergrove, British Columbia) at 3% wet weight of fish daily. The quantity of feed given was adjusted monthly following the recording of standard length and weight of each fish.

#### **Videocamera Set-up**

Locomotory and agonistic behaviours were recorded using a colour pro843 RCA videocamera supported by a 4-wheeled aluminium stand placed on two aluminium tracks. This stand enabled the videocamera to be positioned lens down approximately 75 cm above the rim of each experimental tank. A cable to a Panasonic video monitor, allowed fish behaviours to be observed while being videorecorded.

## Fish Identification

The fish were marked by attaching a coloured bead to each individual. The beads were attached 10 days prior to the start of the behavioural recordings. The fish were anaesthetized by being immersed in a buffered 0.03% w/v solution of methane tricaine sulfonate (MS 222, Syndel Laboratories, Vancouver, Canada). When a fish was nearly motionless, on its side, and respiring slowly, the fish was removed from the solution and placed on a moist sponge. A 0.25 mm diameter nylon monofilament, with one bead tied onto one end, was sewn through the musculature at the front end of the dorsal fin using a sewing needle. The bead was secured onto the fish as described in Kroon (1997). The fish was returned to the freshwater and allowed to recover. Five light-coloured beads were used: yellow, white, blue, green, and pink. These bead colours were chosen because they were in sharp contrast to the dark surroundings (i.e., dark body colouration and sand).

The presence of brightly coloured beads on the fish apparently did not change the motivational state of the neighbouring fish: there appeared to be no increase in the frequency of agonistic acts directed towards beaded fish (pers. obs.). It was important to resolve this issue because body colour patterns are important in the visual communication of cichlids and the pattern of colouration changes according to the motivational state of the fish (Billy, 1982; Nelissen, 1991). For a more detailed description of colour patterns in tilapias see Billy (1982).

### Determination of Sex

The sex of the fish was initially determined by the external examination of the genital papilla (Afonso and Lebouté, 1993) and then verified later by the dissection of the gonads. The distinctive features of the genital papilla of the male and female tilapia are described by Maar *et al.* (1966). Briefly, the male has two orifices situated just forward of the anal fin. One is the anus, the other is the urogenital aperture which usually forms into a small papilla. The female, in contrast, has three orifices, namely the anus, a transverse genital opening and a microscopic urinary orifice which is scarcely visible to the naked eye (Balarin and Hatton, 1979). The anaesthetized fish was placed belly-up on a moist sponge and a dye (potassium permanganate) was applied onto the genital papilla with a Q-tip, as suggested by L.O.B. Afonso (pers. comm.). This dye was used to highlight a slit (genital opening) present only in the females (Afonso and Lebouté, 1993). The anaesthetized fish was then placed under a dissecting microscope (magnification: 7-10X) to inspect the genital papilla. A fish was considered to be a female when the slit was observed. The sex determination procedure commenced on May 19th and was repeated and thereby verified during the monthly recordings of the weight and length measurements.

### Procedure for Recording Weight and Length Measurements

Weight and length measurements were recorded monthly. The anaesthetized fish were placed on a wet Plexiglas surface alongside a metric ruler, and their standard length was recorded. The anaesthetized fish was then placed in a large petri dish on a weight scale to record their weight.

## Behavioural Measures

Detailed descriptions of cichlid behaviour can be found in Baerends and Baerends-van Roon (1950), Billy (1982) and Fryer and Iles (1972). For the purpose of this experiment, the activity was measured on the basis of the following twelve behaviours:

### *Swimming*

Swimming is a movement of the fish in any direction in the water column without any interactions with other fish;

### *Resting*

A fish is considered to be resting when it stays in the same position, either in the water column or on the gravel bottom, long enough for the computer key used to encode resting behaviour to be pressed by the observer;

### *Chasing/Escaping*

A fish swimming after another fish at a high velocity is described as chasing, while escape behaviour is carried out by the fish swimming away from the aggressor;

### *Tail-beating*

Tail-beating occurs when a fish presents the lateral aspect of its body to an opponent, head to tail, and uses its caudal fin to beat the water sideways over the head of its opponent (Baerends and Baerends-van Roon, 1950; Billy, 1982; Fryer and Iles, 1972). The tail-beating individual does not actually touch the opponent. Tail-beating is used as a threat signal by a territorial male towards an intruding male (Billy, 1982); presumably, this act communicates the animal's strength

(Baerends and Baerends-van Roon, 1950). Tail-beating also serves as a courtship signal by a territorial male towards a female entering his territory (Billy, 1982);

### *Nipping*

Biting directed towards a fin and/or the body of a neighbouring fish is referred to as nipping. Occasionally, nipping results in fin amputation and body scarring (Billy, 1982);

### *Confronting*

Confronting occurs between territorial males during boundary disputes. Opposing males rush at each other ending their charges at the common boundary (nest rim). The males then oscillate back and forth in synchrony, with one male (fins collapsed) retreating while its opponent (fins raised) advances a few centimetres. This back and forth motion is completed several times in rapid succession, after which the males separate or attack (e.g., jaw lock) (Billy, 1982);

### *Jaw Lock*

A jaw lock is performed when the fish grip each others mouth, and start pushing and pulling each other to and fro (Fryer and Iles, 1972);

### *Opercular Flare*

Opercular flaring occurs when a fish erects the operculae and branchiostegal membrane, and reveals its dorsally-situated black opercular spots;

### *Gulping*

The action of a fish swimming to the water surface and taking in surface water with its mouth is termed gulping. This behaviour increases oxygen uptake, i.e., complements gill breathing (Weber and Kramer, 1983);

### *Feeding*

A fish is considered to be feeding when sand is picked up with its mouth, sifted (i.e., separates food particles from sand), and then dropped indiscriminately.

### *Nesting*

A male fish establishes a territory by digging a nest pit in the substrate. Nesting occurs when a fish swims head down into the substrate, secures a mouthful of sand, swims a short distance from the centre of the pit, and spits out the substrate. In contrast to feeding, no sifting is performed. The displaced substrate is deposited on the edge of a territory, where it accumulates and forms a raised rim around the nest. This raised rim defines territorial boundaries. Localized digging produces a pit which a male occupies and defends from intruders while attempting to attract spawning partners. Nesting is used to maintain the nest rim and to remove debris from the pit. Each male digs throughout its residency in a territory, with the frequency of digging at a peak when the territory is being established. The female fish also nest, but only in the later stages of courtship prior to spawning (Billy, 1982).

The total duration of swimming and resting was recorded, while the number of bouts of chasing, escaping, tail-beating, nipping, confronting, jaw-locking, opercular flaring, gulping, feeding and nesting were recorded. The data on locomotory and agonistic behaviours were then analysed using The Observer version 3.0 computer software (Noldus Information Technology, Wageningen, Netherlands).

## Statistical Analyses

Linear regression equations were used to test for significant differences in the growth curves (weight and length). The Mann-Whitney U-test was used in the comparison of independent measures of fish from the GIFT and control strain. These tests were one-tailed unless otherwise stated. The chi-square goodness of fit test was used to determine if there were significant differences between the actual number of fish from four experimental groups (i.e., female control, male control, female GIFT and male GIFT) that performed behavioural activities, and a theoretically even distribution. If the chi-square analysis detected significant departures from the even distribution, the chi-square analysis was subdivided to determine whether the significant difference between observed and expected frequencies was concentrated in certain of the experimental groups, or whether the difference was due to the effects of the data in all of the four experimental groups (Zar, 1996). When the observed frequencies were small, the use of the two-tailed Fisher exact test was preferred over the chi-square analysis. The level of significance was set at  $\alpha=0.05$  for all statistical analyses.



### CHAPTER III

Experiment I: Growth, behavioural activity, and sexual maturation in the control and GIFT strains of Nile tilapia

#### Introduction

The examination of the relationship between maturity, size, and age in fish has yielded conflicting results. Alm (1959) noted some cases in which the slower growing forms matured earlier and at a smaller size than the faster-growing forms, and many more cases in which the opposite was true. In tilapia, particularly in Nile tilapia, the female fish tend to have a lower growth rate than the male fish (Balarin and Hatton, 1979; Lowe-McConnell, 1982). Furthermore, in culture ponds, fish of the GIFT strain of Nile tilapia grow faster than control fish (Pullin, 1998, and see p. 7). To examine these growth differences in Nile tilapia, the following questions were asked: Do the differences in the growth rate of GIFT and control fish persist under controlled laboratory conditions? Does the difference apply to both male and female? Can any growth differences be related to a difference in behavioural activity, and the onset of sexual maturity?

To address the last question, nesting activity, a behaviour which is often the first indication of the sexual maturity of fish, was studied. This behaviour was used to examine the relationship between growth rate and the onset of sexual maturity in both strains of Nile tilapia.

## Materials and Methods

Small mixed sex groups (5 fish per tank) of GIFT and control strains were established in 55 L aquaria on March 7th. At this time, the mean weight and standard length of the mixed sex GIFT and control fish were  $5.3 \pm 1.6$  g and  $5.3 \pm 0.6$  cm, and  $4.8 \pm 1.8$  g and  $5.1 \pm 0.7$  cm, respectively. Initially, the fish could not be sexed, and hence the mixed sex design; however, as the experiment progressed and the fish grew, sex determination became possible.

At the start of the experiment (April 19th), each aquarium contained five fish. However, as the experiment progressed, some aquaria had less than five fish present as a result of mortality. The aquaria with four fish were retained in the experiment. Groups with fewer than four fish were excluded. Preliminary observations showed that the fish in aquaria with four or five fish had similar activity levels, while the surviving fish in the tanks with less than four fish were very aggressive. This resulted, in most cases, in only one fish remaining in the tank.

On day 1, the weight and standard length measurements were recorded. The locomotory and aggressive activities of the control and GIFT fish were videorecorded on day 10 and day 12 (trials #1 and 2, respectively) during a 300 second observation period. On day 31, length and weight measurements were repeated. This experimental schedule was repeated three times over the three month study period (April-June). The mean growth and behavioural measurements of all fish in an experimental group were compared, instead of

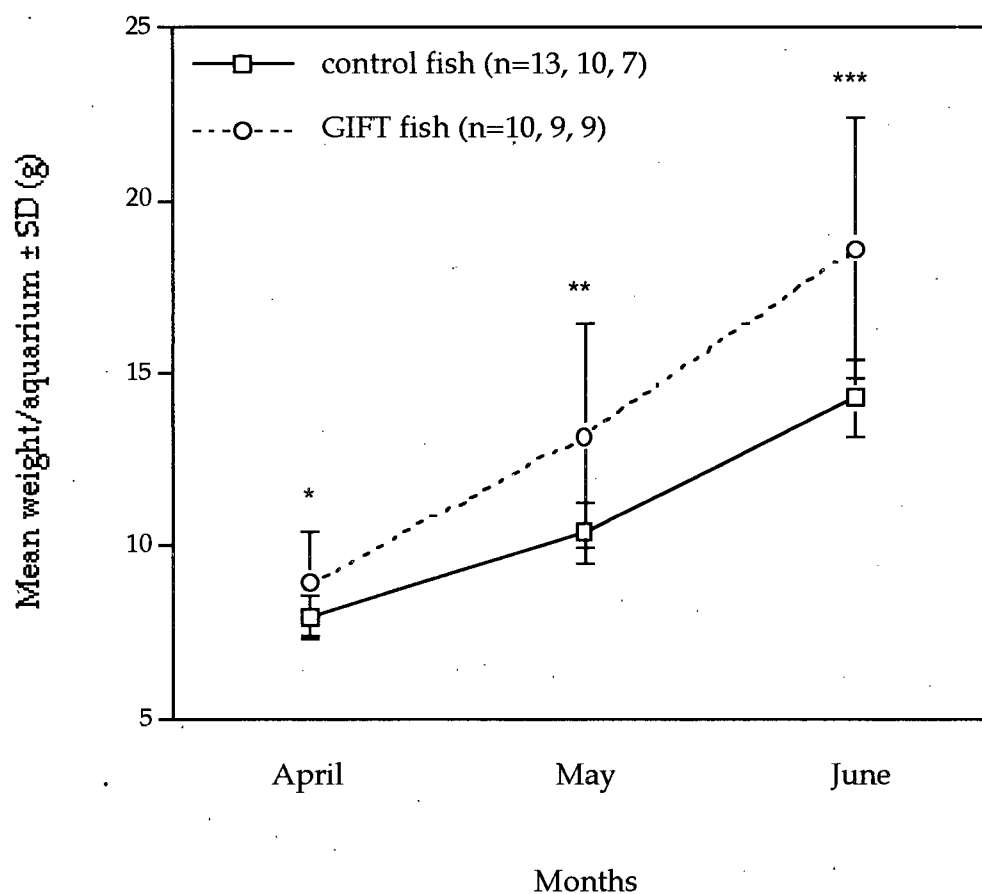
individual measures because growth and behaviour of individual fish in each aquarium were not independent of the behaviour of other members of the group. Due to my inability to identify individual fish in the videorecordings of the first trial in April, only trial #2 could be used to compare activity levels between the female and male fish of each strain. Furthermore, size-specific mortality in male and female fish could only be examined in May and June because, in April, the sex of the fish could be determined neither by the external examination of the genital papilla due to the small size of fish, nor by the dissection of the gonads, due to the cannibalistic practice of live tank mates towards dead fish.

## Results

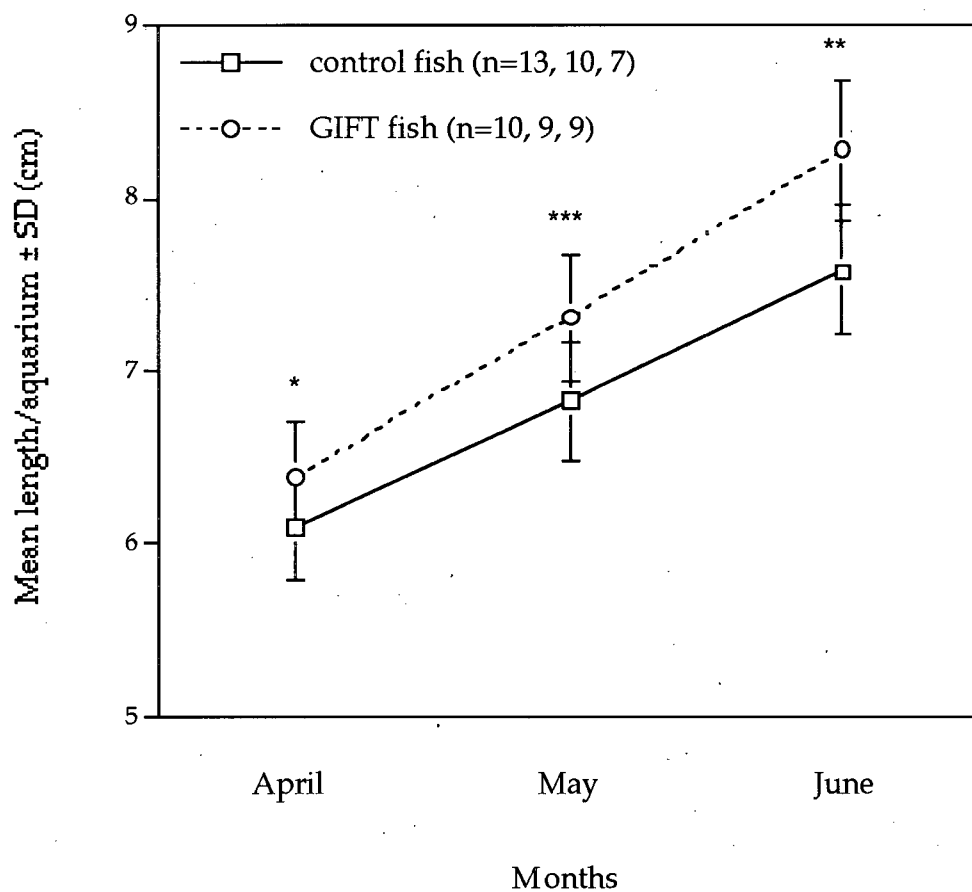
During the three month study period (April-June), the GIFT fish were observed to have significantly faster growth rates than the control fish (one-tailed comparison of simple linear regression equations; weight:  $P < 0.05$ , length:  $P < 0.005$ ) (Figure 1 and 2). GIFT fish gained 4.9 g/month and increased in length by 0.9 cm/month, while the values for the control fish were 3.2 g/month and 0.7 cm/month, respectively. Furthermore, the weight and length of the GIFT fish were found to be significantly greater than the control fish at each measurement (Figure 1 and 2).

The GIFT fish also spent less time swimming and more time resting than the control fish (Table I). The differences in swimming/resting behaviours between the control and GIFT fish were significant in April and May, but not in June

**Figure 1.** Weight (mean  $\pm$  SD) of fish from two strains of Nile tilapia (control and GIFT). All experimental aquaria had four or five fish present and the number of aquaria used during the study period is represented by the n-values (data from aquaria with less than four fish present were not used in the mean weight calculations). The Mann-Whitney U-test (one-tailed) was used to test for significant differences in the weight of fish of both strains. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P = 0.005$ .



**Figure 2.** Length (mean  $\pm$  SD) of fish from two strains of Nile tilapia (control and GIFT). All experimental aquaria had four or five fish present and the number of aquaria used during the study period is represented by the n-values (data from aquaria with less than four fish present were not used in the mean length calculations). The Mann-Whitney U-test (one-tailed) was used to test for significant differences in the length of fish of both strains. \*  $P < 0.025$ , \*\*  $P = 0.005$ , \*\*\*  $P = 0.0025$ .



MONTHS	STRAINS OF NILE TILAPIA	TOTAL TIME (SEC) SPENT PERFORMING BEHAVIOURS PER 300 SECOND TRIAL (MEAN $\pm$ SD)	
		Swimming	Resting
April	control (n=13)	76.4 $\pm$ 81.0 ***	213.4 $\pm$ 85.3 ****
	GIFT (n=10)	19.3 $\pm$ 33.0	279.8 $\pm$ 33.2
May	control (n=10)	51.9 $\pm$ 45.8 *	233.3 $\pm$ 60.4 **
	GIFT (n=9)	10.7 $\pm$ 12.6	287.8 $\pm$ 15.3
June	control (n=7)	41.4 $\pm$ 46.1	252.2 $\pm$ 57.7
	GIFT (n=9)	19.1 $\pm$ 27.1	280.1 $\pm$ 29.0

**Table I.** Total time (mean  $\pm$  SD) two strains of juvenile Nile tilapia (control and GIFT) performed swimming and resting acts each month of the three month study. Each month two 300 second behavioural trials were recorded one day apart. All experimental aquaria had four or five fish present and the number of aquaria used is represented by the n-values (data from the aquaria with less than four fish present were not used). The Mann-Whitney U-test (one-tailed) was used to test for significant differences in the total time the control and GIFT fish allotted to swimming and resting acts each month. \*  $P < 0.025$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.005$ , \*\*\*\*  $P = 0.0025$ .

