

1 Genomic prediction for commercial traits using univariate and  
2 multivariate approaches in Nile tilapia (*Oreochromis niloticus*)

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14

## 15 Abstract

### 16 Background

17 *Over the past three decades, Nile tilapia industry has grown into a significant*  
18 *aquaculture industry spread over 120 tropical and sub-tropical countries around the*  
19 *world accounting for 7.4% of global aquaculture production in 2015. Across species,*  
20 *genomic selection has been shown to increase predictive ability and genetic gain,*  
21 *also extending into aquaculture. Hence, the aim of this paper is to compare the*  
22 *predictive abilities of pedigree- and genomic-based models in univariate and*  
23 *multivariate approaches, with the aim to utilize genomic selection in a Nile tilapia*  
24 *breeding program. A total of 1444 fish were genotyped (48,960 SNP loci) and*  
25 *phenotyped for body weight at harvest (BW), fillet weight (FW) and fillet yield (FY).*  
26 *The pedigree-based analysis utilized a deep pedigree, including 14 generations.*  
27 *Estimated breeding values (EBVs and GEBVs) were obtained with traditional*  
28 *pedigree-based (PBLUP) and genomic (GBLUP) models, using both univariate and*  
29 *multivariate approaches. Prediction accuracy and bias were evaluated using 5*  
30 *replicates of 10-fold cross-validation with three different cross-validation approaches.*  
31 *Further, impact of these models and approaches on the genetic evaluation was*  
32 *assessed based on the ranking of the selection candidates.*

### 33 Results

34 *GBLUP univariate models were found to increase the prediction accuracy and*  
35 *reduce bias of prediction compared to other PBLUP and multivariate approaches.*  
36 *Relative to pedigree-based models, prediction accuracy increased by ~20% for FY,*  
37 *>75% for FW and >43% for BW. GBLUP models caused major re-ranking of the*  
38 *selection candidates, with no significant difference in the ranking due to univariate or*  
39 *multivariate GBLUP approaches. The heritabilities using multivariate GBLUP models*

40 *for BW, FW and FY were  $0.19 \pm 0.04$ ,  $0.17 \pm 0.04$  and  $0.23 \pm 0.04$  respectively. BW*  
41 *showed very high genetic correlation with FW ( $0.96 \pm 0.01$ ) and a slightly negative*  
42 *genetic correlation with FY ( $-0.11 \pm 0.15$ ).*

### 43 *Conclusion*

44 *Predictive ability of genomic prediction models is substantially higher than for*  
45 *classical pedigree-based models. Genomic selection is therefore beneficial to the*  
46 *Nile tilapia breeding program, and it is recommended in routine genetic evaluations*  
47 *of commercial traits in the Nile tilapia breeding nucleus.*

## 48 Background

49 Over the past three decades, Nile tilapia (*Oreochromis niloticus*) industry has grown  
50 into a significant aquaculture industry spread over 120 tropical and sub-tropical  
51 countries around the world accounting for 7.4% of global production in 2015 [1]. Nile  
52 tilapia has also been called the “aquatic chicken” [2] as it is well-suited for  
53 aquaculture in wide range of trophic and ecological adaptations, from backyards to  
54 intensive cages. Since the early days, the industry has recognized the potential  
55 gains from selective breeding and the challenge was to develop a strain, suitable for  
56 production across varieties of production environments. This led to the establishment  
57 of the Genetically Improved Farmed Tilapia (GIFT) base strain in early 1990s by the  
58 crossing of 8 different Nile tilapia strains from Africa and Asia [3]. This GIFT strain  
59 has been widespread over the world and serves as the base in majority of the  
60 farmed Nile tilapia. GenoMar Supreme Tilapia (GST®) strain was derived from GIFT  
61 and has undergone 27 generations of selection for growth, fillet yield and  
62 robustness.

63 For a long time, the aquaculture breeding industry has relied on pedigree information  
64 for genetic improvement, but in the last half-decade, top international breeding  
65 companies have started to use routine genomic selection and other genomic  
66 technologies in their genetic improvement programs for Atlantic salmon [4], catfish  
67 [5], common carp [6] and rainbow trout [7]. Tilapia has two genome assemblies [8,9],  
68 five linkage maps of varying resolutions constructed using different types of markers  
69 [10–14] and two recent 50K SNP-Arrays [14,15]. With these recent developments in  
70 SNP-Arrays and HD linkage maps being supported by the commercial industries, it is  
71 believed that this has opened a new door of the genomic era in Nile tilapia also.

