Impact of a divergent selective breeding programme on individual feed conversion ratio in Nile tilapia Oreochromis niloticus measured in groups by video-recording

Hugues de Verdal, Pierrick Haffray, Vincent Douchet, Marc Vandeputte

Impact of a divergent selective breeding programme on individual feed conversion ratio in Nile tilapia *Oreochromis niloticus* measured in groups by video-recording

Hugues de Verdal[abcd*], Pierrick Haffray[e], Vincent Douchet[ab], Marc Vandeputte[fg]

[a]CIRAD, UMR ISEM, F-34398 Montpellier, France;

[b]ISEM, Université de Montpellier, CNRS, EPHE, IRD, 34095 Montpellier, France

[c]CIRAD, UMR AGAP Institut, F-34398 Montpellier, France

[d]UMR AGAP Institut, Université de Montpellier, CIRAD, INRAE, Institut Agro, 34095 Montpellier, France

[e]SYSAAF, Station LPGP/INRAE, Campus de Beaulieu, 35000 Rennes, France

[f]MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, 34250 Palavas-les-Flots, France

[g]Université Paris-Saclay, INRAE, AgroParisTech, GABI, 78350 Jouy-en-Josas, France

*Corresponding author

Email addresses:

HdV: hugues.de_verdal@cirad.fr; phone number: +33 7 87 93 10 59

PH: pierrick.haffray@inrae.fr

VD: Vincent.douchet@ifremer.fr

MV: Marc.Vandeputte@inrae.fr

Abstract

Feed conversion ratio (FCR) is an important trait to target in breeding programs in order to improve fish farming sustainability and increase environmental efficiency. Due to the complexity of accurately measuring the individual feed consumption of fish, developing a selective breeding programme to improve FCR is a challenge. Using video-recordings of several consecutive meals in tilapia groups, we selected two divergent lines of Nile tilapia for high (FCR+) and low (FCR-) FCR at juvenile stage (12.2 g) combining BLUP and within family selection. After two generations, we observed a 12 % realised difference in FCR between both divergent lines, indicating that the inclusion of FCR in a selective breeding programme can be efficient in practice. This divergence was in line with a realized heritability of 0.19 for FCR. The divergence in estimated breeding values of FCR between the two lines was reduced (3%) but still present. Another important result was that the realized genetic correlation between FCR and Daily Weight Gain (DWG) was highly negative (rg = -0.69 ± 0.16), meaning that improving growth by selective breeding would also indirectly improve FCR in juvenile Nile tilapia, although direct selection for FCR would be more efficient than indirect selection through growth to improve FCR.

Keywords: feed efficiency, aquaculture, genetic parameters, selection response

1. Introduction

Feed conversion ratio (FCR), the ratio of feed intake (FI) to body weight gain (BWG) is one of the main traits to be improved in order to develop sustainable aquaculture (Aubin et al., 2009; Besson et al., 2017; de Verdal et al., 2018a). However, there are currently no commercial breeding programs that report introduction of FCR in their selection index because this trait is difficult to select for. To estimate FCR, FI must be accurately measured at the individual level, which is particularly challenging in fish reared in groups and in a three-dimensional system and an aquatic environment. Furthermore, the FI of an individual fish may vary from day to day (Jobling and Koskela, 1996; de Verdal et al., 2017). Therefore, an optimal method for estimating individual FCR should enable the measurement of FI for each meal over several consecutive days to be accurate and well represent the individual performance of the fish. Under these constraints, two methods have recently been adapted and upscaled to measure individual FI in several hundred fish, which is a necessary amount to enable selective breeding. The first method involves rearing fish individually, with each fish isolated in an aquarium. Growth and the amount of feed consumed are accurately measured for each fish (Besson et al., 2019). This method gives a good estimate of individual FCR but removes all social interactions between fish, which can have an impact on their own FCR, depending on the fish species (Rodde et al., 2021). Moreover, the measure can only be done on the individuals that accept this environmental condition (Besson et al., 2019). Others methods have been developed in fish to accurately measure FI, like the “X-ray” method, but cannot be applied in consecutive days (Kause et al., 2006; Grima et al., 2008), which limits the repeatability of measurements. The last method (see review by Jobling et al., 2001) and adapted for genetic studies by de Verdal et al. (2017) is to use small groups of fish reared in aquariums. Using pellet-by-pellet feeding and video recording of several consecutive meals, it

65 is possible to count the number of pellets consumed by each fish and estimate individual FI
66 without removing social interactions between fish (de Verdal et al., 2017).

67 Phenotyping FCR is clearly a challenge in fish, but there are other important points to
68 consider before adding this trait to a breeding programme. It is essential to estimate the
69 genetic parameters of this trait, i.e. the heritability, and the genetic correlations with other
70 important traits, such as growth, in the population selected for the breeding programme. Few
71 studies have estimated the genetic parameters of FCR in fish. Using different methods for
72 measuring FI during several consecutive days (individual rearing or video analyses),
73 heritability has been estimated to range between 0.25 and 0.32 using pedigree-based models
74 (de Verdal et al., 2018b; Besson et al., 2019), with an interesting level of phenotypic variance
75 (22% coefficient of variation in both studies). It therefore seems possible to develop a
76 selective programme on this trait.

77 The main objective of the present study was to evaluate selection response in a small size
78 selective breeding programme, as a proof of concept to assess the real potential of such
79 selection to improve FCR in fish. Nile tilapia *Oreochromis niloticus* was naturally chosen to
80 develop such a programme because, besides the fact that it is one of the major aquaculture
81 species (Cai et al., 2019) with potentially major economic impact of FCR improvement,
82 several studies have already been conducted to accurately measure FI and evaluate the
83 potential of such genetic selection (de Verdal et al., 2017, 2018b; Rodde et al., 2020, 2021). In
84 addition, Nile tilapia has a relatively short generation interval, thus fish can be selected for
85 two generations in a relatively short period of time. As Nile tilapia is a sociable fish species
86 showing high between-individual interactions (de Verdal et al., 2019), the video-analysis
87 method was preferred to the rearing of isolated fish, as it had been previously shown that the
88 correlation of FCRs measured by these two methods was low in this species (Rodde et al.,
89 2021). A last aspect is that tilapias are mostly reared and selected in developing countries and

90 that affordable strategies of selection, such as within-family selection, have to be considered
91 as they are simpler and more robust than too complex programs based on family selection
92 (Doyle and Herbinger, 1994).

93

94 ## 2. Material and Methods

95 ### 2.1.Ethics statement

96 This study was carried out in accordance with the recommendations of Directive 2010-63-EU
97 on the protection of animals used for scientific purposes. The protocols were approved by
98 C2EA–36 ("Comité d'éthique en expérimentation animale Languedoc-Roussillon") under
99 authorizations APAFiS n° 2018082008567792 #16582 v2 and n°2019101512138909 #22423
100 v4.