(Table I). The time the control fish spent swimming decreased by 46% during the three month period, while the level of swimming activity for the GIFT fish remained relatively constant (Table I). In contrast, the control fish increased the time spent resting by 18% during the study, while the resting values for the GIFT fish again remained relatively constant (Table I).

Moreover, control fish performed more chasing and escaping behaviours than the GIFT fish (Table II). The differences were significant in April and May, but not in June (Table II). The frequency of chasing and escaping exhibited by control fish increased in May by 23% and 10% of April values, respectively, and then declined in June by 55% and 52%, respectively (Table II). In the GIFT fish, the frequency of chasing increased by 29% during the study, while escaping increased in May by 20% of April values, and then declined in June by 37% (Table II). A higher frequency of tail-beating was characteristic of the control fish compared to the GIFT fish; the differences were only significant in April (Table II). Tail-beating frequency of control fish increased by 61% during the study while, in GIFT fish, the frequency increased in May by 327% of April values, and then declined by 70% in June (Table II). Furthermore, nipping frequency was found to be significantly higher in the control fish than the GIFT fish during the three month study period. The nipping frequency of control and GIFT fish increased in May by 169% and 129% of April values, respectively, and then declined in June by 73% and 94%, respectively (Table II). Confronting and jaw-locking behaviours were performed only by the control fish and the frequency of confronting declined by 73% during the study, while jaw-locking remained

MONTHS	STRAINS OF NILE TILAPIA	NUMBER OF BOUTS OF LOCOMOTORY AND AGONISTIC BEHAVIOURS (MEAN $\pm$ SD)								
		Chasing	Escaping	Tail-beat.	Nipping	Confront.	Jaw-lock.	Gulping	Feeding	Nesting
April	control (n=13)	1.2 $\pm$ 1.3 ***	1.7 $\pm$ 1.8 *****	0.6 $\pm$ 0.8 **	0.3 $\pm$ 0.3 *	0.1 $\pm$ 0.3	0.01 $\pm$ 0.03	1.0 $\pm$ 3.1	0.2 $\pm$ 0.4	0.1 $\pm$ 0.3
	GIFT (n=10)	0.2 $\pm$ 0.4	0.3 $\pm$ 0.5	0.1 $\pm$ 0.4	0.1 $\pm$ 0.1	0	0	0	0.1 $\pm$ 0.3	0
May	control (n=10)	1.5 $\pm$ 1.4 ***	1.9 $\pm$ 1.7 *****	0.9 $\pm$ 1.2	0.7 $\pm$ 0.6 ****	0.1 $\pm$ 0.2	0.02 $\pm$ 0.06	2.1 $\pm$ 5.3	0.4 $\pm$ 1.0	0.2 $\pm$ 0.5
	GIFT (n=9)	0.2 $\pm$ 0.5	0.3 $\pm$ 0.8	0.5 $\pm$ 1.4	0.2 $\pm$ 0.2	0	0	0.01 $\pm$ 0.03	0.1 $\pm$ 0.3	0.01 $\pm$ 0.03
June	control (n=7)	0.7 $\pm$ 0.9	0.9 $\pm$ 1.4	1.0 $\pm$ 2.1	0.2 $\pm$ 0.3 **	0.03 $\pm$ 0.05	0	0	0	0.4 $\pm$ 0.8
	GIFT (n=9)	0.2 $\pm$ 0.6	0.2 $\pm$ 0.5	0.1 $\pm$ 0.3	0.01 $\pm$ 0.03	0	0	0	0	0.03 $\pm$ 0.10

**Table II.** Number of bouts of locomotory and agonistic behaviours (mean  $\pm$  SD) the control and GIFT strains of juvenile Nile tilapia performed each month of the three month study. Each month two 300 second behavioural trials were recorded one day apart. The number of control and GIFT aquaria used each month is represented by the n-values. The Mann-Whitney U-test (one-tailed test, except for gulping and feeding behaviours) was employed to test for significant differences between the number of acts performed by the fish from the control and GIFT aquaria for each month. \* P=0.05, \*\* P<0.025, \*\*\* P<0.01, \*\*\*\* P<0.005, \*\*\*\*\* P<0.0025.

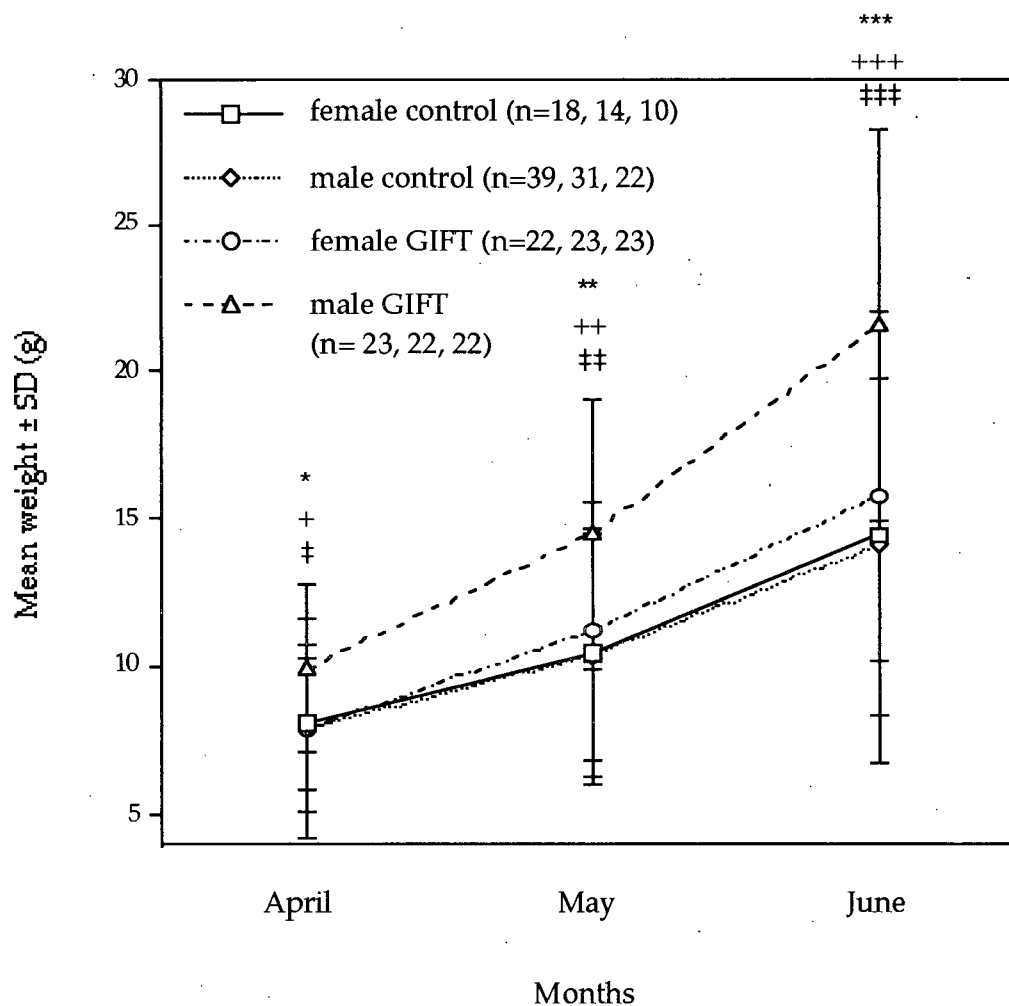


relatively constant (Table II). No opercular flares were performed during the behavioural trials so this behaviour was excluded from analyses.

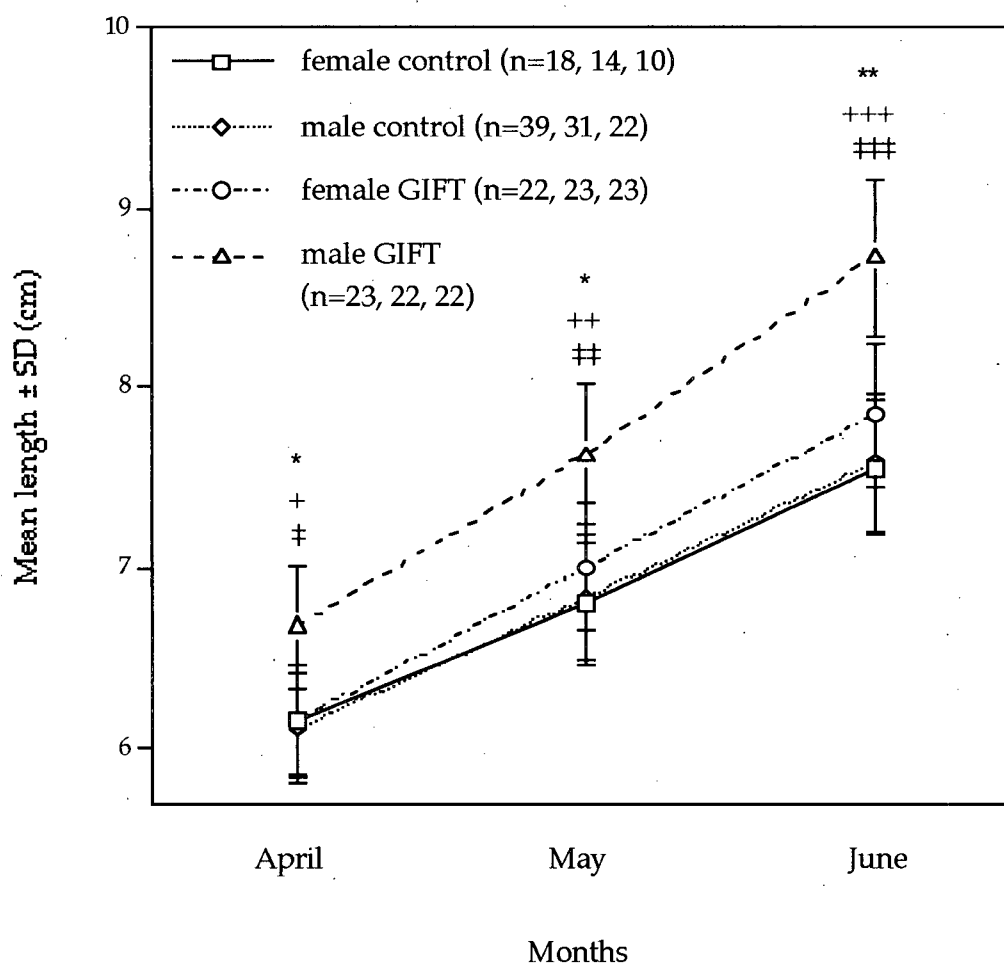
Gulping was also found to be mostly performed by the control fish (Table II). An increase (114%) in the frequency of gulping was observed in May, and then dropped to zero in the behavioural sessions of June (Table II). Feeding behaviour was performed more often by control fish than GIFT fish especially in May, but the differences were not significant (Table II). The feeding frequency of control fish increased in May by 150% of April values while, in the GIFT fish, the frequency remained relatively constant (Table II). In the behavioural sessions of June, no feeding behaviour was recorded by either control or GIFT fish (Table II).

As the experiment progressed and the sex of each fish could be determined, the weight and length, and activity levels of male and female fish of both strains were compared. During the three month study period, the male GIFT were observed to have a faster growth rate than the female GIFT (Figure 3 and 4). The difference was significant only for growth in length (one-tailed comparison of simple linear regression equations;  $P < 0.05$ ). The male GIFT fish gained 5.8 g/month and increased in length by 1.0 cm/month, while the corresponding values for the female GIFT were 3.9 g/month and 0.9 cm/month, respectively. In contrast, the growth rates of the male and female control fish were similar (Figure 3 and 4). The male control fish gained 3.1 g/month and increased in length by 0.7 cm/month, and the values for the female control fish were 3.2 g/month and 0.7 cm/month, respectively. The growth rate in weight of female

**Figure 3.** Weight (mean  $\pm$  SD) of females and males from two strains of Nile tilapia (control and GIFT). The number of females and males from both strains used during the three month study is represented by the n-values. The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the weight of females and males of same strain (GIFT: \*  $P < 0.025$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.0025$ ), females or males of different strains (males: +  $P < 0.01$ , ++  $P < 0.001$ , +++  $P < 0.0005$ ), and females and males of different strains (GIFT male vs. control female: †  $P < 0.025$ , ††  $P < 0.01$ , †††  $P < 0.0025$ ).



**Figure 4.** Length (mean  $\pm$  SD) of females and males from two strains of Nile tilapia (control and GIFT). The number of females and males from both strains used during the three month study is represented by the n-values. The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the length of females and males of same strain (GIFT: \*  $P < 0.025$ , \*\*  $P < 0.0025$ ), females or males of different strains (males: +  $P < 0.01$ , ++  $P < 0.0025$ , +++  $P < 0.0005$ ), and females and males of different strains (GIFT male vs. control female: †  $P < 0.025$ , ††  $P < 0.005$ , †††  $P < 0.0025$ ).



however, in the male GIFT, the growth rate in weight was found to be significantly higher (one-tailed comparison of simple linear regression equations; comparison of female and male control to male GIFT fish:  $P < 0.05$ ,  $P < 0.05$ , respectively). Furthermore, the growth rates in length of the female and male GIFT were significantly different to the male and female control fish (one-tailed comparison of simple linear regression equations; comparison of female and male control to female GIFT fish:  $P < 0.025$ ,  $P < 0.005$ , respectively; comparison of female and male control to male GIFT fish:  $P < 0.025$ ,  $P < 0.025$ , respectively).

The weight and length of the male GIFT were significantly higher than the female GIFT during the three month study period. In contrast, the weight of the male control was slightly lower than the female control during the study. The length of the male control also was slightly lower than the female control fish in April, but then increased slightly above length values of female control in May and June (Figure 3 and 4). Furthermore, the weight and length of male GIFT fish were significantly greater than either the male or female controls, while the measurements of the female GIFT fish were slightly higher than either the female or male controls (Figure 3 and 4). The only exception was in April where the weight of the female GIFT fish was found to be slightly lower than in the female controls.

The male control fish also spent more time swimming and less time resting than the female control fish; however, a significant difference in the allotment of time

**Table III.** Total time in seconds (mean  $\pm$  SD) the female and male juvenile Nile tilapia (control and GIFT strains) performed swimming and resting acts each month of the three month study. Each month two 300 second behavioural trials were recorded one day apart. Due to unforeseen circumstances, only data from the behavioural trial #2 in April were tabulated. The number of female and male fish of both strains used each month is represented by the n-values (i.e., # of fish in April, May, June, respectively). In each table cell, the top values represent the sex/strain of Nile tilapia of the column heading, while the bottom values represent the sex/strain of Nile tilapia of the row. The Mann-Whitney U-test (one-tailed) was employed to test for significant differences in the total time the female and male fish of both strains allotted to swimming and resting acts each month. \*  $P < 0.05$ , +  $P < 0.025$ , \*\*  $P = 0.01$ , ++  $P < 0.01$ , \*\*\*  $P < 0.005$ , +++  $P < 0.001$ , \*\*\*\*  $P < 0.0005$ .

SEXES/STRAINS OF NILE TILAPIA	female control (n=18,14,10)				male control (n=39,31,22)				male GIFT (n=23,22,22)			
	April	May	June		April	May	June		April	May	June	
female GIFT (n=22,23,23)	Swimming	70.3 ± 79.8 *	35.1 ± 43.2	19.2 ± 16.5	84.7 ± 99.7 ***	62.9 ± 51.4 ****	55.5 ± 56.7 *		35.3 ± 64.3	10.0 ± 18.3	12.8 ± 24.6 +	
	Resting	35.1 ± 55.1	11.5 ± 12.7	25.1 ± 27.6	35.1 ± 55.1	11.5 ± 12.7	25.1 ± 27.6		35.1 ± 55.1	11.5 ± 12.7	25.1 ± 27.6	
male GIFT (n=23,22,22)	Swimming	221.0 ± 81.1 *	256.5 ± 52.3 *	279.7 ± 18.2	202.4 ± 97.6 +++	218.0 ± 69.7 ****	234.8 ± 71.4 +		261.2 ± 65.3	288.3 ± 23.7	286.0 ± 28.4 +	
	Resting	264.0 ± 55.2	287.3 ± 13.9	274.6 ± 28.3	264.0 ± 55.2	287.3 ± 13.9	274.6 ± 28.3		264.0 ± 55.2	287.3 ± 13.9	274.6 ± 28.3	
male control (n=39,31,22)	Swimming	70.3 ± 79.8 +	35.1 ± 43.2 ++	19.2 ± 16.5 **	84.7 ± 99.7 ***	62.9 ± 51.4 ****	55.5 ± 56.7 ****		-----	-----	-----	
	Resting	35.3 ± 64.3	10.0 ± 18.3	12.8 ± 24.6	35.3 ± 64.3	10.0 ± 18.3	12.8 ± 24.6		-----	-----	-----	
male control (n=39,31,22)	Swimming	221.0 ± 81.1 +	256.5 ± 52.3 ***	279.7 ± 18.2 **	202.4 ± 97.6 +++	218.0 ± 69.7 ****	234.8 ± 71.4 ****		-----	-----	-----	
	Resting	261.2 ± 65.3	288.3 ± 23.7	286.0 ± 28.4	261.2 ± 65.3	288.3 ± 23.7	286.0 ± 28.4		-----	-----	-----	
male control (n=39,31,22)	Swimming	70.3 ± 79.8	35.1 ± 43.2 *	19.2 ± 16.5	-----	-----	-----		-----	-----	-----	
	Resting	84.7 ± 99.7	62.9 ± 51.4	55.5 ± 56.7	-----	-----	-----		-----	-----	-----	
male control (n=39,31,22)	Swimming	221.0 ± 81.1	256.5 ± 52.3 *	279.7 ± 18.2	-----	-----	-----		-----	-----	-----	
	Resting	202.4 ± 97.6	218.0 ± 69.7	234.8 ± 71.4	-----	-----	-----		-----	-----	-----	

to swimming and resting was only found in May (Table III). In contrast, the male GIFT fish spent less time swimming and more time resting than the female GIFT fish, except in April (Table III). The differences in swimming and resting behaviours were significant only in June (Table III). Furthermore, the male control fish spent significantly more time swimming and less time resting than either female or male GIFT fish (Table III). The female control fish also spent more time swimming and less time resting than either female (except in June) or male GIFT fish (Table III). The differences in swimming and resting behaviours between the female control and male GIFT fish were significant throughout the three month study. The differences in swimming behaviour between the female control and GIFT fish were only significant in April, while the differences in resting behaviours were significant in both April and May (Table III).