72 Genomic selection helps to utilise the within- and between-family variation in the  
73 population, even for sib-evaluated traits. For such traits, the pedigree-based classical  
74 selection methods are just able to utilise between-family variation [16]. Across  
75 species, including aquaculture, genomic selection methods has been shown to  
76 increase the predictive ability and genetic gain by deriving more accurate breeding  
77 values [17,18]. Hence, the first aim of this paper is to perform genetic analysis using  
78 either genomic and pedigree-based information in univariate and multivariate  
79 statistical models for the commercial traits in Nile tilapia. The second objective is to  
80 compare the predictive abilities of the pedigree- and genomic-based models.

## 81 [Methodology](#)

### 82 [Experimental design and rearing procedure](#)

83 The study was carried out on generation 26 of the GST® strain of Nile tilapia, which  
84 is a continuation of the GIFT program [3]. Each generation of GST® consists of 8  
85 batches that follow a revolving breeding scheme where males from batch  $n$  are  
86 mated to females from batch  $n-1$ . This way only about 30 families are produced in  
87 each batch, significantly reducing the age difference within a batch compared to  
88 spawning all the 250 families in a generation at once. The families in one batch were  
89 created by mating the selected parents in a 1:1 mating design, where one male and  
90 one female were placed in a small breeding hapa. After mating, eggs were collected,  
91 and the families were kept separate until hatching.

92 After hatching, 40 fries were randomly selected from each family and pooled  
93 together, which were then reared in a nursery pond for 4 weeks and treated with  
94 hormones to produce an all-male population, mimicking the normal practice in

95 commercial operations. After the nursery stage, they were then transferred to larger  
96 pond for a 30 week grow-out period.



98 Figure 1: Dates showing different stages of lifecycle in Nile tilapia. The population  
99 were reared in 8 different batches during 2017-18

#### 100 Harvesting

101 Fish from the experiment were grown for the entire 30-week period without any  
102 selection. At the end, all the surviving fish were slaughtered and measured for three  
103 commercial traits: body weight at harvest (BW), fillet weight (FW) and fillet yield (FY).

#### 104 Pedigree

105 True pedigree was unavailable, since all the offspring were reared communally  
106 immediately after hatching to reduce the maternal environmental and/or full-sib  
107 and/or tank effects. Thus, lateral fin clips were obtained for microsatellite parentage  
108 assignment and pedigree was constructed as described in [19]. This is the routine  
109 pedigree construction method in the commercial production of GST® strain and  
110 micro-satellite constructed pedigrees were available for the last 14 generations (i.e.  
111 pedigree back to generation 12 with the records of 110,900 fish). Since one male  
112 was mated to 1 female in each of the 253 families, only full-sibs were present in the  
113 dataset.

#### 114 Genotypes:

115 Lateral fin clips were obtained for DNA extraction during harvesting. DNA extraction  
116 was done at BioBank (<https://biobank.no/>) and sent to CIGENE lab, NMBU  
117 (<https://cigene.no/>) for genotyping using Oni150® array [14]. The raw dataset  
118 contained 58,466 SNPs. Of these, 50,275 SNPs (86.75%) were classified as  
119 “PolyHighResolution” (formation of three distinctive clusters of homozygous and  
120 heterozygous genotype) and “NoMinorHom” (formation of two distinctive clusters  
121 with one homozygous genotype missing) using Axiom Analysis Suite Software [20].



122 These high-resolution genotypes were further cleaned for low minor allele frequency  
123 (MAF <0.05) using PLINKv1.07 [21] and the remaining 48,960 SNPs (83.74%) were  
124 used for genomic analysis. Similarly, 3 animals were filtered for low genotyping call  
125 rate (individual call rate <0.9) and only the 1444 animals with the phenotype,  
126 pedigree and genotypes were used for further statistical analysis. The final dataset  
127 contained 188 full-sib families with an average of 7.68 offspring per full-sib family  
128 (range 1 to 15; standard deviation = 4.48).