101 ### 2.2.Origin and rearing of the base generation

102 The Nile tilapia used in this study were produced from a cross between Cirad-IRD dams,
103 initially originating from Egypt, kept in the Cirad-IRD facility (Montpellier, France) for
104 several generations, and sires from FishGen commercial strain introduced in 2018 in Cirad
105 facilities in Palavas-les-Flots (France). In the F0 founders, only FishGen males were
106 phenotyped at the juvenile stage, for practical reasons. Three hundred and fifty-one males
107 were reared in tanks until they reached an average of 10g body weight (BW). When they
108 reached this body weight, they were divided into two groups, with each group being measured
109 in sequence, due to space required to measure the fish. Indeed, for logistical reasons, it was
110 not possible to have more than 20 aquariums in the rearing room. The fish of each batch were
111 distributed in 38 L aquariums (maximum 10 fish per aquarium). After anaesthesia with clove
112 oil, each fish was tagged in the dorsal muscle with a unique combination of two coloured T-
113 bar tags (Avery Dennison tags, 25 mm), one tag on each side of the body, using an Avery

Dennison Mark III pistol Grip tool to identify them individually regardless of which side of the body was shown and recorded in video. The fish were fed a commercial pelleted feed (Le Gouessant, “Tilapia Starter Flot 1” and “Tilapia Starter Flot 2”) containing 38% crude proteins, 8% crude fat, 3.9% crude fibre and 7% moisture throughout the experiment. The water temperature was maintained at 28°C throughout the experiment.

2.3.Phenotyping for FCR

The experimental design was previously developed and reported in de Verdal et al. (2017, 2018b). Briefly, after seven days of adaptation to the group aquarium, all fish were anaesthetized and weighed individually (BWi). The fish were then fed twice a day with 100% daily feed ration (DFR, in percentage of body weight), except on the day of weighing when they were fed once in the afternoon for the first two generations (G0 and G1) and twice the last generation (G2). The DFR was calculated according to the formula published by Mélard et al. (1997): $DFR = 14.23 \times BWi^{-0.322}$. Although this formula is not perfect, using a formula rather than an “*ad-libitum*” ration had some advantages. As different experimenters were involved in the feeding process, a calculated ration was more reproducible from one experimenter to another than an “*ad-libitum*” ration. This calculated ration was also useful to ensure that the same maximal feed ration was given at each meal and in all aquariums. The DFR was shared equally for each of the two daily meals. The feed was given through two pipes to the aquarium, which reduced stress, as the fish did not see the experimenter when they received the feed. The fish generally did not eat the whole ration and the choice was made to stop the feeding when some pellets remained uneaten after about one minute on the surface of the aquarium (which in fact corresponds to an ad-libitum ration). The uneaten pellets were removed from the aquarium with a dip net. At the end of the measurement period (after seven days, 12-13 meals), the fish were anesthetized a second time and weighed to calculate their daily body weight gain (DWG). At that time, all fish were tagged with a

139 passive integrated transponder (PIT-tag, Biolog-ID®) for individual identification. The fish
140 were then placed in two 300L tanks until the phenotyping process was completed. All video-
141 recorded meals were analysed by counting the number of pellets consumed by each fish.
142 Assuming that all the pellets had the same weight (16.2 ± 1.8 mg), it was possible to estimate
143 the daily FI (DFI) of all fish individually during the measurement period. The FCR of all the
144 individual fish was estimated as the ratio of individual DWG to individual DFI.

145 2.4.Selective breeding scheme

146 With FCR phenotypes of all fish, estimated breeding values (EBV) were computed with a
147 classical pedigree-based model for all the fish using the BLUPF90 family of programs
148 (Misztal et al., 2014). The following model was used:

149 $$y_{ijk} = \mu + Batch_i + Aquarium_j + Animal_k + e_{ijk}$$

150 where y_{ijk} is the FCR of animal k, μ is the overall mean, $Batch_i$ is a fixed effect of batch i (i
151 =1 to 3), $Aquarium_j$ is a random environmental effect corresponding to the common
152 environmental effect, $Animal_k$ is the random additive genetic effect of animal k and e_{ijk} the
153 random residual for animal k. At each generation, the pedigree file was updated to add the
154 new generation, and the model was fitted using all available information. The selective
155 breeding scheme is summarized in Figure 1. At the G0 generation, only males were
156 phenotyped and selected. Once selected, the selected fish were isolated individually in 40L
157 aquariums. The spawns from the non-phenotyped G0 females were divided in two to be
158 fertilized with one selected G0 male from those with the lowest EBV and one G0 male from
159 those with the highest EBV. Each G1 full-sib family was then reared separately. Fish were
160 sexed when they reached more than 30g of body weight and sex-ratio was almost balanced
161 with on average 51.5 % of males and 48.5 % of females. Two aquariums were used for each
162 family where ten full-sibs were reared and phenotyped per aquarium. The worst two (for the

non-efficient line) or best (for the efficient line) males and females were then selected within each family (11-12 families per line, Figure 1) and the candidates were isolated individually until they matured. Once mature, G1 males and females (one in each family) were crossed by artificial fertilisation, taking care not to cross together fish from the same family. Only seven G2 families could be produced in each of the lines (Figure 1) due to some difficulties in maturing the fish and in performing artificial fertilisation.

2.5.Statistical analyses

2.5.1. Descriptive statistics

Descriptive statistics, including the number of observations, means and their standard deviations and coefficient of variation (CV) were used to summarise all traits. All statistical analyses were performed using the R software (R Development Core Team, 2018). Outliers were highlighted using the boxplot.stats function of the R package "stats" (R Development Core Team, 2018) and were not included in the analyses. Outliers were due to incorrect entered or measured data (negative DWG, DFI or FCR estimates). Analysis of variance was computed using the lm function of the R package "stats" (R Development Core Team, 2018). Analysis of variance was performed at each generation to test for the fixed effect of line (FCR+ or FCR-).

2.5.2. Retrospective analysis of genetic parameters and breeding values

Using the whole G0, G1 and G2 dataset, genetic parameters and phenotypic correlations for all traits (BWi, BWf, DWG, DFI and FCR) were estimated by the REML (Restricted Maximum Likelihood) method using VCE6 (Neumaier and Groeneveld, 1998; Kovac et al., 2008). The following model was used for all the traits:

$$y_{ijk} = \mu + Generation_i + Aquarium_j + Animal_k + e_{ijk}$$

where y_{ijk} is the phenotype of the animal k, μ is the overall mean, $Generation_i$ is a fixed effect of the generation i (i = 0 to 2), $Aquarium_j$ is a random environmental effect of the aquarium j corresponding to the common environmental effect, $Animal_k$ is the random additive genetic effect of the animal k and e_{ijk} the random residual for animal k. The pedigree file included all individuals from the F0 base generation to the second generation of selection. The solutions for the animal effect were used as a posteriori estimates of breeding values, and averaged for each generation x line combination to estimate genetic trends for the traits of interest. As we have the complete matrix of additive relationships back to the base population, this approach is expected to yield more unbiased estimates of both breeding values and genetic parameters in the base population (Sorensen and Kennedy, 1986). In this a posteriori analysis, transformations were applied to the data to improve the normality of distributions. A logarithm transformation was applied to BWi, BWf and FCR, while a square root transformation was applied to DWG and DFI.