During the three month study, the total time male and female control fish spent swimming declined by 35% and 73% of starting (April) values, respectively, while the time spent resting increased by 16% and 27%, respectively (Table III). In contrast, the amount of time the male and female GIFT fish spent swimming declined in May by 72% and 67% of the April values, respectively, but then increased in June by 29% and 119%, respectively (Table III). Moreover, the total time male and female GIFT fish spent resting increased from April to May by 10% and 9%, respectively, but then declined slightly (i.e., by 1% and 4%, respectively) in June (Table III).

Male fish performed more agonistic behaviours than the female fish (except in

**Table IV.** Number of bouts of agonistic and escape behaviours (mean  $\pm$  SD) performed by the female and male juvenile Nile tilapia (control and GIFT strains) each month of the three month study. Each month two 300 second behavioural trials were recorded one day apart. The five behaviours included under the agonistic category are chasing, tail-beating, nipping, confronting, and jaw-locking. Due to unforeseen circumstances, only data from the behavioural trial #2 in April were tabulated. The number of female and male fish of both strains used each month is represented by the n-values (e.g., # of fish in April, May, June, respectively). In each table cell, the top values represent sex/strain of Nile tilapia of the column heading, while the bottom values represent the sex/strain of Nile tilapia of the row. The Mann-Whitney U-test (one-tailed) was employed to test for significant differences in the number of bouts of agonistic and escaping behaviours the female and male fish of both strains performed each month. \*  $P < 0.05$ , +  $P < 0.025$ , \*\*  $P < 0.01$ , ++  $P < 0.005$ , \*\*\*  $P < 0.0025$ , +++  $P < 0.001$ , \*\*\*\*  $P < 0.0005$ .



SEXES/STRAINS OF NILE TILAPIA		female control (n=18,14,10)			male control (n=39,31,22)			male GIFT (n=23,22,22)		
		April	May	June	April	May	June	April	May	June
female GIFT (n=22,23,23)	Agonistic	0.1 ± 0.1	0.1 ± 0.3	0.2 ± 0.6	0.5 ± 1.4 *	0.9 ± 1.4 ++	0.6 ± 1.6 ++	0.3 ± 0.9	0.3 ± 1.1	0.1 ± 0.5
	Escaping	0.03 ± 0.09	0.1 ± 0.1	0.04 ± 0.13	0.03 ± 0.09	0.1 ± 0.1	0.04 ± 0.13	0.03 ± 0.09	0.1 ± 0.1	0.04 ± 0.13
male GIFT (n=23,22,22)	Agonistic	3.0 ± 3.7 ***	1.6 ± 1.9	0.6 ± 1.0	2.2 ± 3.9 +	2.1 ± 3.0	1.2 ± 2.1 *	0.7 ± 1.6	0.2 ± 0.8	0.1 ± 0.6
	Escaping	0.4 ± 1.0	0.4 ± 1.4	0.2 ± 0.6	0.4 ± 1.0	0.4 ± 1.4	0.2 ± 0.6	0.4 ± 1.0	0.4 ± 1.4	0.2 ± 0.6
male control (n=39,31,22)	Agonistic	0.1 ± 0.1	0.1 ± 0.3	0.2 ± 0.6	0.5 ± 1.4	0.9 ± 1.4 ++	0.6 ± 1.6 ++	-----	-----	-----
	Escaping	0.3 ± 0.9	0.3 ± 1.1	0.1 ± 0.5	0.3 ± 0.9	0.3 ± 1.1	0.1 ± 0.5	-----	-----	-----
male control (n=39,31,22)	Agonistic	3.0 ± 3.7 **	1.6 ± 1.9 ++	0.6 ± 1.0	2.2 ± 3.9	2.1 ± 3.0 ****	1.2 ± 2.1 ++	-----	-----	-----
	Escaping	0.7 ± 1.58	0.2 ± 0.8	0.1 ± 0.6	0.7 ± 1.6	0.2 ± 0.8	0.1 ± 0.6	-----	-----	-----
male control (n=39,31,22)	Agonistic	0.1 ± 0.1	0.1 ± 0.3	0.2 ± 0.6	-----	-----	-----	-----	-----	-----
	Escaping	0.5 ± 1.4	0.9 ± 1.4	0.6 ± 1.6	-----	-----	-----	-----	-----	-----
male control (n=39,31,22)	Agonistic	3.0 ± 3.7	1.6 ± 1.9	0.6 ± 1.0	-----	-----	-----	-----	-----	-----
	Escaping	2.2 ± 3.9	2.1 ± 3.0	1.2 ± 2.1	-----	-----	-----	-----	-----	-----

June between male GIFT and female control); however, only the differences between the male control and female GIFT fish were significant (Table IV). When males of both fish strain were compared, the male control performed more agonistic behaviour than the male GIFT fish (Table IV). The differences were significant in May and June, but not in April. When the females were compared, the control also performed more agonistic behaviour than the GIFT fish, but the differences were not significant (Table IV). The frequency of agonistic behaviour exhibited by male control, and female and male GIFT fish increased in May by 65%, 100% and 4% of the April values, respectively, then declined in June by 27%, 33% and 48%, respectively, while the frequency of agonistic behaviour exhibited by female control increased by 243% during the study. The number of male control fish performing agonistic behaviours was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: April,  $P < 0.01$ ; May,  $P < 0.001$ ; June,  $P < 0.005$ ).

Escape behaviour was performed by both female and male fish (Table IV). Both the male and female control fish performed more escape behaviour than the male and female GIFT fish (Table IV). The differences in escape behaviour between the female control and GIFT fish were only significant in April, while the differences between female control and male GIFT were significant in both April and May (Table IV). In the comparison of the male control to the female and male GIFT, significant differences were found in April and June, and May and June, respectively (Table IV). When female and male control fish were

compared, male fish exhibited less escape behaviour in April than female fish, but in May and June, male fish performed more escape behaviour than female fish. In contrast, male GIFT fish exhibited more escape behaviour in April, but performed less escape behaviour than female GIFT fish in May and June. No significant difference in escape behaviour was found between female and male of either the control or GIFT strain. The frequency of escape behaviour exhibited by the female and male control, and the female and male GIFT fish declined during the study by 82%, 47%, 42%, and 80% of the April values, respectively. The number of male control fish performing escape behaviour was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: April,  $P < 0.025$ ; May,  $P < 0.001$ ; June,  $P < 0.025$ ).

Gulping was mostly performed by the male control fish; however, in May, the female control fish also performed gulping behaviour (Table V). A slight increase in the gulping frequency of male control and GIFT fish was observed in May, but it dropped to zero in June. The number of male control fish gulping was greater than either the number of female control, male GIFT or female GIFT fish; however, the differences were not significant.

A greater number of feeding bouts was performed by the male control and GIFT fish than the female fish; however, in May, the feeding frequency of the female control was higher than male GIFT. The feeding frequency of male control fish also was greater than male GIFT fish; the difference was significant only in May

MONTHS	SEXES/STRAINS OF NILE TILAPIA	NUMBER OF BOUTS OF LOCOMOTORY BEHAVIOURS (MEAN $\pm$ SD)		
		Gulping	Feeding	Nesting
April	female control (n=18)	0	0	0
	male control (n=39)	2.7 $\pm$ 13.4	0.5 $\pm$ 1.9	0
	female GIFT (n=22)	0	0.1 $\pm$ 0.5	0
	male GIFT (n=23)	0	0.3 $\pm$ 1.1	0
May	female control (n=14)	1.3 $\pm$ 4.7	0.2 $\pm$ 0.8	0
	male control (n=31)	2.8 $\pm$ 9.7	0.4 $\pm$ 1.2	0.3 $\pm$ 1.3
	female GIFT (n=23)	0	* 0.1 $\pm$ 0.2	0
	male GIFT (n=22)	0.02 $\pm$ 0.11	0.1 $\pm$ 0.5	0.02 $\pm$ 0.11
June	female control (n=10)	0	0	0
	male control (n=22)	0	0	0.4 $\pm$ 1.7
	female GIFT (n=23)	0	0	0
	male GIFT (n=22)	0	0	0.1 $\pm$ 0.3

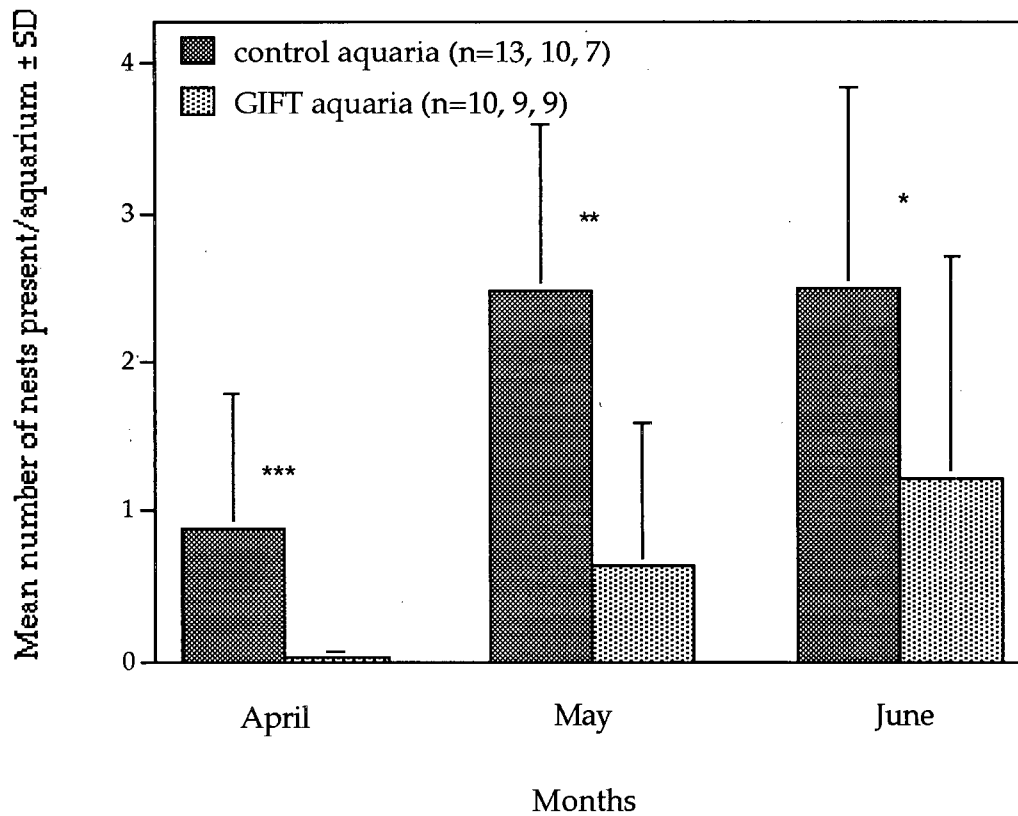
**Table V.** Number of bouts of locomotory behaviours (mean  $\pm$  SD) performed by the female and male juvenile Nile tilapia (control and GIFT strains) each month of the three month study. Each month two 300 second behavioural trials were recorded one day apart. Due to unforeseen circumstances, only data from the behavioural trial #2 in April were tabulated. The number of female and male fish of both strains used each month is represented by the n-values. The Mann-Whitney U-test (two-tailed test, except for nesting behaviour) was employed to test for significant differences between the number of acts performed by the female and male fish from the control and GIFT aquaria for each month.

\*  $P < 0.05$ .

(Table V). In contrast, female GIFT performed more feeding bouts than female control in April, while female control performed more feeding bouts than female GIFT in May. The feeding frequency of male control, and female and male GIFT fish declined in May by 4%, 50%, and 63% of April values, and then dropped to zero in June. The number of male control fish feeding during the behavioural trials was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: May,  $P < 0.01$ ).

To assess the sexual maturity of fish, nesting behaviour, and the number of bowers present in both the control and GIFT aquaria were recorded during the three month study period. Nests were first observed on April 1st in three of the control tanks; and by the eve of the first behavioural trial in April, bowers were present in 11 of the 13 control tanks compared to only 1 GIFT tank out of a total of 10. During the three month study period, nesting behaviour was performed more frequently by the control fish than the GIFT fish, but the differences were not significant (Table II). A large increase (236%) in nesting frequency of control fish, was observed during the study, while the nesting frequency of GIFT fish increased slightly (Table II). Only males of both the GIFT and control strains were observed to perform nesting behaviour. The nesting frequency of male control increased from May to June by 45%, while the frequency of male GIFT increased slightly (Table V). The number of male control fish nesting was greater than either the number of female control, male GIFT or female GIFT fish; however, the differences were not significant. Furthermore, significantly more

**Figure 5.** Number of nests (mean  $\pm$  SD) present in the experimental aquaria (control and GIFT strain of Nile tilapia). All experimental aquaria had four or five fish present and the number of aquaria used during the three month study is represented by the n-values (data from aquaria with less than four fish present were not employed in the mean calculations). The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the number of nests present in the control and GIFT aquaria for each month. \*  $P=0.05$ , \*\*  $P<0.005$ , \*\*\*  $P<0.0005$ .



bowers were present in the control aquaria than GIFT aquaria during the three month study (Figure 5). Control fish also built more bowers earlier in study (i.e., April) than GIFT fish; it took the GIFT fish till June to reach the number of bowers found in the control aquaria in April (Figure 5).

Size-specific mortality was observed in both strains (Table VI). The dead control fish had lower weights and lengths than the live fish present in the same experimental aquaria; the differences were significant in May and June, but not in April (Table VI). The dead GIFT fish also had smaller weight and length measurements than the live fish in the same experimental aquaria; however, no rigorous analyses could be performed due to the low number of dead fish (Table VI). The weight and length of dead and live male control fish were significantly different in both May and June, while the dead and live female fish were similar (Table VII). Therefore, size-specific mortality occurred in only male fish.

STRAINS OF NILE TILAPIA		WEIGHT (g)			LENGTH (cm)		
		April	May	June	April	May	June
control	DEAD	6.5 ± 3.5 (n=6)	7.7 ± 2.9 (n=11) **	10.0 ± 2.4 (n=7) *	5.7 ± 1.2 (n=6)	6.1 ± 0.9 (n=11) ***	6.8 ± 0.6 (n=7) *
	LIVE	7.9 ± 4.1 (n=19)	13.2 ± 5.3 (n=9)	19.2 ± 6.8 (n=5)	6.1 ± 1.0 (n=19)	7.4 ± 1.0 (n=9)	8.5 ± 1.2 (n=5)
GIFT	DEAD	7.0 ± 3.2 (n=4)	-----	-----	6.0 ± 0.9 (n=4)	-----	-----
	LIVE	11.4 (n=1)	-----	-----	7.0 (n=1)	-----	-----

Table VI. Size-specific mortality in the two strains of Nile tilapia (control and GIFT) during the three month study period. The number of control and GIFT fish used in the analyses is represented by the n-values. No GIFT fish died in the month of May or June so the table cells were left with a set of dashes. The Mann-Whitney U-test (one-tailed) was used to test for significant differences in the weight and length of dead and live fish of the control strain. No statistical analyses was performed on the GIFT fish due to the low n-values (i.e., low mortality) observed during the three month study period. \*  $P < 0.025$ , \*\*  $P = 0.005$ , \*\*\*  $P < 0.005$ .



CONTROL STRAIN NILE TILAPIA		female dead (n=4,3)		male dead (n=7,4)	
		May	June	May	June
female live (n=2,1)	Weight (g)	9.2	8.9	-----	-----
		8.9	9.6	-----	-----
	Length (cm)	6.6	6.5	-----	-----
		6.6	6.7	-----	-----
male live (n=7,4)	Weight (g)	-----	-----	6.8 ***	10.8 *
		-----	-----	14.4	21.6
	Length (cm)	-----	-----	5.9 **	7.1 *
		-----	-----	7.6	9.0

**Table VII.** Size-specific mortality in the male and female fish of the control strain Nile tilapia. Due to unforeseen circumstances, only data from May and June were tabulated. The results of GIFT fish were not tabulated due to zero mortality observed during May and June. The number of dead and live fish of both sexes used each month is represented by the n-values (e.g., # of fish in May, and June, respectively). In each table cell, the top values represent sex/state (dead or live) of Nile tilapia of the column heading, while the bottom values represent the sex/state of Nile tilapia of the row. The Mann-Whitney U-test (one-tailed) was used to test for significant differences in weight and length of dead and live fish of both sexes. \*  $P < 0.025$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.005$ .

## CHAPTER IV

### Experiment II: Aggressive behaviour of males from the control and GIFT strains of Nile tilapia in response to a mirror image

#### Introduction

In juvenile coho and chinook salmon, the reactions to mirror images have been correlated with the reactions to conspecifics (Rosenau, 1984; Taylor and Larkin, 1986; Rosenau and McPhail, 1987; Taylor, 1988; Swain and Holtby, 1989). Fish that spend more time performing mirror-elicited agonistic behaviours were also found to be more aggressive in social interactions under more natural circumstances. In my first experiment, male control fish were observed to perform more agonistic behaviours than male GIFT fish (see Chapter III). However, the effect that social interactions in mixed sexed groups have on behavioural measures (see Toguyéni *et al.*, 1997) may have complicated the results of my first experimental study. Therefore, offensive aggression was quantified using the mirror image stimulation (MIS) tests (Gallup, 1968). These tests have the advantage that individuals are tested against 'opponents' of exactly the same size and motivational state and that adequate replication is practical (Swain and Riddell, 1990). Male fish were only examined in this MIS test because female fish were observed to perform relatively little agonistic behaviour in mixed sexed groups (Experiment I), and in all-female stock aquaria (pers. obs.).