### 129 *Statistical analysis*

130 Statistical analysis for three commercial traits was performed using two different  
131 approaches, namely univariate and multivariate, and two different models (PBLUP  
132 and GBLUP) within each approach; as described below

#### 133 *Univariate approach*

134 DMUv6 [22] was used to fit mixed linear models, using REML to estimate the  
135 variance components, heritability and the breeding values. Univariate BLUP models  
136 were used for the three commercial Nile tilapia traits described as;

$$137 \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

138 where,  $\mathbf{y}$  is the vector of phenotypes,  $\mathbf{b}$  is the vector of fixed effects that account for  
139 batch (7 levels), difference of age during harvesting (15 levels), filleter for the traits  
140 FW and FY (2 levels);  $\mathbf{u}$  is the vector of random genetic effects;  $\mathbf{e}$  is the vector of the  
141 residual errors; and  $\mathbf{X}$  and  $\mathbf{Z}$  are the corresponding design matrices for the fixed and  
142 random effects. For PBLUP, the distributional assumption of the random effects was  
143 multivariate normal, with mean zero and

$$\text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 \\ 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

144 Where,  $\sigma_a^2$  and  $\sigma_e^2$  are additive genetic variances and residual variance respectively,  
 145 **A** is the numerator relationship matrix obtained using micro-satellite generated  
 146 pedigree and **I** is an identity matrix. The phenotypic variance was calculated as  
 147  $\sigma_p^2 = \sigma_a^2 + \sigma_e^2$  and the heritability ( $h^2$ ) was calculated as the ratio of  $\sigma_a^2$  and  $\sigma_p^2$ .

148 For GBLUP, the numerator relationship matrix **A** was replaced with the genomic  
 149 relationship matrix (**G**). The **G** matrix was constructed [23] as follows:

$$\mathbf{G} = \frac{\mathbf{H}\mathbf{H}'}{\sum_1^i \sum 2p_i(1 - p_i)}$$

150 where **H** is a centered marker matrix, the sum in the denominator is over all loci and  
 151  $p_i$  is the allelic frequency at locus  $i$ .

### 152 *Multivariate approach*

153 Multivariate models were built on the univariate models and are described as;

$$\begin{bmatrix} \mathbf{y}_{\text{BW}} \\ \mathbf{y}_{\text{FW}} \\ \mathbf{y}_{\text{FY}} \end{bmatrix} = \begin{bmatrix} \mathbf{X} & 0 & 0 \\ 0 & \mathbf{X} & 0 \\ 0 & 0 & \mathbf{X} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{BW}} \\ \mathbf{b}_{\text{FW}} \\ \mathbf{b}_{\text{FY}} \end{bmatrix} + \begin{bmatrix} \mathbf{Z} & 0 & 0 \\ 0 & \mathbf{Z} & 0 \\ 0 & 0 & \mathbf{Z} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{\text{BW}} \\ \mathbf{u}_{\text{FW}} \\ \mathbf{u}_{\text{FY}} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{BW}} \\ \mathbf{e}_{\text{FW}} \\ \mathbf{e}_{\text{FY}} \end{bmatrix}$$

154 where, the symbols represent the same vectors as described in the univariate  
 155 analysis, with the subscripts BW, FW and FY denoting the traits the vectors are  
 156 associated with. For PBLUP models in multivariate approach, the distributional  
 157 assumption of the random effects are structured as;

$$\begin{bmatrix} \mathbf{u}_{\text{BW}} \\ \mathbf{u}_{\text{FW}} \\ \mathbf{u}_{\text{FY}} \end{bmatrix} \sim N \left( \mathbf{0}, \begin{bmatrix} \sigma_{a_{\text{BW}}}^2 & \sigma_{a_{\text{BW,FW}}} & \sigma_{a_{\text{BW,FY}}} \\ \sigma_{a_{\text{BW,FW}}} & \sigma_{a_{\text{FW}}}^2 & \sigma_{a_{\text{FW,FY}}} \\ \sigma_{a_{\text{BW,FY}}} & \sigma_{a_{\text{FW,FY}}} & \sigma_{a_{\text{FY}}}^2 \end{bmatrix} \right) \otimes \mathbf{A}$$

$$\begin{bmatrix} \mathbf{e}_{\text{BW}} \\ \mathbf{e}_{\text{FW}} \\ \mathbf{e}_{\text{FY}} \end{bmatrix} \sim N \left( \mathbf{0}, \begin{bmatrix} \sigma_{e_{\text{BW}}}^2 & \sigma_{e_{\text{BW,FW}}} & \sigma_{e_{\text{BW,FY}}} \\ \sigma_{e_{\text{BW,FW}}} & \sigma_{e_{\text{FW}}}^2 & \sigma_{e_{\text{FW,FY}}} \\ \sigma_{e_{\text{BW,FY}}} & \sigma_{e_{\text{FW,FY}}} & \sigma_{e_{\text{FY}}}^2 \end{bmatrix} \right) \otimes \mathbf{I}$$