The following equation was used to estimate the realized heritability under a within-family selection scheme (Falconer and MacKay, 1996):

$$h_r^2 = \frac{R_w}{i\sigma_p(1-r)\sqrt{\left[\frac{n-1}{n(1-t)}\right]}}$$

where h_r^2 is the heritability of individual values, R_w is the observed response to selection (corresponding to the slope of the regression line of the selection differential between FCR+ and FCR- lines), i is the intensity of selection (i = 1.81 on average, representing 9.55 % of selection pressure on average) , σ_p is the standard deviation of phenotypic values, r is the genetic relationship (r=1/2 with full-sib families), n is the mean number of individuals in each family and t is the intra-class correlation of phenotypic values of members of the families, estimated as $t = 1 - (\sigma_w^2/\sigma_t^2)$ with σ_w^2 and σ_t^2 being the within-family and total variances.

209

210 ## 3. Results

211 ### 3.1.Basic statistics

212 Fish were phenotyped for FCR at the juvenile stage (Tables 1 and 2) with an average initial
213 weight (BWi) and final weight (BWf) of 12.2 ± 4.20 and 14.8 ± 5.02 g. This represents an
214 average individual daily growth of 0.38 ± 0.19 g and an average daily FI of 0.33 ± 0.13 g.
215 Combining all generations and lines (N = 993), the FCR averaged 0.97 ± 0.35, with a CV of
216 36.3%, comparable to that of the weight measurements.

217

218 ### 3.2. Response to selection and genetic parameters

219 The selection response was first estimated by comparing the LSmeans of the two selection
220 lines (FCR+, FCR-) across generations (Figure 2). There was a large year effect on FCR,
221 which affected both lines: the overall FCR decreased in generation 1, and increased in
222 generation 2. However, after two generations of selection (actually, one and a half
223 generations, as the females were not phenotyped and selected at the G0 generation), FCR
224 differed significantly (P = 0.01) between line FCR+ (1.08) and line FCR- (0.96) lines,
225 corresponding to a 12 % difference of FCR between both lines. Thus, the divergence between
226 the two lines occurred as expected. When we looked at the genetic trends (the average EBVs
227 of each line in each generation for each trait - Table 2), the divergence was smaller, as
228 log(FCR) was increased by 0.012 in line FCR+ in G2 while it decreased by 0.017 in line
229 FCR-, which corresponds to a ≈ 3 % difference.

230 The present selection experiment also had impacts in terms of DWG and DFI, with a
231 reduction in DFI in both lines, with a stable DWG for the FCR- line and a decreased DWG in

232 the FCR+ line (Figure 2). Considering the genetic trends, the tendency was clearly divergent,
233 with a decrease of both DWG and DFI in the FCR+ line, and an increase of both traits in the
234 FCR- line (Table 2).

235 Genetic parameters and phenotypic correlations for growth, DFI and FCR are presented in
236 Table 3. With the exception of FCR for which heritability was limited (0.10 ± 0.05),
237 heritability estimates were different to 0 and moderate to high, ranging from 0.27 ± 0.07 for
238 DWG to 0.53 ± 0.07 for BWi.

239 For all traits, the genetic correlations were consistent with the phenotypic correlations, except
240 between DFI and FCR, where the genetic correlation was much more negative than the
241 phenotypic correlation, albeit with a high standard error (r_g = -0.43 ± 0.25 *vs.* r_P = -0.05).
242 Body weight (initial and final), DWG and DFI were significantly and highly correlated. Feed
243 conversion ratio was negatively genetically correlated with DWG (rg = -0.69 ± 0.16). The
244 estimate for the realized heritability of FCR (h^2_R = 0.19) was higher than the mixed model
245 estimate for the same trait (0.10 ± 0.05).

246

247 **4. Discussion**

248 The overall objective of the present study was to evaluate the response to direct selection for
249 improved FCR in Nile tilapia, following previous research that showed 1) the ability to
250 accurately measure individual FCR in this species in using video-assisted technology (de
251 Verdal et al 2017), and 2) the existence of significant genetic variation for this trait (de Verdal
252 et al., 2018). To our knowledge, this is the first study to evaluate the realised response to
253 direct selection for FCR on FCR, growth and feed consumption in fish. For this purpose, two
254 divergent lines were selected for high or low FCR during two generations. The genetic
255 parameters of the traits were estimated in the two generations pedigree, and the response to

selection was evaluated, both as the phenotypic difference between lines and as the divergence in breeding values, estimated with a mixed model. Due to logistical limitations, the selective breeding programme conducted in this study was only a proof of concept, with a small number of families, and focused only on the juvenile stage.

The average individual FCR measured in the different generations of the present study (0.97 ± 0.35) on about 1,000 fish was close to previous FCR estimates made on the GIFT (Genetically Improved Farmed Tilapia, Ponzoni et al., 2011) strain of Nile tilapia. With the latter strain, selected for more than 15 generations for improved growth, de Verdal et al. (2018b) estimated that the average individual FCR measured at a juvenile stage was 0.94 ± 0.21. Although we used a cross between two populations (as it was not possible to import extra-European tilapia germplasm in the facility), the average FCR in our experiment was thus close to that of the most common commercial line, and thus is industry relevant.

After an equivalent of 1.5 generation of divergent selection for FCR (as only F0 males were selected in the base population), a difference of 12% was shown for FCR between FCR- and FCR+ lines. If we consider that the response was symmetrical to the initial FCR of the G0 generation, the realised gain per generation when compared to the mean G0 FCR of the line can then be estimated to be 6% for 1.5 generation and thus 4 % per generation. Selection response in divergent selection is expected to be symmetrical, although this is not always the case in practice (see e.g Aggrey et al., 2003), especially in short term selection experiments where stochasticity of response can be high (Nicholas, 1980; Pélabon et al., 2021). Ideally, as the practical aim of selection for FCR is to decrease FCR relative to its present value, we should have compared the FCR- line to an unselected control line. However, as we expected a low to moderate difference between lines, this would have increased the risk of not being able to identify significant differences between the lines. Thus, we chose the divergent selection approach, which yields higher differences, at the cost of the uncertainty regarding the

281 symmetry of response. When we evaluated selection response as the average EBV for logFCR
282 of each group, the divergence was +0.012 in G2 for line FCR+, and -0.017 in for line FCR-,
283 thus a ≈ 3% divergence, which was symmetrical as expected (and thus, the improvement in
284 that case can be estimated to be 1% per generation for directional selection). The lower
285 divergence observed on EBVs could be due to the lack of pedigree information on the animals
286 from the FishGen males and Cirad females base populations, which are considered a random
287 sample of unrelated individuals from the same base population in the animal model, while it is
288 quite clear that they are from a limited number of (unknown) families, and that males and
289 females from generation G0 are not from the same population. Another possible reason could
290 be that as there is only one family per aquarium in G1 and G2 (but two aquariums per family),
291 the animal model estimate may be biased by suboptimal separation of family and permanent
292 environmental effects.

293 Under the symmetrical response hypothesis, the 4% improvement of phenotypic FCR per
294 generation can be considered an important gain, with a potential major economic impact.
295 With 2.8-3.7 million metric tons of feed consumed each year by the Nile tilapia industry
296 worldwide (de Verdal et al., 2017), these 4% would represent 112.000-148.000 tons of feed
297 saved each year, and thus a major economic benefit. Even with the conservative 1%
298 improvement per generation estimated with the animal model, the impact at the global level
299 would still be major, especially considering this will be a cumulative impact when generations
300 of selection will increment on each other.