## Materials and Methods

Biting and tail-beating behaviours were distinguished in the MIS tests. These two behaviours are similar to the nipping and tail-beating behaviours previously mentioned (see Behavioural Measures), except that they are directed towards a mirror instead of a conspecific.

Small populations (5 fish per tank) of mixed sex GIFT and control strains were re-established in individual 55 L aquaria in mid-November (Nov. 15th). These fish had been previously used in the growth experiment approximately four and a half months earlier. On day 1 (Nov. 19th), the weight and standard length measurements of all male fish were recorded; during the two week study period, the mean weight and standard length of the male control and GIFT fish were  $26.2 \pm 9.8$  g and  $9.5 \pm 1.3$  cm, and  $34.0 \pm 10.6$  g and  $10.2 \pm 1.2$  cm, respectively. On day 3, one day prior to the start of behavioural observations, male control and GIFT fish were individually placed in 55 L aquaria; the mean water temperature of the experimental aquaria was  $23.7 \pm 0.3^\circ\text{C}$  during the two week study period. Each experimental aquarium was divided in two by an opaque partition; the fish was placed on the left side with a boxed filter, while the mirror was positioned on the right side behind the partition.

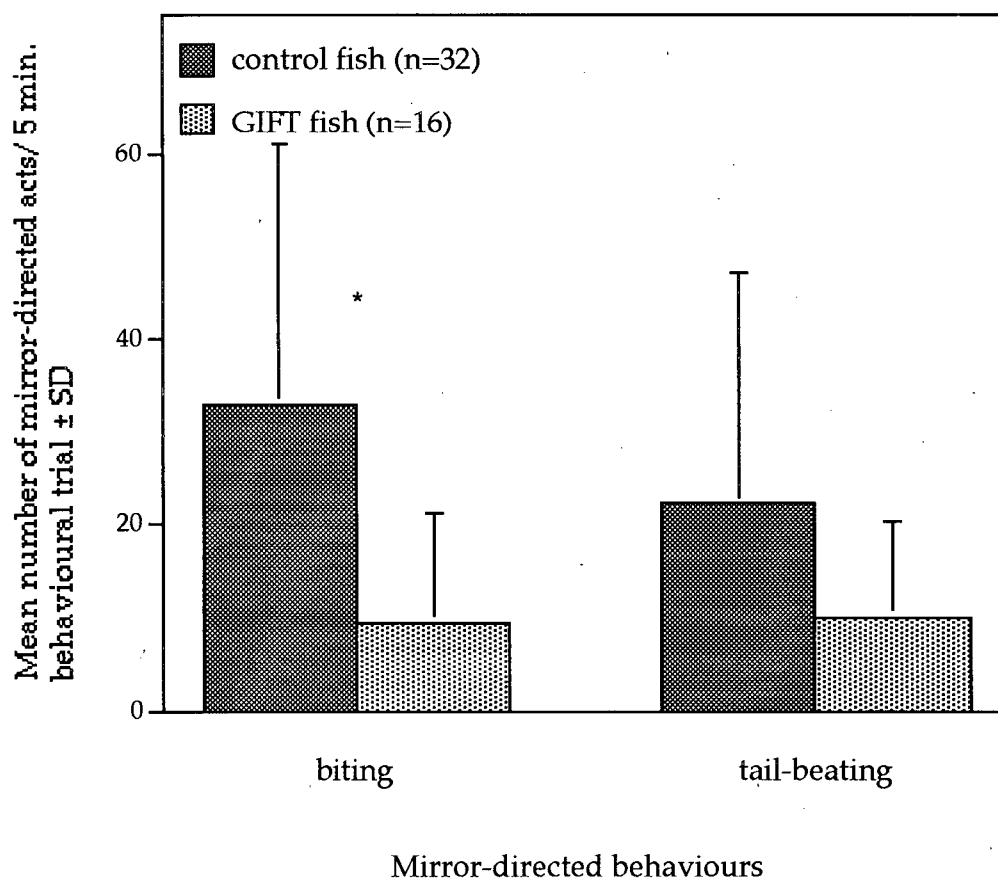
On day 4, at the start of each behavioural session, the partition was lifted exposing the mirror to the fish. A 300 second observation period began when the male fish was observed, on the video monitor, swimming towards the mirror and performing either biting or tail-beating behaviours. At the end of the day

when all behavioural sessions were recorded, the fish were returned to their appropriate stock tanks and new fish were transferred to the experimental aquaria for the next day. Each male was tested twice about a week apart between the two trials, so the data provided is a mean of the two trials.

## Results

During the two week study period, the male control fish performed a higher number of bouts of mirror-directed biting and tail-beating than the male GIFT fish (Figure 6). Only the differences in mirror-directed biting was significant (Figure 6).

**Figure 6.** Number of mirror-directed biting and tail-beating (mean  $\pm$  SD) performed by the male fish from two strains of Nile tilapia (control and GIFT) during the two behavioural trials. Each behavioural trial was five minutes in duration and the two trials were spread out over a one week period. The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the number of mirror-directed acts performed by the male control and GIFT fish during the behavioural trials. \*  $P < 0.001$ .



## CHAPTER V

### Experiment III: Nest building in male fish of the control and GIFT strains of Nile tilapia

#### Introduction

The time(s) of day nests are built, the total time required to build nests and size of completed nests have rarely been studied in fish. Fryer and Iles (1972), and Balarin and Hatton (1979) have described the nest shapes and sizes of some tilapia species; however, the details of fish nesting activity were not documented. In this third experiment, the nesting behaviour of the two strains of Nile tilapia was closely examined. More specifically, the total time required for males to complete a nest, the size of the nest at completion, and the number of nests built per fish were recorded. The time of day nests are built was also noted in both strains of Nile tilapia to see if nesting behaviour is a diurnal and/or nocturnal activity.

#### Materials and Methods

Eleven days before observations began, the weight and standard length were recorded; the mean weight and standard length of the male control and GIFT fish were  $31.6 \pm 12.5$  g and  $10.0 \pm 1.5$  cm, and  $46.1 \pm 12.1$  g and  $11.2 \pm 1.0$  cm, respectively.

At the start of each recording session, a male control and a GIFT fish were individually placed in one of two 55 L aquaria with a mean water temperature of  $25.5 \pm 1.1^{\circ}\text{C}$ . Each experimental aquaria was divided in two by a clear partition; the fish was placed on the left side of the partition, while the boxed filter was on the right side. This partition was used to limit the amount of space occupied by each fish, so two fish in separate aquaria could be monitored simultaneously by one videocamera. Also, the clear partition allowed for sufficient light to enter the test area of aquarium and no shadows to be present.

In my preliminary experiment, nesting activity occurred during both the day and night, so round-the-clock recordings were undertaken in this study. However, it was not possible to view fish under complete darkness. Complete darkness was replaced by low light sufficient to allow videorecordings. One light strip, positioned upwards and mounted 2 m above the row of experiment aquaria, was used to illuminate the laboratory. This dim light level was sufficiently dark to signal to the fish that it was night time (i.e., the fish positioned themselves lower in the water column), and thus still maintained fish under a 12-h photoperiod.

A Sanyo monochrome videocamera was positioned approximately 42 cm on top of the rim of the two experimental aquaria and was connected to a VCR with a 24-h recording potential. Nesting behaviour was recorded from 17:30 to 17:00 on the next day. In some cases, the behavioural sessions were extended to a 48 hour period when no nests were present at 17:00. The videorecordings of nesting activity was then examined (see Behavioural Measures) to determine the time of

day nests are built, the total time required to build nests and the size of nests at completion.

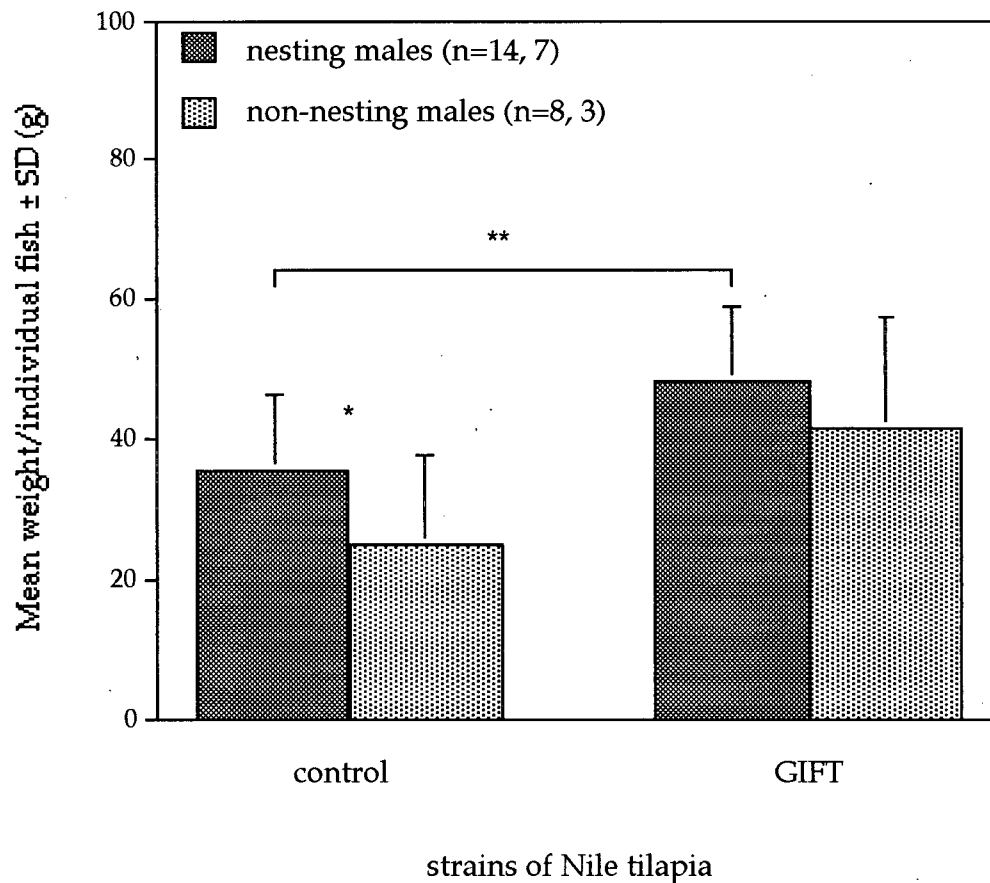
The start point of nest building behaviour was demarcated by the fish performing nesting behaviour and a black spot gradually being seen on the videomonitor (i.e., indicating that the fish had removed enough sand, exposing the glass bottom of the aquarium), while the nest was considered complete when the size of the nest did not increase during the rest of the recording session. The size of nest was determined by attaching a grid (each square is approximately 1 cm x 1 cm) to the screen of a Panasonic videomonitor and recording the number of squares comprising the nest. The conversion factor of 5.2 cm on screen of the videomonitor equals to 7 cm on the aquarium was used to determine the 'actual' area of nest present in each experimental aquaria (i.e., 'actual' nest size = 1.81 x screen nest size). To control for fish size (i.e., male GIFT larger than control fish), the ratio of nest diameter relative to fish length was calculated. The nest diameter was calculated using the following formulas:  $\text{area} = \pi \times r^2$ , where  $\pi = 3.14$  and 'r' is the radius, and  $\text{diameter} = r \times 2$ .

## Results

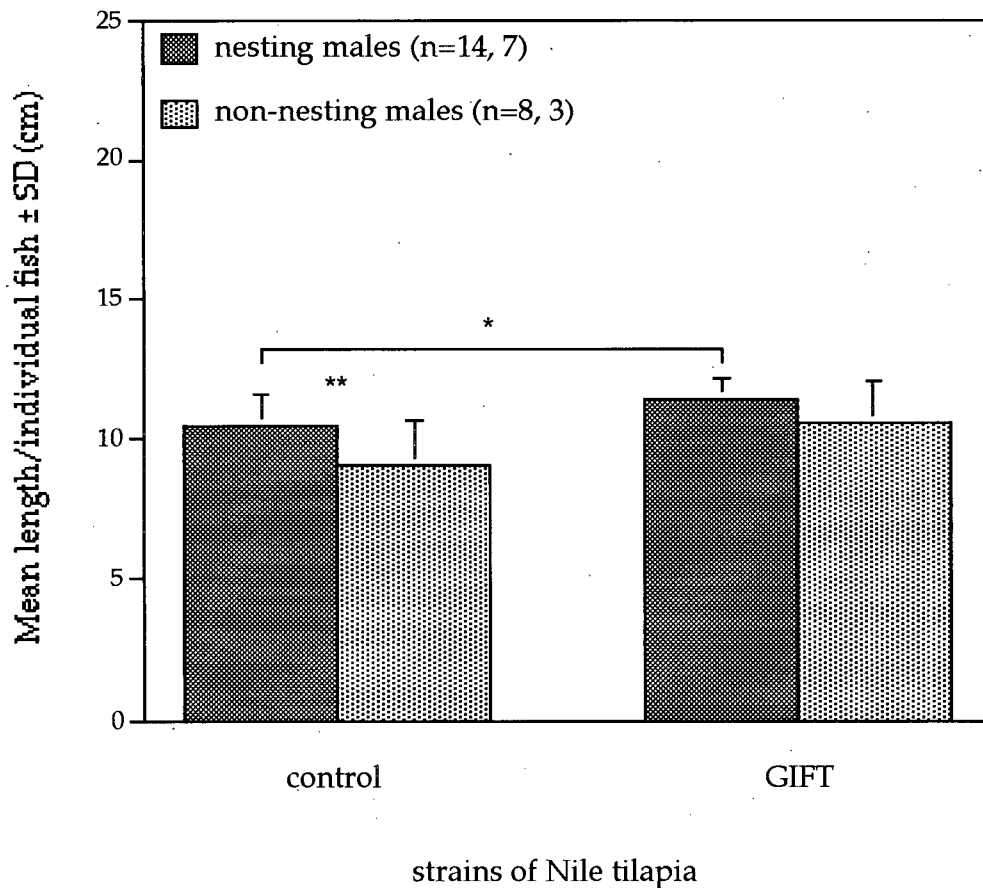
The weights and lengths of the nesting fish were higher than those of the non-nesting fish of the same strain (differences significant only in fish from the control strain) (Figure 7 and 8). Furthermore, the weights and lengths of the nesting GIFT fish were significantly greater than the nesting control fish (Figure 7 and 8). This result was not surprising because GIFT fish were bigger than



**Figure 7.** Weight (mean  $\pm$  SD) of the nesting and non-nesting male fish from two strains of Nile tilapia (control and GIFT). The number of nesting and non-nesting control and GIFT fish used during the study is represented by the n-values (i.e., # of control fish, # of GIFT fish). The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the weight of the nesting and non-nesting male fish of the same strain (control fish: \*  $P < 0.05$ ), and the nesting or non-nesting male fish of different strains (nesting males: \*\*  $P < 0.025$ ).



**Figure 8.** Length (mean  $\pm$  SD) of the nesting and non-nesting male fish from two strains of Nile tilapia (control and GIFT). The number of nesting and non-nesting control and GIFT fish used during the study is represented by the n-values (i.e., # of control fish, # of GIFT fish). The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the length of the nesting and non-nesting male fish of the same strain (control fish: \*  $P=0.025$ ), and the nesting or non-nesting male fish of different strains (nesting males: \*\*  $P<0.05$ ).



control fish at the start of the study. The measurements of the non-nesting GIFT fish were not significantly greater than the non-nesting control fish (Figure 7 and 8).

There were no significant differences in the nesting behaviour of the control and GIFT strains; however, there were a number of suggestive differences in various measures of nesting activity. The male GIFT fish required more time to complete nest(s) compared to the control male (Table VIII). The total nest size (i.e., the addition of all nest sizes present in the experimental aquarium) and the mean nest size (i.e., the total nest size/the number of nests present in the experimental aquarium) were also higher in male GIFT than control fish (Table VIII). However, the mean ratio of nest diameter relative to fish length for both male control and GIFT fish was similar (Table VIII). Furthermore, the number of nests built by the male control fish was greater than the GIFT fish (Table VIII). Lastly, it was noted that the control and GIFT fish nested during both the low light and day portions of the recording period; however, the fish often started and completed its nest(s) during the day time.

NESTING CHARACTERISTICS	STRAINS OF NILE TILAPIA	
	control (n=14)	GIFT (n=7)
Total time (hour) required to complete nest	8.1 ± 6.3	11.2 ± 7.6
Total nest area (cm <sup>2</sup> )	74.3 ± 54.1	92.9 ± 60.0
Mean nest area (cm <sup>2</sup> )	56.9 ± 58.3	74.2 ± 65.4
Ratio of nest diameter relative to fish length	0.8 ± 0.3	0.8 ± 0.4
Number of nest(s) built/fish	1.6 ± 0.7	1.4 ± 0.5

**Table VIII.** Total time required to build a nest, the size of the nest at completion, nest diameter relative to fish length, and the number of nests built per fish (mean ± SD) were examined in the male fish of two strains of Nile tilapia (control and GIFT). The number of male control and GIFT fish used during the study is represented by the n-values. Each fish was videorecorded from 17:30 to 17:00 on the next day. In some cases, the recording sessions were extended to a 48 hour period when no nests were present at 17:00. The total nest area was calculated by the addition of all nest sizes present in the experimental aquarium, while the mean nest area was calculated by the division of the total nest area value by the number of nests present in the experimental aquarium. The nest diameter was calculated using the following formulas: area =  $\pi \times r^2$ , where  $\pi = 3.14$  and 'r' is the radius, and diameter =  $r \times 2$ . The Mann-Whitney U-test (two-tailed) was employed to test for significant differences in various measures of nesting activity of the control and GIFT fish; no significant differences were found.

## CHAPTER VI

### Discussion

Under laboratory conditions, the GIFT fish grew faster than the fish from the control strain. It was not surprising that growth performance was higher in the GIFT than control fish, as the former had been subjected to intentional selection for that trait (Pullin, 1998, and see p. 7). The results from my behavioural experiment on Nile tilapia suggest that behavioural activity may contribute to this effect on growth. In the following paragraphs, behavioural effects on growth, possible hormonal causes in relation to sex, and other confirmatory findings as well as nest building will be discussed.