158 The symbols represent the same variance components as described in the  
159 univariate analysis with the subscripts denoting the trait the variance components  
160 are associated with. The elements  $\sigma_{a_{Tr1,Tr2}}$  and  $\sigma_{e_{Tr1,Tr2}}$  denotes the genetic and  
161 residual covariances between two traits, with the subscripts.

162 For GBLUP models, the numerator relationship matrix was replaced by the genomic  
163 relationship matrix (**G**).

#### 164 Predictive ability

165 Comparison between the predictive ability of PBLUP and GBLUP models was  
166 performed by both univariate and multivariate approaches using 5 replicates of 10-  
167 fold cross validation in different cross-validation methods. 10-fold cross validation  
168 allows us to mask the phenotypes of ~10% of animals, which is predicted using the  
169 phenotypes of the rest of the 90% phenotypes.

170 Three different cross-validation methods were used to quantify the prediction  
171 accuracy of the models. With the “random cross-validation” method, the dataset was  
172 randomly divided into 10 batches, predicting one batch at a time using the  
173 phenotypes of the remaining 9 batches. Similarly, with “within family cross-validation”  
174 method, the phenotypes of (as close as possible to) 10% of the animals within a full-  
175 sib family are masked and phenotypes of the unmasked members of the family and  
176 other families are used to predict the masked phenotype. This scenario is important  
177 with the sib-testing strategy usually done for invasively measured traits like FY.  
178 Finally, with the “across family cross-validation” method, the phenotypes of all the  
179 animals in a full-sib are masked and the phenotypes of the individuals from other  
180 families are used to predict the masked phenotype. This scenario is appropriate

181 where phenotype collection for all the population is very expensive and we measure  
182 the phenotypes in few families only or in different cohorts of fish.

183 Predictive ability of the GBLUP and PBLUP models were calculated as the  
184 Pearson's correlation between GEBVs or EBVs of all predicted phenotypes adjusted  
185 for the fixed effects in one replicate. Results were averaged over the 5 replicates.  
186 The obtained mean value of correlation was converted to the expected prediction  
187 accuracy by dividing the correlation coefficient by the square root of the heritability.  
188 Heritabilities obtained from multivariate genomic models were used to assess the  
189 prediction accuracy. Standard error of prediction accuracy was calculated as [24];

$$\frac{1 - \text{prediction accuracy}^2}{\sqrt{\text{No. of validation animals} - 1}}$$

190 In addition, regression coefficient of phenotypes adjusted for the fixed effects on  
191 GEBVs or EBVs were used as to assess the bias of the prediction. Theoretically, a  
192 regression coefficient of 1 indicates unbiased prediction, whereas the value <1  
193 indicates inflation of GEBV or EBV and >1 indicates deflation of GEBV or EBV. The  
194 mean value and standard error of the mean of the regression coefficient was  
195 calculated from the five replicates.

196

197 **Results**

198 **Descriptive Statistics**

199 Descriptive statistics for the three traits: BW, FW and FY are presented in Table 1.  
200 The mean ( $\pm$  standard deviation) phenotypic measurements for BW, FW and FY  
201 were 817.37 ( $\pm$  261.11) g, 300.01( $\pm$  107.34) g and 36.40% ( $\pm$  2.5%), respectively.  
202 The coefficient of variation ranged from about 7% for FY to as high as 36% for fillet  
203 weight. The scatterplot and phenotypic correlations between the traits are presented  
204 in Supplementary Figure S1.

205 **Table 1:** Descriptive statistics for the three commercial traits of Nile tilapia

	Units	Min	Max	Median	Mean	Mean (SE)	SD	CV%
<b>BW</b>	g	138.70	1893.70	780.30	817.37	6.87	261.11	31.95
<b>FW</b>	g	39.10	754.60	284.25	300.01	2.82	107.34	35.78
<b>FY</b>	%	20.83	46.64	36.56	36.40	0.07	2.50	6.90

206 **Note:** Min is the smallest phenotype, Max is the largest phenotype, SD is the  
207 standard deviation, SE is the standard error and CV is the coefficient of variation  
208 expressed as percentage. The traits BW represents body weight at harvest, FW  
209 represents fillet weight and FY represents fillet yield.