301 In the present study, the realized heritability of FCR (h_r^2 = 0.19), was higher than that
302 estimated with the animal model (0.10 ± 0.05), probably for the same reasons of limited
303 deepness of the pedigree and partial confusion of family and environment effects, as
304 discussed above, that limit the genetic gains estimated with the animal model. Genomic

information could have been useful here both to assess the real genetic relationship between G0 individuals and to better use within-family variance data to improve heritability estimates.

The realized heritability of FCR was in the lower range of previous heritability estimates obtained in the GIFT strain of Nile tilapia using video recording and pedigree-based models of 0.32 ± 0.11 and 0.21 ± 0.09 (de Verdal et al., 2018b; Barria et al., 2021) or in European sea bass *Dicentrarchus labrax* using individual rearing (0.25, Besson et al., 2019). They are close to estimates in the GIFT strain of Nile tilapia using video recording and genomic-based models (0.12 ± 0.06, Barria et al., 2021) and higher than estimates in salmonids obtained with the X-ray method (0.04-0.07 in Quinton et al., 2007; 0.07-0.10 in Kause et al., 2016). Furthermore, our heritability estimate for DWG (0.27 ± 0.07) was close to estimates on body weight gain from previous study on the GIFT strain of Nile tilapia in the same type of experimental settings (0.27 ± 0.08 in de Verdal et al., 2018b). The reason why realized heritability, and even more animal model heritability across generations, was lower than the single generation estimates obtained in Nile tilapia (0.21-0.32, see before) could be due to the fact that selection was performed on the ratio (FCR), which is known not to be optimal, as variation in a ratio can be obtained from different combined variations of its component traits (DFI and DWG) as highlighted by several authors (Lin, 1980; Gunsett, 1984, 1987; Lin and Aggrey, 2013). Indeed, it is not uncommon that selection on a ratio yields lower response than expected from the genetic parameters of the ratio (see e.g. Webb and King, 1983, for FCR in pigs, Campo and Rodríguez, 1990, for the egg mass to body weight ratio in *Tribolium castaneum*, or Vandeputte et al., 2019, for fillet yield in rainbow trout *Oncorhynchus mykiss*).

Divergent selection also had a significant impact on DFI and DWG, which are the component traits of FCR, as FCR = DFI / DWG. Phenotypic DWG was stable over generations in the FCR- line and decreased in the FCR+ line, while DFI decreased in both lines. However, the genetic trends for DWG and DFI showed a different picture, with an increase of both traits in

330 the FCR- (efficient) line, and a decrease of both in the FCR+ line (Table 2). This shows that
331 the phenotypic trends shown in Figure 2 are likely due to fixed effects of year on the
332 measurement, which are clearly visible for FCR, which goes down in the first generation then
333 increases in G2. For DFI or DWG, the year effects are not clearly visible on Figure 2, but do
334 exist, as phenotypic response is not symmetrical in the FCR- and FCR+ lines, as would be
335 expected. The divergent EBVs for DFI and DWG in the FCR+ and FCR- lines are also in
336 agreement with the negative genetic correlation of both traits with FCR. There was a negative
337 genetic correlation of DWG with FCR (-0.69 ± 0.16), similar to other results in obtained in
338 Nile tilapia by Barria et al. (2021) using genomic-based models (r_g = -0.60 ± 0.16). However,
339 with the GIFT strain, de Verdal et al. (2018b) did not find significant genetic correlations
340 between growth and FCR using pedigree-based model. The decrease of DFI across
341 generations was substantial in both lines, which was not expected given the negative
342 (although non-significant) genetic correlation between DFI and FCR (-0.43 ± 0.25). When
343 looking at the genetic trends, there was a decrease in DFI in the FCR+ line, but an increase in
344 the FCR- line (Table 2), again highlighting the fact that the general decreasing trend in both
345 lines was probably caused by fixed effects of year on the measurements as the experimental
346 protocol which may have been marginally modified. Still, it has to be highlighted that an
347 opposite (positive) genetic correlation between DFI and FCR was found with the GIFT strain
348 (r_g = 0.67 ± 0.15; de Verdal et al., 2018b) in a previous study, while in the recent study by
349 Barria et al. (2021) using genomic-based models, the genetic correlation between FCR and FI
350 is also positive (r_g = 0.24 ± 0.25), although not significant.

351 All in all, our results show that selection for low FCR caused an increase in growth rate, and it
352 can thus be expected that selection for faster growth rate would also lead to improvements in
353 FCR in Nile Tilapia as also highlighted by the negative genetic correlation between DWG and
354 FCR. Improvement of FCR through selection for a better growth has also been reported in

355 different livestock species (Emmerson, 1997; Knap and Kause, 2018) and the response is
356 higher when considering at the same BW (and not the same age). However, in tilapia, the
357 abundant literature on response to selection for growth (Bolivar and Newkirk, 2002; Ponzoni
358 et al., 2005; Charo-Karisa et al., 2006; Thodesen et al., 2012; Thodesen (Da-Yong Ma) et al.,
359 2013; Thodesen et al., 2013; Bentsen et al., 2017) has never reported changes in FCR,
360 probably because it is difficult to precisely estimate in the production environment.

361 The interest of selecting for FCR directly or through indirect selection for growth can be
362 evaluated through the relative efficiency of selection (RES) with the growth predictor, defined
363 as RES=h1|rA| where h1is the square root of the heritability of the predictor, and |rA| is the
364 absolute value of the genetic correlation existing between the predictor and FCR (Vandeputte
365 et al., 2017). Using the genetic parameters from Table 3, the RES for BWi is 0.11, while the
366 RES for DWG is 0.36. This means that for a same selection intensity, FCR improvement
367 through selection for BW will be only 11% of that obtained with direct selection for FCR, and
368 this will rise to 36% if selection is performed on DWG. Of course, it is much easier to
369 evaluate a large number of fish for BW or DWG than for individual FCR, thus selection can
370 be stronger. If the selection intensity differs between direct selection for FCR and indirect
371 selection, the relative response (RR) between direct and indirect selection will be
372 $RR=RES.i_{IND}/i_{FCR}$, with i_{IND} the selection intensity with the indirect trait, and i_{FCR} the
373 selection intensity for direct selection with FCR. If we consider a reasonable selection
374 pressure of 0.20 for direct selection for FCR, the value of i_{FCR} would be 1.40. A very strong
375 selection for growth (1%) would correspond to i_{IND}=2.67. With such values, the relative
376 response in FCR with BWi would be 21% of that obtained with direct selection for FCR, and
377 would reach 69% with DWG. The interest of choosing one option or another will depend on
378 economic evaluation, but it is clear that direct selection for FCR has to be considered if FCR
379 is the breeding goal. In any case, selection for growth is applied in all fish breeding programs

(Chavanne et al., 2016) and should thus result at least in tilapia in indirect improvement of FCR.