The fast growth of GIFT fish was associated with a lower activity level compared to control fish. GIFT fish performed less swimming and more resting behaviour than control fish. These findings are similar to the study by Koebele (1985) on juvenile *Tilapia zillii*, which suggested that an increase in activity such as swimming may have resulted in a slight decrease in their mean growth. The fast-growing GIFT fish also exhibited a lower frequency of agonistic behaviour than the slow-growing control fish. This connection between growth and aggression has been previously documented. Ruzzante and Doyle (1991) observed in the medaka, *Oryzias latipes*, that fish 'indifferent' to other neighbouring fish (i.e., not involved in aggressive behaviour) grew the fastest. In addition, a negative correlation between aggression and growth was found in

the tilapia hybrid, *Oreochromis mossambicus* x *O. hornorum* (Robinson and Doyle, 1990) and Atlantic salmon (Holm and Fernö, 1986). Swimming activity, and especially agonistic interactions are energetically costly, and thus passive (i.e., GIFT) fish, with a relatively lower metabolic expenditure, should gain a growth advantage over active (i.e., control) fish. Increased demand for energy during exercise has been confirmed in several studies on oxygen consumption, which reflect behavioural activities in fish (Beamish, 1980; Nahhas *et al.*, 1982; Butler, 1985).

The fact that the more active control fish are compromised in their growth performance suggest that the amount of energy generated in the control fish is limited. The limitation of energy output can be attributed to many factors. A hypothesis to explain various features of fish growth in terms of growth limitation by oxygen supply was proposed by Pauly (1981; see also Pauly, 1984, 1994). He proposed that in addition to food, oxygen plays an important role in limiting fish growth as they derive the energy for the synthesis of body substances exclusively from the oxidation of energy-rich assimilates (Pauly, 1981). It has been observed by Stewart *et al.* (1967) that largemouth bass held in hypoxic waters usually had a lower percent dry weight than fish held at concentrations near the air-saturation level. Balarin and Hatton (1979) also found, in tilapia, that at low oxygen levels, growth decreased. This decrease in growth is due chiefly to the inability of fish to store but small quantities of oxygen for later use (Pauly, 1981); most fish die within a short period of time when kept in anoxic water. Thus, anything, in a given population, that causes a higher metabolic

expenditure (e.g., high activity level), will result in a reduced fish size. It is thought that the high activity level of the control fish, which limited amount of oxygen allocated to growth, may have resulted in their reduced size.

Gulping was mostly performed by the active, slow-growing control fish. It has been observed that aquatic surface respiration (i.e., gulping) is initiated at higher oxygen concentrations than absolutely necessary for survival, and thus this behaviour can provide an energetic advantage to fish (Weber and Kramer, 1983). The fish approaching the water surface and aerating their gills with more oxygen-saturated water increase oxygen uptake rate and/or decrease the work required for ventilation, as compared to subsurface respiration (Weber and Kramer, 1983). An increase in the oxygen uptake rate of fish would permit greater food intake (Weber and Kramer, 1983). The control fish was also observed to perform more feeding behaviour than the GIFT fish. Intraspecific comparisons between wild and hatchery-reared Atlantic salmon have shown that wild fish generally feed more than hatchery fish (Fenderson *et al.*, 1968; Sosiak *et al.*, 1979).

A possible explanation for the higher gulping of control fish in April and May could be due to the higher oxygen requirement due to high activity and feeding frequency compared to GIFT strain. However, in June, no gulping was performed by the control fish during the behavioural recordings, which may be the result of a decline in locomotory and agonistic activity of control fish. Furthermore, it has been noted that as fish increase in size, more energy is

needed to maintain bodily functions (i.e., higher standard metabolic rate) (Wootton, 1990). It is thought that as the active control fish became larger in size, less energy was available for performing behavioural activity because it was being re-directed into standard metabolism and growth. Thus, this change in the allocation of energy resulted in the observed decline in the activity level of control fish. However, in the case of the passive GIFT fish, as they increased in size, sufficient amount of energy was still available for the higher standard metabolic rate, so the low activity level of GIFT fish remained relatively unchanged.

The divergence in locomotory and agonistic behaviour of the GIFT and control fish is not surprising, because behavioural traits are among the first traits to respond to domestication; it is usually the frequency or intensity with which a particular behaviour is expressed that is affected by domestication (Price, 1984). In the Philippines, both fish strains tested were reared under similar hatchery conditions (e.g., pH, salinity, temperature). Thus, the difference in activity level between GIFT and control fish must have been due to a genetic difference between the two types or to prefertilization environmental differences (environmental maternal effects) rather than a phenotypic/environmental effect (Swain and Riddell, 1990). A genetic basis has been demonstrated for behavioural differences among families (Bakker, 1986), populations (Rosenau and McPhail, 1987), and closely-related species of fish (Ferguson and Noakes, 1982, 1983), but no scientific studies have indicated an effect of the prefertilization, maternal environment on behaviour (Swain and Riddell, 1990).



Thus, it is likely that the behavioural differences reported between GIFT and control fish are the result of the selection program described by Pullin (1998).

In the comparison of female and male GIFT fish, the growth performance of males was higher than females. The growth advantage experienced by male GIFT fish was connected with a lower activity level. Male GIFT performed less swimming and escaping, and more resting behaviour than female GIFT. Even though a higher frequency of agonistic behaviour (excluding escape behaviour) was exhibited by the fast-growing male GIFT fish, the difference in male and female frequencies was not significant, and the number of bouts of agonistic behaviour performed by the male GIFT fish was up to 4.5 times less than male control values. The mirror image stimulation tests supported the finding that male control fish are more aggressive than male GIFT fish. When female and male fish of the GIFT and control strains were compared, the connection between growth and activity level was still observed, suggesting that differences in growth between sexes may be to some extent mediated by behavioural differences. However, in the control fish, the growth rates, and size of male and female fish were similar even though the male control fish performed more swimming and escaping behaviour, and less resting than the female control fish. The male controls also exhibited a higher frequency of agonistic activity than the female controls.

In the comparison of female and male fish, low growth of fish was also associated with a high activity level; however, a few experimental observations

seemed to deviate from this relationship. For example, the fast-growing male GIFT exhibited a higher frequency of agonistic activity (excluding escape behaviour) compared to slow-growing female GIFT, and in the control fish, growth of male and female fish was relatively similar even though, the male control fish performed more locomotory and agonistic acts than the female control fish. Physiological differences between sexes, such as due to different hormone levels, may be the underlying cause of this observed deviation from the relationship between growth and behavioural activity.

Higher growth in males has been attributed to androgens or male sex hormones (Donaldson *et al.*, 1979; Ufodike and Madu, 1986). The anabolism-enhancing effect of androgens has been observed in Nile tilapia (Ufodike and Madu, 1986), goldfish (Yamazaki, 1976), and all salmonids (see Donaldson *et al.*, 1979). Varadaraj and Pandian (1988) suggested, in 'normal' (phenotypic and genetic), and phenotypic males *Oreochromis mossambicus*, that androgens stimulated growth by increasing food intake or food conversion efficiency.

Thyroid hormones ( $T_3$  and  $T_4$ ) are also involved in controlling growth and development of fish (see Donaldson *et al.*, 1979). Toguyéni *et al.* (1996, 1997) observed, in the Nile tilapia, that plasma  $T_3$  levels were higher in males than females, and thus could account for the males' growth advantage over females. It was suggested that  $T_3$  increases the efficiency of food utilisation by males, and thus their growth as well (Toguyéni *et al.*, 1997). Eales and Shostak (1985) also observed, in a population of Arctic charr, that plasma  $T_3$  levels are strongly

correlated with both food ration and growth, which supports the notion that increased  $T_3$  production induced by food intake may exert some role in promoting growth.

In this study, male GIFT fish, even with a higher agonistic activity than female GIFT, could still have a growth advantage because of both the growth-promoting effects of androgens and thyroid hormones, and their relative low level of locomotory activity. In the case of the male controls, the growth-promoting effects of androgens and thyroid hormones could balance out the inhibitory effects of high levels of locomotory and agonistic activity on growth. Therefore, the male controls would be able to maintain growth rates similar to female control fish, even though males expend more energy in behavioural activity than females. To test this hypothesis, further experimentation is necessary to examine the relationship between growth, behavioural activity, and hormone levels in male and female fish.

Nesting behaviour, which is often the first indication of the sexual maturity of fish, was observed only in males. Billy (1982) observed, in *Oreochromis mossambicus*, a species closely related to Nile tilapia, that both female and male fish performed nesting behaviour, but female fish only performed nesting behaviour immediately prior to spawning. Male controls performed more nesting behaviour than male GIFT fish. A significantly higher number of nests also was present in the control than GIFT aquaria. Aggression, as observed mostly in the male control fish, appears to be the prevalent mechanism of

establishing and maintaining nesting sites (Fenderson *et al.*, 1968; Mabaye, 1971; Koebele, 1985), and thus attracting mates (Oliveira *et al.*, 1996). The control fish also built more nests earlier in the study (i.e., April) than the GIFT fish; it took the GIFT fish till June to reach the level of nesting activity observed in the control aquaria in April. These findings indicate, at least in males, that the slow-growing control fish became sexually mature sooner, and at a smaller size than the fast-growing GIFT fish. Siddiqui *et al.* (1997) also observed that in male and female hybrid tilapia, *Oreochromis niloticus* x *O. aureus*, fast-growing fish matured at larger sizes, whereas slow-growing fish matured at smaller sizes.

In contrast, Alm (1959) summarized, in his review of the connection between maturity, size, and age in fish, that larger specimens within a certain age group would mature sooner than smaller specimens. He suggested that this circumstance could be considered the 'rule', since a connection of this kind was found to exist for all species of fish that had been examined (e.g., salmonids, coregonids, perch) (Alm, 1959). However, most of the data about which generalisations were made came from temperate fish species. Therefore, the connection between growth and sexual maturation needs to be further examined in tropical fish species to ascertain if it is similar or different to that of temperate fish species. From the results of my study, the relationship between growth and sexual maturation seems to differ in tropical and temperate fish species; this difference may be associated with their different environmental conditions.

Size-related mortality was found in both strains of Nile tilapia: dead fish were smaller than the survivors (i.e., live fish). On examination of the bodies of the dead fish, many fish had frayed fins (i.e., pectoral, tail). Christiansen and Jobling (1990), Christiansen *et al.* (1991), and Siikavuopio *et al.* (1996) used the incidence of caudal fin damage as an indirect indication of aggressive interactions. If this interpretation is correct, most fish seem to have died from an aggressive encounter with a tank mate or the consequence of the aggression rather than from natural causes. It was suggested that high mortality in small fish may result from starvation as a consequence of the aggression of a few large individuals (Saclauso, 1985). This behaviour could have elicited inhibitory effects (e.g., small fish become less mobile) which denied the smaller conspecifics access to the food even if it was given in excess (Saclauso, 1985).

In the control strain, it was observed that only male control fish experienced size-related mortality. The male control fish could have experienced size-related mortality because they performed more agonistic behaviour than females, and the subordinate males, as suggested by Saclauso (1985), were probably unable to evade damaging and potentially lethal attacks of the dominant fish in closely confined aquaria.

Furthermore, control fish suffered a higher mortality than GIFT fish. The higher mortality of control fish could be correlated with their higher bouts of agonistic behaviour compared to GIFT fish; high mortality rates have been attributed to increase aggressiveness of fish (Saclauso, 1985). Siikavuopio *et al.* (1996)

observed a high mortality and incidence of caudal fin damage amongst wild-caught Arctic charr, while amongst hatchery-reared fish, mortalities were low and little evidence of fin damage was found. In contrast, Vincent (1960), and Flick and Webster (1964) observed a higher mortality rate in the larger and faster growing individuals of the domestic strains of brook trout. This higher mortality rate observed in fast-growing domestic brook trout could be due to them performing more agonistic behaviour, but aggression was not examined. Einum and Fleming (1997) found the farmed Atlantic salmon, with a higher growth rate, tend to be more aggressive. Aggressive behaviour, in the form of nipping, also was reported to be more frequent among fast-growing domesticated brook trout (Moyle, 1969). In all, these results add further support to the conclusion that the slow-growing control fish were more aggressive than the fast-growing GIFT fish during the three month study period.

The weight and length of nesting male fish were higher than non-nesting male fish of the same strain. This finding agrees with the results of previous studies on the sand goby, *Pomatoschistus minutus* (Magnhagen and Kvarnemo, 1989; Kvarnemo, 1995), and the cichlid fish, *Oreochromis mossambicus* (Oliveira *et al.*, 1996) which showed that territorial fish were larger in size than non-territorial fish. It has been suggested that larger males are more successful in defending territories (Downhower and Brown, 1980; DeMartini, 1987; Goto, 1987; Hastings, 1988; Côte and Hunte, 1989, Magnhagen and Kvarnemo, 1989; Oliveira *et al.*, 1996), building nests, and obtaining mates (Magnhagen and Kvarnemo, 1989). In my study, even though small males were isolated in the experimental aquaria

with no male-male interactions, they still had a lower nest building rate than the larger males. Thus, it seems that small fish may not have the physical ability or be at the motivational state to build nests (see Pauly, 1994).

The fast-growing male GIFT fish required more time to complete their nest(s), and built fewer nests than the slow-growing male control fish. Even though the nest diameter to fish length ratios of control and GIFT fish were similar, the total and mean nest areas were higher in the larger male GIFT than control fish. This connection between large males and larger-sized nests has also been observed in the blenny, *Istiblennius enosimae* (Sunobe *et al.*, 1995). However, in mouthbrooding cichlids, size does not appear to be a major consideration in mate choice (McKaye, 1983, 1984). Only nest size is known to be an important correlate of male reproductive success and social status in other lek-breeding cichlids (McKaye *et al.*, 1990; McKaye, 1991). It was observed that a large nest size is preferred by females (Bisazza *et al.*, 1989; McKaye *et al.*, 1990; Sunobe *et al.*, 1995), thus males who build large nest(s) should experience a higher mating success. It was noted that males with larger nests expended more time and energy in defending the nest from other breeding males. They also spent more time and energy defending the nest territory against nonbreeding coloured conspecifics, including 'sneakers' (McKaye, 1983). It was suggested that male's nest size may signal to the female his ability to defend the nest from egg eaters, which are specialized in stealing eggs before the female can put them into her mouth (McKaye, 1984). Thus, nest size probably plays a role in inducing the female to lay eggs with a given male (McKaye *et al.*, 1990). In all, more research

on mouthbrooding cichlids is needed to confirm the importance of body and/or nest size in the breeding success of males.

Nesting activity was recorded during both low light and day portions of the observation period; however, the fish often started and completed its nest(s) during the day. To my knowledge, this is the first study that examined the time of day nesting is performed in fish. More work is needed to discover why the nest is mostly started and completed during the day. Brett (1979) suggested that light stimulates the brain-pituitary responses which radiate through the endocrine and sympathetic systems; this induces the production of growth hormone (GH) and anabolic steroids, and can influence locomotory activity in association with thyroid stimulation. Therefore, light may play a role in regulating nesting activity of fish.



### Concluding Remarks

The rearing of cultured fish has become an increasingly important industry. Fish culturists seek fish strains that possess high growth rates and reach harvestable size before attaining sexual maturation. Sexual maturation of fish can complicate production operations and/or affect product quality. This is especially important for the tilapia which, when they mature precociously, can overpopulate waters with small, stunted fish. Aggressiveness in the form of attacking and fin-nipping, also associated with breeding behaviour, is an undesirable habit for farmed fish (Balarin and Hatton, 1979) and one for important consideration when choosing a tilapiine strain for culture practices. It has been argued that in competitive environments, artificial selection for fast growth may lead to higher levels of overall aggression, and therefore would result in no net gain in assimilation efficiency or growth in the populations (Kinghorn, 1983). By considering the 'energy budgets' of fish under domestication, such as Nile tilapia, the information could be used in selective breeding of this and other fish species. For example, the fast-growing, passive GIFT fish with a delayed maturation would be ideal in fish rearing programs, while the slow-growing, aggressive control fish with a precocious maturation would not be selected. The results of behavioural studies are likely to be of more direct utility to breeders than most physiological and biochemical measures such as food conversion efficiency, and protein, lipid and water contents of body tissues.

The main focus of many breeders is on genetic improvement of farmed fish. If indeed quiet, 'low energy' behaviour reflects an underlying genetic variation and thus amenable to selection (as the GIFT fish seem to demonstrate), then it could be incorporated into or even become a primary basis of fish breeding programs. 'Low energy' behaviour could also be correlated with other desirable traits (e.g., high survival, disease resistance); domestication of some livestock has involved a similar selection strategy.

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**Appendix I.** Total time (sec) and number (#) of bouts of locomotory and agonistic behaviours individual fish from the control (CT) and GIFT strains of Nile tilapia performed each month of the three month study (April-June). Each month, two 300 second behavioural trials were recorded one day apart. All experimental aquaria had four or five fish present (data from the aquaria with less than four fish present were not used). Due to my inability to identify individual fish by bead colour in the videorecordings of the first trial in April, the weight, length, and sex of fish (F, female or M, male) could not be recorded in Table I. However, these findings were included in all other tables. The eleven different activities examined were: swimming (SW), resting (RE), chasing (CH), escaping (ES), tail-beating (TB), nipping (NI), confronting (CO), jaw-locking (JL), gulping (GU), feeding (FE), and nesting (NE). The table cell was left blank if fish did not perform behaviour. ?, sex of fish not determined; -----, data not used in analyses.

Appendix I. Table I. Behavioural activity of GIFT and control fish in April (trial #1).

fish strain/ tank number	behaviours										
	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/2		300.0									
GIFT/2		300.0									
GIFT/2		300.0									
GIFT/2		300.0									
GIFT/2		300.0									
GIFT/4	5.6	294.4									
GIFT/4	6.2	293.8									
GIFT/4	5.4	294.6									
GIFT/4	15.2	284.9									
GIFT/4	2.2	297.8									
GIFT/6		300.0									
GIFT/6	1.6	298.4									
GIFT/6	0.3	299.7									
GIFT/6		300.0									
GIFT/6		300.0									
GIFT/8		300.0									
GIFT/8		300.0									
GIFT/8		300.0									
GIFT/8		300.0									
GIFT/8		300.0									
GIFT/10	3.6	296.4									
GIFT/10	6.5	293.5									
GIFT/10	4.7	295.3									
GIFT/10	8.3	291.7									
GIFT/10	3.3	296.7									
GIFT/14	5.4	294.6									
GIFT/14	9.8	290.2									
GIFT/14	12.0	288.0									
GIFT/14		300.0									

Appendix I. Table I. continued.

fish strain/ tank number	behaviours										
	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/14	15.9	284.1									
GIFT/16		300.0									
GIFT/16		300.0									
GIFT/16		300.0									
GIFT/16		300.0									
GIFT/18	1.8	298.2									
GIFT/18		300.0									
GIFT/18		300.0									
GIFT/18		300.0									
GIFT/18		300.0									
GIFT/24	5.0	294.0	1								
GIFT/24	10.7	289.3									
GIFT/24	4.4	295.6									
GIFT/24	18.1	281.9									
GIFT/24	8.8	291.2									
GIFT/26	13.9	286.1									
GIFT/26	45.8	254.2									
GIFT/26	32.3	267.8									
GIFT/26	40.5	259.5									
GIFT/26	21.8	278.3									
CT/1	233.8	49.9	3	1	5	2	4	1			
CT/1	228.2	63.8	1	2			1				
CT/1	213.4	68.8		4	2		2				
CT/1	236.1	52.3	7		4	3	1				
CT/1	214.0	82.8					2		2	3	
CT/3		300.0									
CT/3		300.0									
CT/3		300.0									

Appendix I. Table I. continued.

fish strain/ tank number	behaviours										
	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/3		300.0									
CT/3	1.1	298.9									
CT/7		300.0									
CT/7		300.0									
CT/7		300.0									
CT/7	3.8	296.2									
CT/7		300.0									
CT/9		300.0									
CT/9		300.0									
CT/9	9.6	290.4									
CT/9	26.7	273.3									
CT/11		300.0									
CT/11		300.0									
CT/11	16.4	283.7									
CT/11		300.0									
CT/13	153.8	146.2									
CT/13	32.6	264.8		2							
CT/13	65.8	234.2									
CT/13	80.5	219.5									
CT/13	21.4	278.6									
CT/15	102.3	182.6	8		7	4					
CT/15	75.1	224.3		1							
CT/15	79.4	218.0		1	6						
CT/15	54.4	245.6									
CT/15	38.5	249.2		7							
CT/17	75.7	11.6	13		4						11
CT/17	256.5	20.7		3					7		
CT/17	238.3	51.8		4							



Appendix I. Table I. continued.

fish strain/ tank number	behaviours										
	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/17	151.1	136.0		2	3						
CT/17	253.5	32.9		6	4	1					
CT/19	224.1	75.9									
CT/19	234.8	63.5		1							
CT/19	254.9	38.9		5			1				
CT/19	203.1	94.9		1	5				12		
CT/19	230.3	54.8	4	4	4	3					
CT/21	100.5	190.7	6		5						
CT/21	41.4	257.0		1		1					
CT/21	39.4	257.4		2							
CT/21	68.8	231.2									
CT/21	68.9	225.7		3							
CT/25	29.5	270.5									
CT/25	3.4	296.6									
CT/25	9.4	290.6									
CT/25	2.7	297.3									
CT/25	6.6	293.4									
CT/27	1.8	298.2									
CT/27	7.8	292.2									
CT/27		300.0									
CT/27		300.0									
CT/29	68.4	228.2		1							
CT/29	80.3	102.4	18		19	2					3
CT/29	29.3	207.3		14							
CT/29	48.4	239.0		3			2				

Appendix I. Table II. Behavioural activity of GIFT and control fish in April (trial #2).

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/2/yellow	M	12.1	7.3	9.0	291.0									
GIFT/2/white	F	10.3	6.9	7.3	292.7									
GIFT/2/blue	M	12.5	7.3	17.4	282.6									
GIFT/2/green	M	8.8	6.5	12.1	287.9									
GIFT/2/pink	M	6.7	5.7	13.3	286.7									
GIFT/4/yellow	M	8.3	6.5	5.0	295.0									
GIFT/4/white	F	8.4	6.3	13.9	286.1									
GIFT/4/blue	M	12.7	7.3	38.2	261.8									
GIFT/4/green	F	10.1	6.7	7.0	293.0									
GIFT/4/pink	F	4.3	5.0	16.5	283.5									
GIFT/6/yellow	M	13.0	7.3	47.3	213.2	10		11						
GIFT/6/white	M	6.4	5.8	64.3	229.8	2	2							
GIFT/6/blue	M	11.1	7.2	14.8	263.1	1	6							
GIFT/6/green	M	6.7	5.8	29.6	267.4		3							
GIFT/6/pink	M	6.9	6.0	48.6	246.5		4							
GIFT/8/yellow	?	3.4	4.7	7.3	292.7									
GIFT/8/blue	?	8.2	6.4		300.0									
GIFT/8/green	?	10.8	6.8	14.9	285.1									
GIFT/8/pink	M	11.4	7.0	5.8	294.2									
GIFT/10/yellow	F	6.2	5.9	24.1	269.1		4							
GIFT/10/white	F	5.9	5.6	24.7	272.6		1							
GIFT/10/blue	F	7.0	6.2	45.4	252.1		2						2	
GIFT/10/green	M	11.8	7.2	15.4	280.8	3			3				2	
GIFT/10/pink	M	10.2	6.9	24.5	275.5								5	
GIFT/14/yellow	F	3.5	4.8		300.0									
GIFT/14/white	M	6.4	6.0		300.0									
GIFT/14/blue	M	10.4	6.8		300.0									
GIFT/14/green	F	5.8	5.5		300.0									

Appendix I. Table II. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/14/pink	M	9.2	6.8		300.0									
GIFT/16/yellow	F	13.1	7.2	4.4	295.6									
GIFT/16/white	F	11.3	7.2	0.4	299.6									
GIFT/16/blue	M	5.3	5.2		300.0									
GIFT/16/green	M	9.8	6.4		300.0									
GIFT/18/yellow	M	12.5	7.1	1.7	298.3									
GIFT/18/white	F	11.4	7.2	8.9	291.1								1	
GIFT/18/blue	F	8.7	6.3	17.5	282.5									
GIFT/18/green	M	8.6	6.3	3.0	297.0									
GIFT/18/pink	F	6.8	5.8	11.4	288.6									
GIFT/24/yellow	F	7.9	6.4	28.3	271.7									
GIFT/24/white	F	7.4	6.1	11.5	288.5									
GIFT/24/blue	F	6.9	6.0	16.0	284.0				1					
GIFT/24/green	F	5.5	5.4	34.0	266.0									
GIFT/24/pink	F	4.5	5.1	8.1	291.9									
GIFT/26/yellow	F	10.1	6.6	154.1	145.9									
GIFT/26/white	F	6.9	5.9	147.2	150.7		2							
GIFT/26/blue	M	11.1	7.1	237.1	60.8		1							
GIFT/26/green	M	17.0	8.0	224.3	75.7									
GIFT/26/pink	F	12.8	7.3	197.1	102.9				2					
CT/1/yellow	F	8.4	6.4	236.6	60.8	1	1							
CT/1/white	F	6.7	5.8	259.5	40.5									
CT/1/blue	M	8.1	6.6	264.8	35.2									
CT/1/green	F?	5.2	5.4	248.3	51.7									
CT/1/pink	M	5.7	5.9	233.9	66.1									
CT/3/yellow	M	12.5	7.2	17.0	256.5	2								
CT/3/white	M	5.7	5.5	2.0	296.6		1							
CT/3/blue	F	11.9	7.3	1.5	293.9		4							

Appendix I. Table II. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours											
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)	
CT/3/green	M	9.0	6.7	20.0	277.4	1	1								
CT/3/pink	M	3.0	4.6	5.1	294.9										
CT/7/yellow	M	11.4	7.2	31.0	224.3	36									
CT/7/white	F	6.0	5.4	76.1	207.5		6								
CT/7/blue	F	7.2	5.3	56.1	229.3		5								
CT/7/green	M	5.7	5.6	39.4	228.9		15								
CT/7/pink	M	8.7	6.5	42.2	245.1		7								
CT/9/yellow	F	9.2	6.6	20.0	269.4	2									
CT/9/white	M	9.8	6.7	12.3	285.4	2		2							
CT/9/blue	F	8.0	6.2	45.6	252.1		1								
CT/9/green	M	9.0	6.4	10.8	275.3		4								
CT/11/yellow	F	9.5	6.6	7.5	292.5										
CT/11/blue	F	10.7	6.8	43.7	254.9		1								
CT/11/green	F	11.1	7.0	54.6	245.4				1						
CT/11/pink	M	3.3	4.6	27.8	272.2										
CT/13/yellow	F	4.3	5.0	2.7	295.6		2								
CT/13/white	M	9.0	6.5	17.9	282.1										
CT/13/blue	M	5.2	5.5	30.9	269.1										
CT/13/green	M	13.7	7.3	13.2	286.8				4						
CT/13/pink	M	6.7	6.0	22.1	278.0										
CT/15/yellow	F	6.7	5.8	22.3	275.0		2		2						
CT/15/white	M	4.2	5.0	19.3	274.9		3						4		
CT/15/blue	M	8.5	6.2	47.3	229.6	4		5	3						
CT/15/green	F	10.7	6.5	10.3	289.7										
CT/15/pink	M	9.3	6.6	7.9	257.2		5	2							
CT/17/yellow	M	5.8	5.4	282.1	6.0		7								
CT/17/white	M	10.9	7.0	274.0	22.7		2					8	3		
CT/17/blue	M	11.9	6.9	188.9	95.8	8						10	11		

Appendix I. Table II. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours											
		F/M	weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/17/green	M		6.3	5.8	282.5	15.8		2					5		
CT/17/pink	M		4.4	5.2	243.9	54.6		1					83		
CT/19/yellow															
CT/19/white	M		19.7	8.2	35.6	264.4			1						
CT/19/blue	M		4.7	5.0	4.9	295.1									
CT/19/green	M		6.8	6.0	42.8	257.2									
CT/19/pink	M		3.2	4.4	34.2	265.8									
CT/21/yellow	M		13.6	7.7	209.9	90.1									
CT/21/white	?		8.6	6.4	252.8	47.3									
CT/21/blue	F		7.4	6.1	190.3	103.7	3								
CT/21/green	M		6.8	5.9	200.2	99.8									
CT/21/pink	M		4.2	5.0	282.2	17.8									
CT/25/yellow	?		11.6	7.2		300.0									
CT/25/white	M		14.5	7.7		300.0									
CT/25/blue	F		6.6	5.9		300.0									
CT/25/green	M		3.3	4.6		300.0									
CT/25/pink	?		8.0	6.5		300.0									
CT/27/yellow	M		5.4	5.6	74.3	220.4	5								
CT/27/white	F		6.6	6.0	106.8	174.7	13								
CT/27/blue	M		7.7	6.2	75.6	208.4	7								
CT/27/green	M		9.7	6.8	87.9	184.3	12	1	1	1					
CT/29/yellow	M		9.7	6.7	44.9	164.4	17	1							
CT/29/white	F		10.0	6.7	84.6	170.4		8							
CT/29/blue	F		4.9	5.3	46.9	222.4		8							
CT/29/green	M		6.9	6.0	22.2	196.9		9							
CT/29/pink	M		5.6	5.6	51.5	200.4		15							

Appendix I. Table III. Behavioural activity of GIFT and control fish in May (trial #1).

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/2/yellow	M	18.5	8.5		300.0									
GIFT/2/white	F	15.2	8.0		300.0									
GIFT/2/blue	M	18.9	8.4		300.0									
GIFT/2/green	M	13.4	7.5		300.0									
GIFT/2/pink	M	9.8	6.6		300.0									
GIFT/4/yellow	M	10.9	7.4	7.3	292.7									
GIFT/4/white	F	11.3	7.1	1.7	298.3									
GIFT/4/blue	M	15.9	8.1		300.0									
GIFT/4/green	F	13.5	7.6	5.8	294.2									
GIFT/4/pink	F	6.3	5.8	7.5	292.5									
GIFT/6/yellow	M	17.1	8.0	3.9	294.9		1							
GIFT/6/white	M	9.4	6.7	0.8	299.2									
GIFT/6/blue	M	19.1	8.3	19.2	280.8				5					
GIFT/6/green	M	8.5	6.4	4.3	295.7									
GIFT/6/pink	M	9.4	6.8	4.0	293.3		1							
GIFT/8/yellow														
GIFT/8/blue														
GIFT/8/green														
GIFT/8/pink														
GIFT/10/yellow	F	7.7	6.3	54.5	245.5									
GIFT/10/white	F	7.0	6.1	71.1	228.9									
GIFT/10/blue	F	8.4	6.8	13.5	286.5									
GIFT/10/green	M	19.7	8.7	16.4	283.6									
GIFT/10/pink	M	14.5	7.8	46.8	253.2									
GIFT/14/yellow	F	5.4	5.5		300.0									
GIFT/14/white	M	9.2	6.8		300.0									
GIFT/14/blue	M	16.6	7.9		300.0									
GIFT/14/green	F	8.8	6.5	0.8	299.2									

Appendix I. Table III. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
	F/M	weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/14/pink	M	15.4	8.0		300.0									
GIFT/16/yellow	F	17.9	8.2	10.2	289.8				2					
GIFT/16/white	F	15.2	7.9	2.0	298.0									
GIFT/16/blue	M	8.4	6.3		300.0									
GIFT/16/green	M	13.9	7.3		300.0									
GIFT/16/pink	F	21.8	8.6	2.9	297.1									
GIFT/18/yellow	M	19.6	8.5		300.0									
GIFT/18/white	F	14.3	7.9		300.0									
GIFT/18/blue	F	11.4	7.0		300.0									
GIFT/18/green	M	11.4	7.0		300.0									
GIFT/18/pink	F	9.0	6.6	3.5	296.5									
GIFT/24/yellow	F	10.9	7.2	52.9	246.3		1		2					
GIFT/24/white	F	9.1	6.7	19.9	279.7		1							
GIFT/24/blue	F	9.2	6.8	39.1	260.9				3					
GIFT/24/green	F	6.5	6.0	39.6	260.4									
GIFT/24/pink	F	6.9	5.9	4.3	295.7									
GIFT/26/yellow	F	16.1	7.8	24.9	275.1				2					
GIFT/26/white	F	9.5	6.8	20.8	243.8		8							
GIFT/26/blue	M	14.5	7.8	25.3	259.0		7							
GIFT/26/green	M	25.2	9.0	82.4	163.7	12		29					3	1
GIFT/26/pink	F	16.5	7.9	24.7	262.3	1	3						1	
CT/1/yellow														
CT/1/white														
CT/1/blue														
CT/1/green														
CT/1/pink														
CT/3/yellow	M	15.5	8.0	9.7	290.3				2					
CT/3/white	M	8.9	6.6		300.0									

Appendix I. Table III. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/3/blue	F	13.6	7.6	7.6	292.4									
CT/3/green	M	10.8	7.1	12.8	284.9	1	1		2					
CT/3/pink	M	4.4	5.3	7.3	287.5		1							
CT/7/yellow	M	14.4	7.8	46.8	244.7	3			1				1	
CT/7/white	F	8.0	6.2	43.0	256.0		1							
CT/7/blue	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
CT/7/green	M	8.4	6.4	27.4	270.7		1							
CT/7/pink	M	11.0	7.1	16.0	278.0		1							
CT/9/yellow	F	11.9	7.3		300.0									
CT/9/white	M	16.4	8.0	6.8	293.2									
CT/9/blue	F	8.7	6.4	2.5	297.5									
CT/9/green	M	9.6	6.8	1.6	298.4									
CT/11/yellow	F	10.4	7.0	7.4	291.1		1		2					
CT/11/blue	F	10.7	7.0	61.7	237.5		1							
CT/11/green	F	21.0	8.8	12.1	287.9				3					
CT/11/pink	M	3.3	4.7	27.2	272.8									
CT/13/yellow	F	5.0	5.5	283.1	9.9		3							
CT/13/white	M	13.3	7.6	221.6	33.9		6							
CT/13/blue	M	6.2	5.9	257.6	42.4									
CT/13/green	M	21.3	8.5	195.0	73.9	8			5				1	
CT/13/pink	M	9.1	6.8	138.3	147.0	1	5							
CT/15/yellow	F	9.7	6.7	17.7	266.3		3							
CT/15/white	M	6.6	5.9	1.8	281.3		5							
CT/15/blue	M	10.4	6.7	127.9	71.8	14		19	15					4
CT/15/green	F	14.4	7.2	1.8	266.7		9							
CT/15/pink	M	13.6	7.5	2.7	279.7		5							
CT/17/yellow	M	6.6	6.0	147.2	140.1		3							
CT/17/white	M	14.2	7.8	138.4	124.4	1	12							



Appendix I. Table III. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
	F/M	weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/17/blue	M	16.3	7.8	107.4	38.6	10							1	9
CT/17/green	M	8.6	6.5	171.3	101.1		4							
CT/17/pink	M	5.7	5.7	228.3	66.8		2							
CT/19/yellow														
CT/19/white														
CT/19/blue														
CT/19/green														
CT/19/pink														
CT/21/yellow	M	18.1	8.5	98.0	183.1	10		2	1				4	
CT/21/white														
CT/21/blue	F	8.7	6.5	65.0	235.1									
CT/21/green	M	6.9	6.1	64.0	236.0			8	2					
CT/21/pink	M	4.8	5.3	82.2	203.8		5							
CT/25/yellow														
CT/25/white														
CT/25/blue														
CT/25/green														
CT/25/pink														
CT/27/yellow	M	7.5	6.3	112.7	169.0		8						3	
CT/27/white	F	7.4	6.3	98.8	174.4		9	8	1	1			6	
CT/27/blue	M	9.7	6.9	40.1	221.1	7	7	2	6	1			6	
CT/27/green	M	12.7	7.5	77.6	156.5	20			2	1			11	
CT/29/yellow	M	12.0	7.5	47.5	204.1	14		2	6					
CT/29/white	F	11.1	7.0	13.1	281.6	1	1							
CT/29/blue	F	5.6	5.7	14.7	169.6		4							
CT/29/green	M	8.4	6.6	3.6	288.4		2							
CT/29/pink	M	7.5	6.5	5.7	260.0		7							