The method developed by de Verdal et al. (2017) and used in the present study was accurate in measuring the FI of fish for several consecutive days. A positive aspect of this method is that it allows fish to maintain social interactions which each other, which seems to be important in Nile tilapia. With this species, it has been previously shown that FCR measured at the individual level in isolation, method described in Besson et al.(2019), was not significantly correlated with FCR measured using the video methodology (Rodde et al., 2021). However, the negative aspect is that this method is particularly time-consuming as it is necessary to feed the fish pellet by pellet, and then it is essential to analyse all the videos of the meals. Improvements to add FCR to breeding programmes could be to simplify the video analyses method using machine learning and convolutional neural networks. Such automation of video analysis could greatly speed up the method and provide a real opportunity to improve FCR in several aquaculture species.

Another constraint is related to the fish species chosen for this breeding programme. Nile tilapia has the advantage of growing faster than most of the aquaculture fish species, but the main disadvantage is that it is not possible, to our knowledge, to synchronize spawning date efficiently. This reduces the possibility to develop factorial designs and contemporaneous families, and therefore common-garden rearing practices are not recommended, as not all fish are at the same stage of development, and cannibalism could occur if different families arte mixed at different body weight. This is a real problem as it is not possible in many cases to distinguish the common environmental effects from the effects of variation between families. An alternative is to index only males for which sperm is more easily available during several weeks, but this compromise limits selection pressure to the male pathway by 50 %.

The present experiment was carried out on juvenile Nile tilapia rather than on adult fish even though adults consume more feed and the financial cost of feed is higher for rearing adults than juveniles. The genetic correlation between juvenile and commercial sizes need to be estimated to transfer our results to bigger sizes. We first relied on the study by Rodde et al. (2020) estimating that the FCR measured at juvenile stage (36 g) was correlated with the FCR measured during the whole rearing period, from 36 to 260g body weight on average. But there are several other logistical reasons for this choice: i) Nile tilapia mature early before commercial BW and breed at a young age (Coward and Bromage, 2000) and females keep their eggs and free-swimming fry in their mouths for about a week without eating (Coward and Bromage, 2000). It is therefore important, in the case of mixed groups, to conduct experiments before the maturation stage; ii) the volume of water (i.e. aquarium size) required to rear Nile tilapia is smaller when studying juvenile fish rather than adults. With a limited facility size, it was preferable to choose to phenotype a larger number of juvenile fish than a smaller number of larger fish; and iii) as all meals were video-recorded and video were analysed to count the number of pellets eaten by each fish, it was preferred to focus on juvenile fish, eating less in quantity than adults, even though adults ate larger pellets.

It may now be interesting to compare the performance and feed efficiency related traits of FCR+ and FCR- lines reared in large groups in tanks to better evaluate the potential of such selection programme. Another future area of development would be to evaluate the impact of such selection in other Nile tilapia rearing environment, i.e. in large groups in earthen ponds or in recirculated systems. The selection environment, small groups reared in aquarium was rather different from the classical rearing environment and it is thus questionable how important the interactions between genetics and environment are.

This work provides favourable results for future experiment with more family to estimate genetic parameters and accuracy estimated breeding values in keeping inbreeding to an acceptable level.

5. Conclusion

Improving FCR in fish through genetics is feasible. After only1.5 equivalent generations of selection for this trait, a phenotypic divergence of 12 %, and a breeding value difference of 3% were observed between more efficient and less efficient lines, in a proof of concept selective breeding programme with a reduced number of fish and families phenotyped in each generation. If confirmed at a larger scale, selection for FCR could be greatly improved in Nile tilapia, substantially and positively influencing the sustainable production of this fish species, the second fish species consumed in the world. The transfer of video-assisted technology to improve FCR will probably need adaptation to potential interspecific difference in feeding behaviour, size or social interaction.

Author contributions

HDV designed the experiment; HDV and VD performed the experiment; HDV and MV analysed the data; HDV, PH and MV wrote the manuscript. All authors read and approved the final manuscript. All authors contributed to the article and approved the submitted version.

Funding

This publication was made possible through support provided by the project DADA-EAT, partly supported by the European Marine and fisheries Fund (EMFF) and French government.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

We thank Marc Canonne (CIRAD) for his help and support in maintaining the experimental infrastructure.

6. References

Aggrey, S., Ankra-Badu, G., Marks, H., 2003. Effect of long-term divergent selection on growth characteristics in Japanese quail. Poultry Science 82, 538–542. https://doi.org/10.1093/ps/82.4.538

Aubin, J., Papatryphon, E., Van der Werf, J.H.J., Chatzifotis, S., 2009. Assessment of the environmental impact of carnivorous finfish production systems using life cycle assessment. Journal of Cleaner Production 17, 354–361.

Barria, A., Benzie, J.A.H., Houston, R.D., de Koning, D.J., de Verdal, H., 2021. Genomic selection and genome-wide association study for feed-efficiency related traits in a farmed Nile tilapia (*Oreochromis niloticus*) population. Frontiers in Genetics 12, 1796. https://doi.org/10.3389/fgene.2021.737906

Bentsen, H.B., Gjerde, B., Eknath, A.E., de Vera, M.S.P., Velasco, R.R., Danting, J.C., Dionisio, E.E., Longalong, F.M., Reyes, R.A., Abella, T.A., Tayamen, M.M., Ponzoni, R.W., 2017. Genetic improvement of farmed tilapias: Response to five generations of selection for increased body weight at harvest in Oreochromis niloticus and the further

472 impact of the project. Aquaculture 468, 206–217.
473 https://doi.org/10.1016/j.aquaculture.2016.10.018
474 Besson, M., de Boer, I.J.M., Vandeputte, M., van Arendonk, J.A.M., Quillet, E., Komen, H.,
475 Aubin, J., 2017. Effect of production quotas on economic and environmental values of
476 growth rate and feed efficiency in sea cage fish farming. PLoS ONE 12, e0173131.
477 https://doi.org/doi:10.1371/journal. pone.0173131
478 Besson, M., Allal, F., Chatain, B., Vergnet, A., Clota, F., Vandeputte, M., 2019. Combining
479 Individual Phenotypes of Feed Intake With Genomic Data to Improve Feed Efficiency
480 in Sea Bass. Frontiers in Genetics 10, 1–14. https://doi.org/10.3389/fgene.2019.00219
481 Bolivar, R.B., Newkirk, G.F., 2002. Response to within family selection for body weight in
482 Nile tilapia (Oreochromis niloticus) using a single-trait animal model. Aquaculture,
483 Genetics in Aquaculture VII 204, 371–381. https://doi.org/10.1016/S0044-
484 8486(01)00824-9
485 Cai, J., Zhou, X., Yan, X., Lucente, D., Lagana, C., 2019. Top 10 species groups in global
486 aquaculture 2017 12.
487 Campo, J.L., Rodríguez, M., 1990. Relative efficiency of selection methods to improve a ratio
488 of two traits in Tribolium. Theoret. Appl. Genetics 80, 343–348.
489 https://doi.org/10.1007/BF00210070
490 Charo-Karisa, H., Komen, H., Rezk, M.A., Ponzoni, R.W., van Arendonk, J.A.M., Bovenhuis,
491 H., 2006. Heritability estimates and response to selection for growth of Nile tilapia
492 (Oreochromis niloticus) in low-input earthen ponds. Aquaculture 261, 479–486.
493
494 Chavanne, H., Janssen, K., Hofherr, J., Contini, F., Haffray, P., Komen, H., Nielsen, E.E.,
495 Bargelloni, L., 2016. A comprehensive survey on selective breeding programs and

496 seed market in the European aquaculture fish industry. Aquaculture International 24,
497 1287-1307. https://doi.org/10.1007/s10499-016-9985-0.
498 Coward, K., Bromage, N.R., 2000. Reproductive physiology of female tilapia broodstock.
499 Reviews in Fish Biology and Fisheries 10, 1–25.
500 https://doi.org/10.1023/A:1008942318272
501 de Verdal, H., Mekkawy, W., Lind, C.E., Vandeputte, M., Chatain, B., Benzie, J.A.H., 2017.
502 Measuring individual feed efficiency and its correlations with performance traits in
503 Nile tilapia, Oreochromis niloticus. Aquaculture 468, 489–495.
504 de Verdal, H., Komen, H., Quillet, E., Chatain, B., Allal, F., Benzie, J.A.H., Vandeputte, M.,
505 2018a. Improving feed efficiency in fish using selective breeding: A review. Reviews
506 in Aquaculture 10, 833–851. https://doi.org/10.1111/raq.12202
507 de Verdal, H., Vandeputte, M., Mekkawy, W., Chatain, B., Benzie, J.A.H., 2018b.
508 Quantifying the genetic parameters of feed efficiency in juvenile Nile tilapia
509 Oreochromis niloticus. BMC genetics 19, 105. https://doi.org/10.1186/s12863-018-
510 0691-y
511 de Verdal, H., O'Connell, C.M., Mekkawy, W., Vandeputte, M., Chatain, B., Bégout, M.L.,
512 Benzie, J.A.H., 2019. Agonistic behaviour and feed efficiency in juvenile Nile tilapia
513 Oreochromis niloticus. Aquaculture 505, 271–279.
514 https://doi.org/10.1016/j.aquaculture.2019.02.067
515 Doyle, R W, Herbinger. C.M., 1994. The Use of DNA Fingerprinting for High-Intensity,
516 within-Family Selection in Fish Breeding. Proceedings 5th World Congress, Genetics
517 Applied to Livestock Production, 364-371.
518 Emmerson, D.A., 1997. Commercial approaches to genetic selection for growthand feed
519 conversion in domestic poultry. Poultry Science 76, 1121–1125.

520 Falconer, D.S., MacKay, T.F.C., 1996. Introduction to quantitative genetics. 4th edition.
521 Longman Scientific & Technical, Burnt Mill, Harlow, United Kingdom.
522 Grima, L., Quillet, E., Boujard, T., Robert-Granié, C., Chatain, B., Mambrini, M., 2008.
523 Genetic variability in residual feed intake in rainbow trout clones and testing of
524 indirect selection criteria. Genetic Selection Evolution 40, 607–624.
525 Gunsett, F.C., 1984. Linear index selection to improve traits defined as ratios. Journal of
526 Animal Science 59, 1185–1193.
527 Gunsett, F.C., 1987. merit of utilizing the heritability of a ratio to predict the genetic change
528 of a ratio. Journal of Animal Science 65, 936–942.
529 Jobling, M., Koskela, J., 1996. Interindividual variations in feeding and growth in rainbow
530 trout during restricted feeding and in a subsequent period of compensatory growth.
531 Journal of Fish Biology 49, 658–667.
532 Jobling, M., Covès, D., Damsgard, B., Kristiansen, H.R., Koskela, J., Petusdottir, T.E., Kadri,
533 S., Gudmundsson, O., 2001. Techniques for measuring feed intake, in: Houlihan, D.,
534 Boujard, T., Jobling, M. (Eds.), Food Intake in Fish. Wiley-Blackwell, pp. 49–87.
535 Kause, A., Tobin, D., Dobly, A., Houlihan, D., Martin, S., Mäntysaari, E.A., Ritola, O.,
536 Ruohonen, K., 2006. Recording strategies and selection potential of feed intake
537 measured using the X-ray method in rainbow trout. Genetic Selection Evolution 38,
538 389–409.
539 Kause, A., Kiessling, A., Martin, S.A.M., Houlihan, D., Ruohonen, K., 2016. Genetic
540 improvement of feed conversion ratio via indirect selection against lipid deposition in
541 farmed rainbow trout (*Oncorhynchus mykiss* Walbaum). Br J Nutr 116, 1656–1665.
542 https://doi.org/10.1017/S0007114516003603

543 Knap, P.W., Kause, A., 2018. Phenotyping for Genetic Improvement of Feed Efficiency in
544 Fish: Lessons From Pig Breeding. Front. Genet. 9.
545 https://doi.org/10.3389/fgene.2018.00184
546 Kovac, M., Groeneveld, E., Garcia-Cortez, A., 2008. VCE 6 User's manual. version 6.0.2.
547 Lin, Y.C., 1980. Relative efficiency of selection methods for improvement of feed efficiency.
548 Journal of Dairy Science 63, 491–494.
549 Lin, C.Y., Aggrey, S.E., 2013. Incorporation of economic values into the component traits of
550 a ratio: Feed efficiency. Poultry Science 92, 916–922. https://doi.org/10.3382/ps.2012-
551 02688
552 Mélard, C., Baras, E., Desprez, D., 1997. Compensatory growth of Nile tilapia Oreochromis
553 niloticus. Fourth International Symposium on Tilapia in Aquaculture 1, 178-185.
554 Misztal, I., Tsuruta, S., Lourenco, D., Aguilar, I., Legarra, A., Vitezica, Z., 2014. Manual for
555 BLUPF90 family of programs 125.
556 Neumaier, A., Groeneveld, E., 1998. Restricted maximum likelihood of covariances in sparse
557 linear models. Genetic Selection Evolution 30, 13–26.
558 Nicholas, F.W., 1980. Size of population required for artificial selection. Genetic Research
559 35, 85–105.
560 Pélabon, C., Albertsen, E., Rouzic, A.L., Firmat, C., Bolstad, G.H., Armbruster, W.S.,
561 Hansen, T.F., 2021. Quantitative assessment of observed vs. predicted responses to
562 selection. Evolution n/a. https://doi.org/10.1111/evo.14284
563 Ponzoni, R.W., Hamzah, A., Tan, S., Kamaruzzaman, N., 2005. Genetic parameters and
564 response to selection for live weight in the GIFT strain of Nile tilapia (Oreochromis
565 niloticus). Aquaculture 247, 203–210.
566 Ponzoni, R.W., Hong Nguyen, N., Khaw, H.L., Hamzah, A., Abu Bakar, K.R., Yee, H.Y.,
567 2011. Genetic improvement of Nile tilapia (Oreochromis niloticus) with special