Appendix I. Table IV. Behavioural activity of GIFT and control fish in May (trial #2).

fish strain/ tank number/ bead colour	sex	measurements		behaviours											
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)	
GIFT/2/yellow	M	18.5	8.5		300.0										
GIFT/2/white	F	15.2	8.0	4.9	295.1										
GIFT/2/blue	M	18.9	8.4	7.4	292.6										
GIFT/2/green	M	13.4	7.5		300.0										
GIFT/2/pink	M	9.8	6.6	4.1	295.9										
GIFT/4/yellow	M	10.9	7.4	13.8	286.2										
GIFT/4/white	F	11.3	7.1	3.1	296.9										
GIFT/4/blue	M	15.9	8.1	31.1	268.9										
GIFT/4/green	F	13.5	7.6	7.0	293.0										
GIFT/4/pink	F	6.3	5.8	11.2	288.8										
GIFT/6/yellow	M	17.1	8.0		300.0										
GIFT/6/white	M	9.4	6.7	0.7	299.3										
GIFT/6/blue	M	19.1	8.3	8.7	291.3										
GIFT/6/green	M	8.5	6.4		300.0										
GIFT/6/pink	M	9.4	6.8	2.5	297.5										
GIFT/8/yellow															
GIFT/8/blue															
GIFT/8/green															
GIFT/8/pink															
GIFT/10/yellow	F	7.7	6.3	23.0	277.0										
GIFT/10/white	F	7.0	6.1	13.7	286.3										
GIFT/10/blue	F	8.4	6.8	13.9	286.1										
GIFT/10/green	M	19.7	8.7	48.5	251.5			2							
GIFT/10/pink	M	14.5	7.8	19.1	280.9										
GIFT/14/yellow	F	5.4	5.5		300.0										
GIFT/14/white	M	9.2	6.8		300.0										
GIFT/14/blue	M	16.6	7.9	3.8	296.2										
GIFT/14/green	F	8.8	6.5		300.0										

Appendix I. Table IV. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
	F/M	weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/14/pink	M	15.4	8.0		300.0									
GIFT/16/yellow	F	17.9	8.2		300.0									
GIFT/16/white	F	15.2	7.9		300.0									
GIFT/16/blue	M	8.4	6.3		300.0									
GIFT/16/green	M	13.9	7.3		300.0									
GIFT/16/pink	F	21.8	8.6		300.0									
GIFT/18/yellow	M	19.6	8.5		300.0									
GIFT/18/white	F	14.3	7.9		300.0									
GIFT/18/blue	F	11.4	7.0		300.0									
GIFT/18/green	M	11.4	7.0		300.0									
GIFT/18/pink	F	9.0	6.6		300.0									
GIFT/24/yellow	F	10.9	7.2	11.6	288.4									
GIFT/24/white	F	9.1	6.7	8.9	291.1									
GIFT/24/blue	F	9.2	6.8	2.4	297.6									
GIFT/24/green	F	6.5	6.0	2.7	297.3									
GIFT/24/pink	F	6.9	5.9	1.6	298.4									
GIFT/26/yellow	F	16.1	7.8	10.3	289.7			4					2	
GIFT/26/white	F	9.5	6.8	13.1	279.3		5							
GIFT/26/blue	M	14.5	7.8	14.1	285.9									
GIFT/26/green	M	25.2	9.0	73.5	224.0	2		9				1	2	
GIFT/26/pink	F	16.5	7.9		300.0									
CT/1/yellow														
CT/1/white														
CT/1/blue														
CT/1/green														
CT/1/pink														
CT/3/yellow														
CT/3/white														

Appendix I. Table IV. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/3/blue	F/M	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
CT/3/green	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
CT/3/pink	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
CT/7/yellow	M	14.4	7.8	30.2	269.8									
CT/7/white	F	8.0	6.2		300.0									
CT/7/blue	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
CT/7/green	M	8.4	6.4	5.2	294.8									
CT/7/pink	M	11.0	7.1	4.8	295.2									
CT/9/yellow	F	11.9	7.3		300.0									
CT/9/white	M	16.4	8.0		300.0									
CT/9/blue	F	8.7	6.4		300.0									
CT/9/green	M	9.6	6.8		300.0									
CT/11/yellow	F	10.4	7.0		300.0									
CT/11/blue	F	10.7	7.0		300.0									
CT/11/green	F	21.0	8.8		300.0									
CT/11/pink	M	3.3	4.7	10.8	289.2									
CT/13/yellow	F	5.0	5.5	0.4	299.6									
CT/13/white	M	13.3	7.6	1.8	298.2									
CT/13/blue	M	6.2	5.9	4.4	295.6									
CT/13/green	M	21.3	8.5	4.7	295.3									
CT/13/pink	M	9.1	6.8	1.3	298.7									
CT/15/yellow	F	9.7	6.7		300.0									
CT/15/white	M	6.6	5.9		300.0									
CT/15/blue	M	10.4	6.7	112.7	187.3			2	4					
CT/15/green	F	14.4	7.2		300.0									
CT/15/pink	M	13.6	7.5		300.0									
CT/17/yellow	M	6.6	6.0	147.5	148.9		2					19		
CT/17/white	M	14.2	7.8	104.2	133.4		16					105		

Appendix I. Table IV. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/17/blue	M	16.3	7.8	87.3	28.6	20			5			6		5
CT/17/green	M	8.6	6.5	109.0	142.8		12					21		
CT/17/pink	M	5.7	5.7	69.7	225.8		3					15		
CT/19/yellow														
CT/19/white														
CT/19/blue														
CT/19/green														
CT/19/pink														
CT/21/yellow	M	18.1	8.5	102.0	198.0			12						
CT/21/white														
CT/21/blue	F	8.7	6.5	67.4	228.2	2								
CT/21/green	M	6.9	6.1	32.4	249.9		4		2					
CT/21/pink	M	4.8	5.3	57.5	225.4		6	2						
CT/25/yellow														
CT/25/white														
CT/25/blue														
CT/25/green														
CT/25/pink														
CT/27/yellow	M	7.5	6.3	9.3	290.7									
CT/27/white	F	7.4	6.3	12.6	287.4									
CT/27/blue	M	9.7	6.9		300.0									
CT/27/green	M	12.7	7.5	19.2	280.8				2					
CT/29/yellow	M	12.0	7.5	154.0	106.8	21		3		1				
CT/29/white	F	11.1	7.0	79.8	199.3		9							
CT/29/blue	F	5.6	5.7	187.1	109.4		3					35		
CT/29/green	M	8.4	6.6	179.0	87.5		5	6		1				
CT/29/pink	M	7.5	6.5	197.5	66.7		5	11		2	2	9		

Appendix I. Table V. Behavioural activity of GIFT and control fish in June (trial #1).

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/2/yellow	M	30.0	9.9		300.0									
GIFT/2/white	F	20.3	8.6		300.0									
GIFT/2/blue	M	30.0	9.8	8.2	291.8									
GIFT/2/green	M	21.1	8.8		300.0									
GIFT/2/pink	M	14.1	7.8	2.2	297.8									
GIFT/4/yellow	M	16.2	8.3	69.8	230.2									
GIFT/4/white	F	16.5	8.0	60.7	239.3			3	1					
GIFT/4/blue	M	21.0	8.9	74.3	225.7			5						
GIFT/4/green	F	17.0	8.2	14.9	285.2									
GIFT/4/pink	F	9.9	6.7	21.4	278.6									
GIFT/6/yellow	M	20.7	8.5	4.3	295.7									
GIFT/6/white	M	14.1	7.6		300.0									
GIFT/6/blue	M	30.2	10.0		300.0									
GIFT/6/green	M	11.3	7.0		300.0									
GIFT/6/pink	M	13.7	7.6		300.0									
GIFT/8/yellow														
GIFT/8/blue														
GIFT/8/green														
GIFT/8/pink														
GIFT/10/yellow	F	11.3	7.2	150.5	144.9		3							
GIFT/10/white	F	10.2	6.8	158.3	135.0		5							
GIFT/10/blue	F	11.3	7.5	113.2	183.5		2							
GIFT/10/green	M	28.4	9.6	146.8	113.0	17		5					3	
GIFT/10/pink	M	24.3	8.9	154.9	130.4		6							
GIFT/14/yellow	F	8.4	6.5		300.0									
GIFT/14/white	M	14.9	8.2		300.0									
GIFT/14/blue	M	23.3	8.8		300.0									
GIFT/14/green	F	14.7	7.6	1.7	298.3									

Appendix I. Table V. continued.

fish strain/ tank number/ bead colour	sex	measurements			behaviours									
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/14/pink	M	23.1	9.3		300.0									
GIFT/16/yellow	F	26.3	9.3		300.0									
GIFT/16/white	F	21.3	9.0		300.0									
GIFT/16/blue	M	14.3	7.5		300.0									
GIFT/16/green	M	23.0	8.7		300.0									
GIFT/16/pink	F	26.5	9.2		300.0									
GIFT/18/yellow	M	30.2	9.8		300.0									
GIFT/18/white	F	21.2	9.0	1.8	298.2									
GIFT/18/blue	F	15.8	8.0		300.0									
GIFT/18/green	M	16.4	7.9	3.3	296.7									
GIFT/18/pink	F	13.7	7.6		300.0									
GIFT/24/yellow	F	13.1	7.7	88.8	211.2									
GIFT/24/white	F	12.5	7.4	119.8	178.4		1							
GIFT/24/blue	F	13.0	7.4	117.4	180.9	3		2						
GIFT/24/green	F	9.0	6.6	74.3	225.8									
GIFT/24/pink	F	11.0	7.0	93.7	206.3									
GIFT/26/yellow	F	23.8	8.8		300.0									
GIFT/26/white	F	13.7	7.8		300.0									
GIFT/26/blue	M	21.3	8.8		300.0									
GIFT/26/green	M	33.5	10.3		300.0									
GIFT/26/pink	F	22.7	8.6		300.0									
CT/1/yellow														
CT/1/white														
CT/1/blue														
CT/1/green														
CT/1/pink														
CT/3/yellow	M	19.4	8.8	11.2	288.8									
CT/3/white	M	13.4	7.4	5.8	294.2									

Appendix I. Table V. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/3/blue	F	16.6	8.1	6.7	293.3									
CT/3/green	M	12.9	7.5	2.9	297.1									
CT/3/pink	M	6.9	6.2	1.4	298.6									
CT/7/yellow	---	---	---	---	---	---	---	---	---	---	---	---	---	---
CT/7/white	---	---	---	---	---	---	---	---	---	---	---	---	---	---
CT/7/blue	---	---	---	---	---	---	---	---	---	---	---	---	---	---
CT/7/green	---	---	---	---	---	---	---	---	---	---	---	---	---	---
CT/7/pink	---	---	---	---	---	---	---	---	---	---	---	---	---	---
CT/9/yellow	F	13.8	7.5		300.0									
CT/9/white	M	23.4	9.2		300.0									
CT/9/blue	F	13.0	7.3		300.0									
CT/9/green	M	13.2	7.5	1.6	298.4									
CT/11/yellow	F	10.5	7.0		300.0									
CT/11/blue	F	12.9	7.5	1.3	298.7									
CT/11/green	F	34.4	10.3		300.0									
CT/11/pink	M	4.0	5.1		300.0									
CT/13/yellow	F	6.8	6.2	11.0	289.0									
CT/13/white	M	18.1	8.6	6.4	293.6									
CT/13/blue	M	8.0	6.5	22.7	277.3									
CT/13/green	M	27.0	9.4	7.0	293.0									
CT/13/pink	M	12.6	7.6	10.1	289.9									
CT/15/yellow	F	11.6	7.2	37.7	256.9		4	14						
CT/15/white	M	9.4	6.6	21.6	266.7		5							
CT/15/blue	M	14.0	7.5	146.2	126.5	9		24	7					
CT/15/green	F	15.4	7.7	28.6	266.6		2							
CT/15/pink	M	16.9	8.1	25.2	267.0		5							
CT/17/yellow	M	9.2	6.6	67.6	222.3		5							
CT/17/white	M	18.8	8.5	232.6	47.6		12							1



Appendix I. Table V. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
	F/M	weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/17/blue	M	21.8	8.7	89.3	13.2	15		5						16
CT/17/green	M	11.7	7.4	153.5	128.8		7							
CT/17/pink	M	8.1	6.5	145.2	144.6		3							
CT/19/yellow														
CT/19/white														
CT/19/blue														
CT/19/green														
CT/19/pink														
CT/21/yellow														
CT/21/white														
CT/21/blue														
CT/21/green														
CT/21/pink														
CT/25/yellow														
CT/25/white														
CT/25/blue														
CT/25/green														
CT/25/pink														
CT/27/yellow	M	12.2	7.4		300.0									
CT/27/white	F	9.2	6.7		300.0									
CT/27/blue	M	12.3	7.5		300.0									
CT/27/green	M	17.2	8.2		300.0									
CT/29/yellow														
CT/29/white														
CT/29/blue														
CT/29/green														
CT/29/pink														

Appendix I. Table VI. Behavioural activity of GIFT and control fish in June (trial #2).

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/2/yellow	M	30.0	9.9	3.9	296.1									
GIFT/2/white	F	20.3	8.6	2.6	297.4									
GIFT/2/blue	M	30.0	9.8	3.5	296.5									
GIFT/2/green	M	21.1	8.8		300.0									
GIFT/2/pink	M	14.1	7.8		300.0									
GIFT/4/yellow	M	16.2	8.3		300.0									
GIFT/4/white	F	16.5	8.0		300.0									
GIFT/4/blue	M	21.0	8.9		300.0									
GIFT/4/green	F	17.0	8.2		300.0									
GIFT/4/pink	F	9.9	6.7		300.0									
GIFT/6/yellow	M	20.7	8.5		300.0									
GIFT/6/white	M	14.1	7.6		300.0									
GIFT/6/blue	M	30.2	10.0	0.8	299.2									
GIFT/6/green	M	11.3	7.0		300.0									
GIFT/6/pink	M	13.7	7.6	4.7	295.3									
GIFT/8/yellow														
GIFT/8/blue														
GIFT/8/green														
GIFT/8/pink														
GIFT/10/yellow	F	11.3	7.2	8.1	291.9									
GIFT/10/white	F	10.2	6.8	7.5	292.5									
GIFT/10/blue	F	11.3	7.5	3.4	296.6									
GIFT/10/green	M	28.4	9.6	18.6	281.4									
GIFT/10/pink	M	24.3	8.9	7.4	292.6									
GIFT/14/yellow	F	8.4	6.5	9.3	290.7									
GIFT/14/white	M	14.9	8.2	12.1	287.9									
GIFT/14/blue	M	23.3	8.8	9.5	290.5									
GIFT/14/green	F	14.7	7.6	3.5	296.5									

Appendix I. Table VI. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
GIFT/14/pink	M	23.1	9.3	3.5	296.5									
GIFT/16/yellow	F	26.3	9.3		300.0									
GIFT/16/white	F	21.3	9.0		300.0									
GIFT/16/blue	M	14.3	7.5		300.0									
GIFT/16/green	M	23.0	8.7		300.0									
GIFT/16/pink	F	26.5	9.2	15.0	285.0									
GIFT/18/yellow	M	30.2	9.8	20.3	279.7									
GIFT/18/white	F	21.2	9.0	20.8	279.2									
GIFT/18/blue	F	15.8	8.0	35.4	264.6									
GIFT/18/green	M	16.4	7.9	15.3	284.7									
GIFT/18/pink	F	13.7	7.6	11.4	288.6									
GIFT/24/yellow	F	13.1	7.7	0.4	299.6									
GIFT/24/white	F	12.5	7.4	3.1	296.9									
GIFT/24/blue	F	13.0	7.4		300.0									
GIFT/24/green	F	9.0	6.6	3.2	296.8									
GIFT/24/pink	F	11.0	7.0		300.0				1					
GIFT/26/yellow	F	23.8	8.8		300.0									
GIFT/26/white	F	13.7	7.8	12.9	287.1									
GIFT/26/blue	M	21.3	8.8		300.0									
GIFT/26/green	M	33.5	10.3		300.0									
GIFT/26/pink	F	22.7	8.6		300.0									
CT/1/yellow														
CT/1/white														
CT/1/blue														
CT/1/green														
CT/1/pink														
CT/3/yellow	M	19.4	8.8	61.8	237.5	1								
CT/3/white	M	13.4	7.4		300.0									

Appendix I. Table VI. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/3/blue	F	16.6	8.1		300.0									
CT/3/green	M	12.9	7.5	16.4	283.6									
CT/3/pink	M	6.9	6.2	16.8	283.2									
CT/7/yellow														
CT/7/white														
CT/7/blue														
CT/7/green														
CT/7/pink														
CT/9/yellow	F	13.8	7.5	1.0	299.0									
CT/9/white	M	23.4	9.2	3.1	296.9									
CT/9/blue	F	13.0	7.3	22.7	277.4									
CT/9/green	M	13.2	7.5	19.1	280.9									
CT/11/yellow	F	10.5	7.0	12.6	287.4									
CT/11/blue	F	12.9	7.5	17.2	282.8									
CT/11/green	F	34.4	10.3	31.4	268.6				4					
CT/11/pink	M	4.0	5.1	22.2	277.8									
CT/13/yellow	F	6.8	6.2	67.9	231.8		1							
CT/13/white	M	18.1	8.6	95.6	202.5		2		1					
CT/13/blue	M	8.0	6.5	98.0	200.9		1							
CT/13/green	M	27.0	9.4	96.0	175.4	8		9						5
CT/13/pink	M	12.6	7.6	8.6	291.4									
CT/15/yellow	F	11.6	7.2	54.8	243.1		1	6						
CT/15/white	M	9.4	6.6	53.2	244.8		1							
CT/15/blue	M	14.0	7.5	168.6	106.0	8		14						
CT/15/green	F	15.4	7.7	48.5	242.3		3							
CT/15/pink	M	16.9	8.1	76.4	218.5		1			1				
CT/17/yellow	M	9.2	6.6	142.5	157.5									
CT/17/white	M	18.8	8.5	140.8	150.6		4							2

Appendix I. Table VI. continued.

fish strain/ tank number/ bead colour	sex	measurements		behaviours										
		weight (g)	length (cm)	SW (sec)	RE (sec)	CH (#)	ES (#)	TB (#)	NI (#)	CO (#)	JL (#)	GU (#)	FE (#)	NE (#)
CT/17/blue	M	21.8	8.7	137.7	124.8	5								2
CT/17/green	M	11.7	7.4	142.8	143.4		3			1				
CT/17/pink	M	8.1	6.5	87.7	211.0		1							
CT/19/yellow														
CT/19/white														
CT/19/blue														
CT/19/green														
CT/19/pink														
CT/21/yellow														
CT/21/white														
CT/21/blue														
CT/21/green														
CT/21/pink														
CT/25/yellow														
CT/25/white														
CT/25/blue														
CT/25/green														
CT/25/pink														
CT/27/yellow	M	12.2	7.4		300.0									
CT/27/white	F	9.2	6.7	42.9	257.1									
CT/27/blue	M	12.3	7.5	33.2	266.0		1							
CT/27/green	M	17.2	8.2	70.1	229.9				2					
CT/29/yellow														
CT/29/white														
CT/29/blue														
CT/29/green														
CT/29/pink														

**Appendix II.** Number of nests present in the experimental aquaria (control and GIFT strain of Nile tilapia) during the three month study period (April-June). All experimental aquaria had four or five fish present (data from the aquaria with less than four fish present were not used). ---, data not used in analyses.