568 reference to the work conducted by the WorldFish Center with the GIFT strain.
569 Reviews in Aquaculture 3, 27–41. https://doi.org/3
570 Quinton, C.D., Kause, A., Koskela, J., Ritola, O., 2007. Breeding salmonids for feed
571 efficiency in current fishmeal and future plant-based diet environment. Genetic
572 Selection Evolution 39, 431–446.
573 R Development Core Team, 2018. R: A Language and Environment for Statistical
574 Computing. Vienna, Austria : the R Foundation for Statistical Computing. ISBN: 3-
575 900051-07-0. Available online at http://www.R-project.org/.
576 Rodde, C., Chatain, B., Vandeputte, M., Trinh, T.Q., Benzie, J.A.H., de Verdal, H., 2020. Can
577 individual feed conversion ratio at commercial size be predicted from juvenile
578 performance in individually reared Nile tilapia Oreochromis niloticus? Aquaculture
579 Reports.
580 Rodde, C., Vandeputte, M., Trinh, T.Q., Douchet, V., Canonne, M., Benzie, J.A.H., de
581 Verdal, H., 2021. The Effects of Feed Restriction and Isolated or Group Rearing on
582 the Measurement of Individual Feed Intake and Estimation of Feed Conversion Ratio
583 in Juvenile Nile Tilapia (Oreochromis niloticus) for Selective Breeding Purposes.
584 Front. Genet. 11, 596521. https://doi.org/10.3389/fgene.2020.596521
585 Sorensen, D.A., Kennedy, B.W., 1986. Analysis of selection experiments using mixed model
586 methodology. J Anim Sci 63, 245–258. https://doi.org/10.2527/jas1986.631245x
587 Thodesen (Da-Yong Ma), J., Rye, M., Wang, Y.-X., Li, S.-J., Bentsen, H.B., Gjedrem, T.,
588 2013. Genetic improvement of tilapias in China: Genetic parameters and selection
589 responses in growth, pond survival and cold-water tolerance of blue tilapia
590 (Oreochromis aureus) after four generations of multi-trait selection. Aquaculture 396–
591 399, 32–42. https://doi.org/10.1016/j.aquaculture.2013.02.010

592 Thodesen, J., Rye, M., Wang, Y.-X., Bentsen, H.B., Gjedrem, T., 2012. Genetic improvement
593 of tilapias in China: Genetic parameters and selection responses in fillet traits of Nile
594 tilapia (Oreochromis niloticus) after six generations of multi-trait selection for growth
595 and fillet yield. Aquaculture 366–367, 67–75.
596 https://doi.org/10.1016/j.aquaculture.2012.08.028
597 Thodesen, J., Rye, M., Wang, Y.-X., Li, S.-J., Bentsen, H.B., Yazdi, M.H., Gjedrem, T., 2013.
598 Genetic improvement of tilapias in China: Genetic parameters and selection responses
599 in growth, survival and external color traits of red tilapia (Oreochromis spp.) after four
600 generations of multi-trait selection. Aquaculture 416–417, 354–366.
601 Vandeputte, M., Puledda, A., Tyran, A.S., Bestin, A., Coulombet, C., Bajek, A., Baldit, G.,
602 Vergnet, A., Allal, F., Bugeon, J., Haffray, P., 2017. Investigation of morphological
603 predictors of fillet and carcass yield in European sea bass (Dicentrarchus labrax) for
604 application in selective breeding. Aquaculture 470, 40–49.
605 Vandeputte, M., Bugeon, J., Bestin, A., Desgranges, A., Allamellou, J.-M., Tyran, A.-S.,
606 Allal, F., Dupont-Nivet, M., Haffray, P., 2019. First Evidence of Realized Selection
607 Response on Fillet Yield in Rainbow Trout Oncorhynchus mykiss, Using Sib
608 Selection or Based on Correlated Ultrasound Measurements. Front. Genet. 0.
609 https://doi.org/10.3389/fgene.2019.01225
610 https://doi.org/10.1016/j.aquaculture.2016.12.014
611 Webb, A.J., King, J.W.B., 1983. Selection for improved food conversion ratio on ad libitum
612 group feeding in pigs. Animal Science 37, 375–385.
613 https://doi.org/10.1017/S0003356100001987
614
615
616

Table 1 – Basic statistics: Number measured (N), Mean± standard deviation (StdDev), minimum (Min), maximum (Max) and raw coefficient of variation (CV) of all the traits measured during the experiment.

Trait[1]	N	Mean ± StdDev	Min - Max	CV (%)
BWi	1,043	12.3 ± 4.29	4.15 - 28.2	34.9
BWf	1,030	14.9 ± 5.13	4.58 - 32.9	34.4
DWG	1,012	0.38 ± 0.19	0.003 – 1.03	48.3
DFI	1,010	0.34 ± 0.13	0.08 – 0.70	38.2
FCR	997	0.97 ± 0.35	0.30 - 2.49	36.3

[1]BWi : body weight in g at the beginning of the FCR measurement period; BWf: body weight in g at the end of the FCR measurement period; DWG: daily body weight gain in g during the FCR measurement period; DFI: daily feed intake in g during the FCR measurement period; FCR: feed conversion ratio measured as the ratio between DFI and DWG.

Table 2 –Phenotypic mean (± standard deviation) and average estimated breeding values (EBV, in italics) of all the traits measured during the experiment for each generation and line. Phenotypic values (Pheno) are on untransformed data, estimated breeding values on transformed data (square root for DWG and DFI, natural logarithm for BWi, BWf and FCR)

Generation	Line		BWi[1]	BWf	DWG	DFI	FCR
0	Base pop	Pheno	14.2 ± 4.54	17.1 ± 5.27	0.41 ± 0.15	0.41 ± 0.12	1.06 ± 0.31
		EBV	*0.001*	*0.001*	*0.001*	*0.001*	*0.000*
1	FCR+	Pheno	10.6 ± 2.94	13.1 ± 3.62	0.35 ± 0.18	0.28 ± 0.10	0.88 ± 0.35
		EBV	*-0.002*	*-0.007*	*-0.017*	*-0.007*	*0.009*
2	FCR+	Pheno	10.4 ± 3.49	12.0 ± 4.04	0.27 ± 0.16	0.26 ± 0.10	1.08 ± 0.43
		EBV	*-0.008*	*-0.013*	*-0.025*	*-0.010*	*0.012*
1	FCR-	Pheno	12.1 ± 3.66	15.1 ± 4.52	0.42 ± 0.19	0.32 ± 0.11	0.85 ± 0.30
		EBV	*0.031*	*0.030*	*0.019*	*0.005*	*-0.008*
2	FCR-	Pheno	11.8 ± 4.93	14.6 ± 6.10	0.40 ± 0.23	0.33 ± 0.13	0.95 ± 0.37
		EBV	*0.059*	*0.063*	*0.052*	*0.030*	*-0.017*

[1]BWi: body weight at the beginning of the FCR measurement period; BWf: body weight at the end of the FCR measurement period; DWG: daily body weight gain during the FCR measurement period; DFI: daily feed intake during the FCR measurement period; FCR: feed conversion ratio measured as the ratio between DFI and DWG.