Date	Experimental Aquaria																							
	GIFT												Control											
	2	4	6	8	10	14	16	18	24	26	1	3	7	9	11	13	15	17	19	21	25	27	29	
April 1														1				1						
April 2														1				1						
April 3														2										
April 5									1									2	1	2				
April 7										2	2							1	1	1			1	
April 8										2	2							2					1	
April 9																		3		1			1	
April 10																		2		1				
April 11										1	1							5	1	1	1		3	
April 12										1	1							4		2	1		4	
April 13										1	2			2				5	1	2	1		4	
April 14											2			2		1	2		1	2	1		2	
April 15											2	1	2	2		3	2	2	1	2	1		2	
April 17											5					3	5	6		2	1		3	
April 18											3	1	1	1		2	7	2	1	5	1		2	
April 20											1						7	6		2				
April 21													1				7	3			2			
April 22																		3			2		3	
April 23																		4		1			3	
April 24				1							1							3	1	2	2		5	
April 25				1							1							4		5			2	
April 26											2									2	2		3	
April 28		3		1							2						2	6			2	2	6	
April 29											2			2			1	1			2	1	6	

Appendix II. continued.

Date	Experimental Aquaria																								
	GIFT												Control												
	2	4	6	8	10	14	16	18	24	26	1	3	7	9	11	13	15	17	19	21	25	27	29		
May 1		1	—							—	3		5				2	5	—	3	—				
May 2				—			1			—	2		5					3	—		—				
May 3				—		1				—	2		2				2	3	—		—				
May 4				—						—	2			5		1	2	3	—		—	1			
May 5	1			—						—	2			5		1	2	3	—		—	1			
May 6				—						—	2			4		3	1	5	—	4	—	1	1		
May 7		2		—						—	3	3	2			4		5	—	5	—		6		
May 8		2		—						—	1	2	2			1		4	—	3	—		4		
May 10			5	—						—	1	4	2			6	3	6	—	4	—	7	5		
May 11		4	4	—						—	2	2	1			5	4		—	4	—	3	2		
May 14		4	1	—						—		2	2			5	4	2	—	5	—	2	3		
May 15		4	3	—						—	1	3	3			7	5	6	—	5	—	7	5		
May 16		3	3	—						—	1	3	3			3	3	6	—	5	—	4	4		
May 17		3	3	—						—	2	4	1			2	4	6	—	3	—	4	1		
May 18		3	2	—			2			—	7	4	2			7	3	2	—		—				
May 19		1		—			1			—	1	3	2			1	2	1	—	5	—		3		
May 25		6	5	—		1	1			—	2	2	1		1	7	5	3	—	5	—	2	9		
May 27		7		—					1	—			2			7	2	4	—	4	—	1	5		
May 28		4	4	—			1			—	2	2	1			7	4	4	—	5	—		5		
May 30		7	5	—	3		2		1	—	5	5	1			7	4	6	—	5	—		2		
May 31		7	3	—	1		3		4	—	3	4				6	4	5	—	3	—	3	5		

Appendix II. continued.

Date	Experimental Aquaria																								
	GIFT												Control												
	2	4	6	8	10	14	16	18	24	26	1	3	7	9	11	13	15	17	19	21	25	27	29		
June 2		7	5	—					4	—	6	—	2			6	2	5	—	—	—	4	—		
June 6		6	4	—					2	—	2	—	1			3	3	5	—	—	—	2	—		
June 9		5		—					1	—	1	—	—				1	3	—	—	—	1	—		
June 12		4		—						—	1	—	—	1			3	4	—	—	—	2	—		
June 15		6	3	—						—	1	—	—	2		8	6	5	—	—	—	6	—		
June 17		6		—						—	1	—	—				3	4	—	—	—	4	—		
June 24		3	2	—	1					—	4	—	—	1		1	4	1	—	—	—		—		
June 25		5	3	—	4	1				—	4	—	—	1		6	5	2	—	—	—		—		
June 26		3	3	—					5	—	2	—	—			5	3	3	—	—	—	5	—		
June 27		4	3	—	2				5	—		—	—	1		7	4	3	—	—	—	2	—		
June 30	5	5	2	—	3	3	1	3	1	—	6	—	—	3	2	6	4	4	—	—	—		—		
July 2	3	2	1	—	4				2	—	4	—	—	3		5	4	3	—	—	—	4	—		



**Appendix III.** Size-specific mortality in the control (CT) and GIFT strains of Nile tilapia during the three month study period (April-June). Weight, length, and sex (F, female or M, male) of dead fish, and that of the live fish present in same aquarium are tabulated. ?, sex of fish not determined; ---, no data for analyses.

fish strain/ tank number/	sex	April			May			June		
		weight (g)	length (cm)	dead/ live	weight (g)	length (cm)	dead/ live	weight (g)	length (cm)	dead/ live
GIFT/8/yellow	?	3.4	4.7	dead	---	---	---	---	---	---
GIFT/8/white	?	5.7	5.9	dead	---	---	---	---	---	---
GIFT/8/blue	?	8.2	6.4	dead	---	---	---	---	---	---
GIFT/8/green	?	10.8	6.8	dead	---	---	---	---	---	---
GIFT/8/pink	M	11.4	7.0	live	---	---	---	---	---	---
CT/1/yellow	F	8.4	6.4	live	11.5	7.3	dead	---	---	---
CT/1/white	F	6.7	5.8	live	8.4	6.5	dead	---	---	---
CT/1/blue	M	8.1	6.6	live	6.8	6.2	dead	---	---	---
CT/1/green	F?	5.2	5.4	dead	---	---	---	---	---	---
CT/1/pink	M	5.7	5.9	live	9.7	6.9	live	---	---	---
CT/7/yellow	M	---	---	---	14.4	7.8	live	19.9	8.8	live
CT/7/white	F	---	---	---	8.0	6.2	dead	---	---	---
CT/7/blue	F	---	---	---	9.0	6.5	dead	---	---	---
CT/7/green	M	---	---	---	8.4	6.4	dead	---	---	---
CT/7/pink	M	---	---	---	11.0	7.1	live	13.8	7.6	dead
CT/19/yellow	F	3.0	4.3	dead	---	---	---	---	---	---
CT/19/white	M	19.7	8.2	live	21.3	8.6	live	---	---	---
CT/19/blue	M	4.7	5.0	live	5.0	5.4	dead	---	---	---
CT/19/green	M	6.8	6.0	live	13.4	7.6	dead	---	---	---
CT/19/pink	M	3.2	4.4	live	4.0	4.8	dead	---	---	---
CT/21/yellow	M	13.6	7.7	live	18.1	8.5	live	24.4	9.5	live
CT/21/white	?	8.6	6.4	dead	---	---	---	---	---	---
CT/21/blue	F	7.4	6.1	live	8.7	6.5	live	9.6	6.7	live
CT/21/green	M	6.8	5.9	live	6.9	6.1	live	7.0	6.1	dead

Appendix III. continued.

fish strain/ tank number/	sex	April			May			June		
		weight (g)	length (cm)	dead/ live	weight (g)	length (cm)	dead/ live	weight (g)	length (cm)	dead/ live
CT/21/pink	M	4.2	5.0	live	4.8	5.3	dead	-----	-----	-----
CT/25/yellow	?	11.6	7.2	dead	-----	-----	-----	-----	-----	-----
CT/25/white	M	14.5	7.7	live	19.4	8.5	live	26.4	9.6	live
CT/25/blue	F	6.6	5.9	live	9.1	6.6	live	8.9	6.2	dead
CT/25/green	M	3.3	4.6	live	5.4	5.3	dead	-----	-----	-----
CT/25/pink	?	8.0	6.5	dead	-----	-----	-----	-----	-----	-----
CT/27/yellow	M	5.4	5.6	live	-----	-----	-----	-----	-----	-----
CT/27/white	F	6.6	6.0	live	-----	-----	-----	-----	-----	-----
CT/27/blue	M	7.7	6.2	live	-----	-----	-----	-----	-----	-----
CT/27/green	M	9.7	6.8	live	-----	-----	-----	-----	-----	-----
CT/27/pink	?	2.8	4.4	dead	-----	-----	-----	-----	-----	-----
CT/29/yellow	M	-----	-----	-----	-----	-----	-----	15.6	8.2	live
CT/29/white	F	-----	-----	-----	-----	-----	-----	10.1	7.1	dead
CT/29/blue	F	-----	-----	-----	-----	-----	-----	7.8	6.3	dead
CT/29/green	M	-----	-----	-----	-----	-----	-----	10.4	7.2	dead
CT/29/pink	M	-----	-----	-----	-----	-----	-----	11.9	7.4	dead

**Appendix IV.** Number of mirror-directed biting (BI) and tail-beating (TB) performed by the male fish of the control (CT) and GIFT strains of Nile tilapia during the two behavioural trials. Each behavioural trial was five minutes in duration and the two trials were spread out over a one week period. The table cell was left blank if fish did not perform behaviour.

fish strain/ tank number/ bead colour	trial #1				trial #2			
	weight (g)	length (cm)	BI (#)	TB (#)	weight (g)	length (cm)	BI (#)	TB (#)
GIFT/2/yellow	40.7	11.3			42.4	11.3		
GIFT/2/blue	40.6	11.0			42.9	11.0	4	2
GIFT/2/green	33.0	10.3			34.0	10.4	2	25
GIFT/2/pink	19.7	8.8	48	16	20.3	8.9	31	20
GIFT/6/yellow	24.3	9.1	6		25.6	9.3		
GIFT/6/blue	47.1	11.6		41	50.9	11.5		19
GIFT/6/green	14.3	7.6			14.8	7.7	11	18
GIFT/8/pink	33.7	10.3			33.8	10.2	19	16
GIFT/14/white	26.8	10.0			27.0	9.9	42	37
GIFT/14/blue	35.3	10.3	10		35.9	10.3	21	
GIFT/14/pink	40.0	11.2	42	31	40.7	11.2		
GIFT/16/blue	22.8	9.0			26.0	9.2		
GIFT/16/green	34.8	10.5			37.6	10.4	35	54
GIFT/18/yellow	47.7	11.5			50.7	11.7	37	39
GIFT/18/green	24.0	9.0			24.9	9.2	3	3
GIFT/26/green	46.6	11.6			48.2	11.5		4
CT/1/pink	22.9	9.6	50	39	24.2	9.7	31	29
CT/3/yellow	21.7	9.1			22.3	9.3	14	
CT/3/white	19.9	8.8			21.3	8.8	21	12
CT/3/green	15.8	8.2			16.2	8.2	94	37
CT/3/pink	10.6	7.2			11.0	7.3		
CT/5/white	19.6	9.2	19		20.1	9.1	78	14
CT/7/yellow	28.9	10.2	36	19	29.5	10.4	20	8
CT/9/white	36.5	10.7			39.3	11.0	51	91
CT/9/green	17.4	8.4	44	5	18.1	8.5	31	18
CT/11/pink	5.7	6.1			6.0	6.0	20	13
CT/13/white	32.4	10.3	35	20	34.5	10.4	6	58
CT/13/blue	10.5	7.2	81	14	11.1	7.2	64	17
CT/13/green	38.8	10.6	15	71	41.4	10.8	6	62
CT/13/pink	22.0	9.1	1	16	22.9	9.3		
CT/15/pink	31.3	10.3	120	14	33.8	10.5	87	22
CT/17/yellow	18.0	8.5	2	101	20.5	8.7	6	65
CT/17/white	29.8	10.0	69	3	32.5	10.1	44	4
CT/17/blue	27.1	9.8	85	16	28.6	9.8	119	19
CT/17/green	18.8	8.7	62	67	20.8	8.9	54	118
CT/17/pink	16.1	8.3	34	14	17.4	8.4	46	8
CT/19/white	44.3	11.2			44.4	11.3	65	68
CT/21/yellow	34.9	10.7	62	1	35.5	10.8	43	28
CT/23/white	38.3	11.0	55	10	39.0	11.2	51	19
CT/27/yellow	28.7	9.9			30.6	10.1		
CT/27/blue	25.2	9.3	10	18	26.0	9.3	3	

## Appendix IV. continued.

fish strain/ tank number/ bead colour	trial #1				trial #2			
	weight (g)	length (cm)	BI (#)	TB (#)	weight (g)	length (cm)	BI (#)	TB (#)
CT/27/green	31.1	10.3	25	13	31.4	10.0	6	
CT/29/yellow	28.5	10.2	22	73	29.1	10.3	44	54
CT/30/yellow	19.7	9.0	58	3	19.8	9.1		
CT/30/white	16.9	8.3			41.6	11.1	28	7
CT/30/blue	40.0	11.0			17.2	8.3	8	97
CT/30/green	27.0	9.8	38	35	28.2	9.7		
CT/30/pink	41.1	11.4	95	2	41.9	11.3	55	1

**Appendix V.** Weight and length of nesting and non-nesting (N/N) male fish of the control (CT) and GIFT strains of Nile tilapia. For the nesting male fish, the total time required to build a nest (start and stop times included), the size of the nest at completion, and the nest diameter relative to fish length were tabulated. The number of nests built per fish is given by the number of nesting (i.e., start/stop) times recorded in the table cell of individual male fish.

fish strain/ tank number/ bead colour	measurements		time of day at start/completion of nesting		total time to build nest(s) (hour)	nest area (cm <sup>2</sup> )	nest diameter relative to fish length
	weight (g)	length (cm)	start	stop			
GIFT/2/yellow	55.3	11.9	N/N	N/N	N/N	N/N	N/N
GIFT/2/blue	50.4	11.5	23:34	9:53	10.3	45.3	0.7
			15:39	16:17	0.6	25.4	0.5
GIFT/2/green	44.3	11.4	18:20	15:22	21.0	52.6	0.7
GIFT/2/pink	23.5	9.1	N/N	N/N	N/N	N/N	N/N
GIFT/6/blue	62.9	12.5	7:49	15:43	7.9	99.7	0.9
GIFT/14/white	28.8	10.1	1:44	13:38	11.9	58.0	0.9
			3:23	15:44	12.4	23.6	0.5
GIFT/14/blue	44.4	11.0	13:39	14:32	0.9	23.6	0.5
GIFT/14/pink	52.2	12.0	18:11	15:05	20.9	212.0	1.4
GIFT/16/green	44.9	11.0	N/N	N/N	N/N	N/N	N/N
GIFT/18/yellow	54.5	11.8	21:04	16:01	19.0	54.4	0.7
			15:38	16:29	0.9	56.2	0.7
CT/1/pink	33.6	10.5	9:56	16:14	6.3	32.6	0.6
			13:03	13:10	0.1	16.3	0.4
CT/3/yellow	27.3	9.7	N/N	N/N	N/N	N/N	N/N
CT/3/white	29.7	9.7	N/N	N/N	N/N	N/N	N/N
0.8CT/3/green	20.3	8.7	N/N	N/N	N/N	N/N	N/N
CT/3/pink	13.3	7.7	9:36	10:31	0.9	30.8	0.8
CT/5/white	22.9	9.3	15:01	16:36	1.6	67.1	1.0
			16:40	17:20	0.7	16.3	0.5
CT/7/yellow	30.5	10.5	2:32	11:03	8.5	63.4	0.9
CT/9/white	47.4	11.7	5:43	13:15	7.5	52.6	0.7
CT/9/green	22.2	9.0	13:34	18:31	5.0	235.6	1.9
CT/11/pink	10.1	6.9	N/N	N/N	N/N	N/N	N/N
CT/13/white	45.4	11.5	9:38	9:53	0.3	10.9	0.3
CT/13/blue	10.7	7.2	N/N	N/N	N/N	N/N	N/N
CT/13/green	46.1	11.3	18:18	16:27	22.2	123.2	1.1
			18:33		21.9		
CT/13/pink	27.1	9.8	17:53	14:28	20.6	39.9	0.7
			15:31	16:35	1.1	27.2	0.6
CT/17/white	42.1	11.1	18:35	14:15	19.7	29.0	0.5
			12:57	15:31	2.6	25.4	0.5
CT/19/white	47.3	11.6	19:39	14:19	18.7	21.8	0.5
			7:10	14:19	7.2	39.9	0.6
CT/23/white	41.6	11.3	17:53	13:12	19.3	14.5	0.4
			9:36	10:35	1.0	18.1	0.4
			10:38	13:36	3.0	18.1	0.4

## Appendix V. continued.

fish strain/ tank number/ bead colour	measurements		time of day at start/completion of nesting		total time to build nest(s) (hour)	nest area (cm <sup>2</sup> )	nest diameter relative to fish length
	weight (g)	length (cm)	start	stop			
CT/27/yellow	40.1	11.0	21:25	14:30	17.1	54.4	0.8
CT/27/blue	29.9	9.9	N/N	N/N	N/N	N/N	N/N
CT/27/green	36.6	11.0	9:24	14:54	5.5	41.7	0.7
			11:19	16:42	5.4	61.6	0.8
CT/30/white	19.5	8.6	N/N	N/N	N/N	N/N	N/N
CT/30/blue	50.6	12.0	N/N	N/N	N/N	N/N	N/N