637

638 Table 3 – Estimates (± standard error) of heritability (highlighted in grey, on the diagonal),
639 genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for
640 measured traits. DWG and DFI were square-root transformed, BWi, BWf, FCR were log-
641 transformed

Trait[1]	BWi	BWf	DWG	DFI	FCR
BWi	**0.53 ± 0.07**	**0.99 ± 0.003**	**0.71 ± 0.09**	**0.75 ± 0.06**	-0.15 ± 0.21
BWf	0.98	**0.48 ± 0.07**	**0.79 ± 0.06**	**0.81 ± 0.05**	-0.26 ± 0.20
DWG	0.58	0.74	**0.27 ± 0.07**	**0.94 ± 0.04**	**-0.69 ± 0.16**
DFI	0.56	0.66	0.75	**0.41 ± 0.07**	-0.43 ± 0.25
FCR	-0.25	-0.38	-0.68	-0.05	**0.10 ± 0.05**

642 [1]BWi : body weight at the beginning of the FCR measurement period; BWf: body weight at
643 the end of the FCR measurement period; DWG: daily body weight gain during the FCR
644 measurement period; DFI: daily feed intake during the FCR measurement period; FCR: feed
645 conversion ratio measured as the ratio between DFI and DWG. Bold indicates that the
646 estimate significantly differs from zero.

Figures

Figure 1- Selective breeding scheme performed to develop divergent lines selected for their low (FCR- in orange) and high (FCR+ in blue) FCR.

Figure 2 – LSmeans (± standard error) of DWG, DFI and FCR according to the line (FCR+ in black, FCR- in grey) and the generation (0 to 2). Error bars represents the standard error of the LSmeans. Asterisks show the significant difference between lines at each generation.

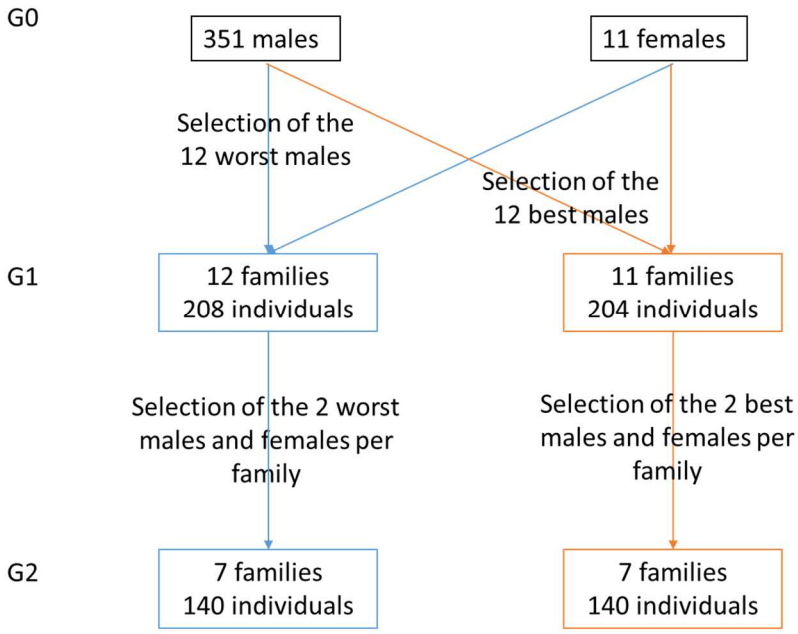
G0
351 males
11 females
Selection of the
12 worst males
Selection of the
12 best males
G1
12 families
208 individuals
11 families
204 individuals
Selection of the 2 worst
males and females per
family
Selection of the 2 best
males and females per
family
G2
7 families
140 individuals
7 families
140 individuals

Figure 1

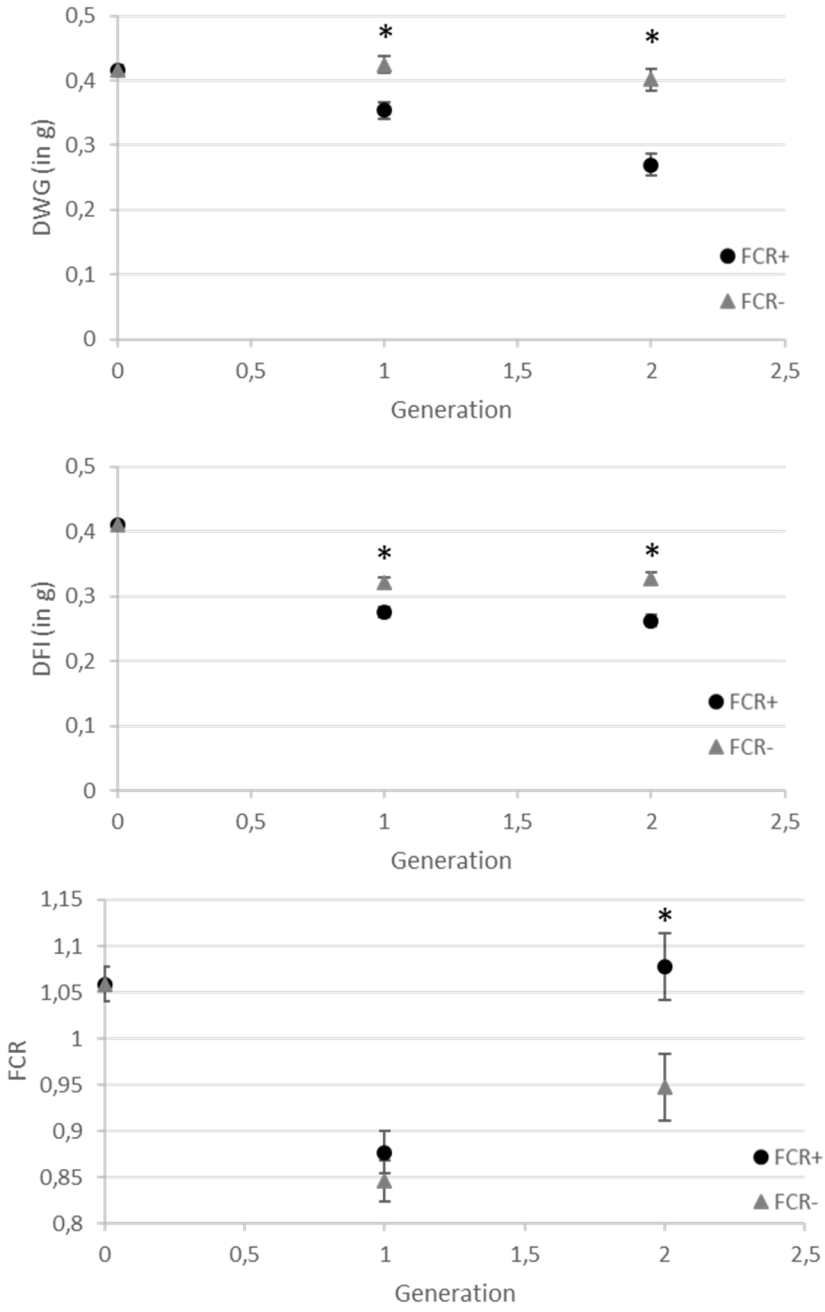
DWG (in g)
0,5
0,4
0,3
0,2
0,1
0
0
0,5
1
1,5
2
2,5
Generation
FCR+
FCR-
*
*
DFI (in g)
0,5
0,4
0,3
0,2
0,1
0
0
0,5
1
1,5
2
2,5
Generation
FCR+
FCR-
*
*
FCR
1,15
1,1
1,05
1
0,95
0,9
0,85
0,8
0
0,5
1
1,5
2
2,5
Generation
FCR+
FCR-
*

Figure 2