210 **Estimates of heritabilities**

211 Estimates of variance components and heritabilities using univariate and multivariate  
212 approaches are presented in Table 2, whereas the genetic and phenotypic  
213 correlation between the traits obtained using multivariate approach is presented in  
214 Table 3. All the traits were found to have medium heritabilities. GBLUP models were  
215 found to give lower heritability estimates compared to PBLUP models in both

216 univariate and multivariate approaches. Heritabilities using multivariate approach  
 217 were slightly higher for the traits BW and FW, compared to univariate approach.

218 The results indicated a slightly unfavorable genetic correlation between FY and BW  
 219 (albeit non-significantly different from 0). The genetic correlations with the trait FY  
 220 was higher for PBLUP models in multivariate approach, compared to GBLUP.

221 Table 2: Heritabilities and variance parameters for PBLUP and GBLUP models using  
 222 univariate and multivariate approaches.

Approaches	Traits	Model	$\sigma_a^2$	$\sigma_e^2$	$\sigma_p^2$	$h^2$	se	$\sigma_a^{2*}$	$h^{2*}$
<b>Univariate</b>	BW	PBLUP	7131	25394	32525	0.22	0.06	7262	0.22
	BW	GBLUP	5467	26742	32209	0.17	0.04	5437	0.17
	FW	PBLUP	1230	4076	5306	0.23	0.06	1253	0.24
	FW	GBLUP	842	4384	5226	0.16	0.04	837	0.16
	FY	PBLUP	1.80	3.69	5.49	0.33	0.07	1.83	0.33
	FY	GBLUP	1.21	4.13	5.34	0.23	0.04	1.21	0.23
<b>Multivariate</b>	BW	PBLUP	9279	24068	33348	0.28	0.06	9449	0.28
	BW	GBLUP	6168	26366	32534	0.19	0.04	6134	0.19
	FW	PBLUP	1488	3930	5419	0.27	0.06	1516	0.28
	FW	GBLUP	899	4369	5268	0.17	0.04	894	0.17
	FY	PBLUP	1.82	3.68	5.50	0.33	0.07	1.85	0.33
	FY	GBLUP	1.26	4.11	5.37	0.23	0.04	1.25	0.23

223 **Note:**  $\sigma_a^{2*}$  and  $h^{2*}$  are the additive genetic variance and heritability corrected to the  
 224 base generation as per [25]. The additive variance was multiplied by mean of  
 225 corresponding diagonal relationship matrix – mean of the corresponding relationship  
 226 matrix and the heritability was calculated based on this variance parameter. The

227 mean of the diagonal and whole matrix for **A** were 1.018322 and 0, and for **G** were  
 228 0.9951903 and 0.000689405 respectively.

229 **Table 3:** Heritabilities, phenotypic and genetic correlation using multivariate  
 230 approach.

PBLUP	BW	FW	FY	GBLUP	BW	FW	FY
<b>BW</b>	<b>0.28</b> ± 0.06	0.96 ± 0.01	0.23 ± 0.02	<b>BW</b>	<b>0.19</b> ± 0.04	0.96 ± 0.01	0.23 ± 0.02
<b>FW</b>	0.96 ± 0.01	<b>0.27</b> ± 0.07	0.47 ± 0.02	<b>FW</b>	0.96 ± 0.01	<b>0.17</b> ± 0.04	0.47 ± 0.02
<b>FY</b>	-0.04 ± 0.17	0.23 ± 0.16	<b>0.33</b> ± 0.07	<b>FY</b>	-0.11 ± 0.15	0.19 ± 0.15	<b>0.23</b> ± 0.04

231 Note: The values on the left (4x4 square) are the estimates from PBLUP models,  
 232 whereas the values on the right (4x4 square) are based on GBLUP. Heritabilities are  
 233 presented in the diagonal, genetic correlations below the diagonal and phenotypic  
 234 correlations above the diagonal. The standard errors are presented after ± sign.

### 235 [Impact on the genetic evaluation](#)

236 The correlation of the EBVs and/or GEBVs using two different approaches, namely  
 237 univariate and multivariate, and two different models (PBLUP and GBLUP) within  
 238 each approach are presented in Figure 2.

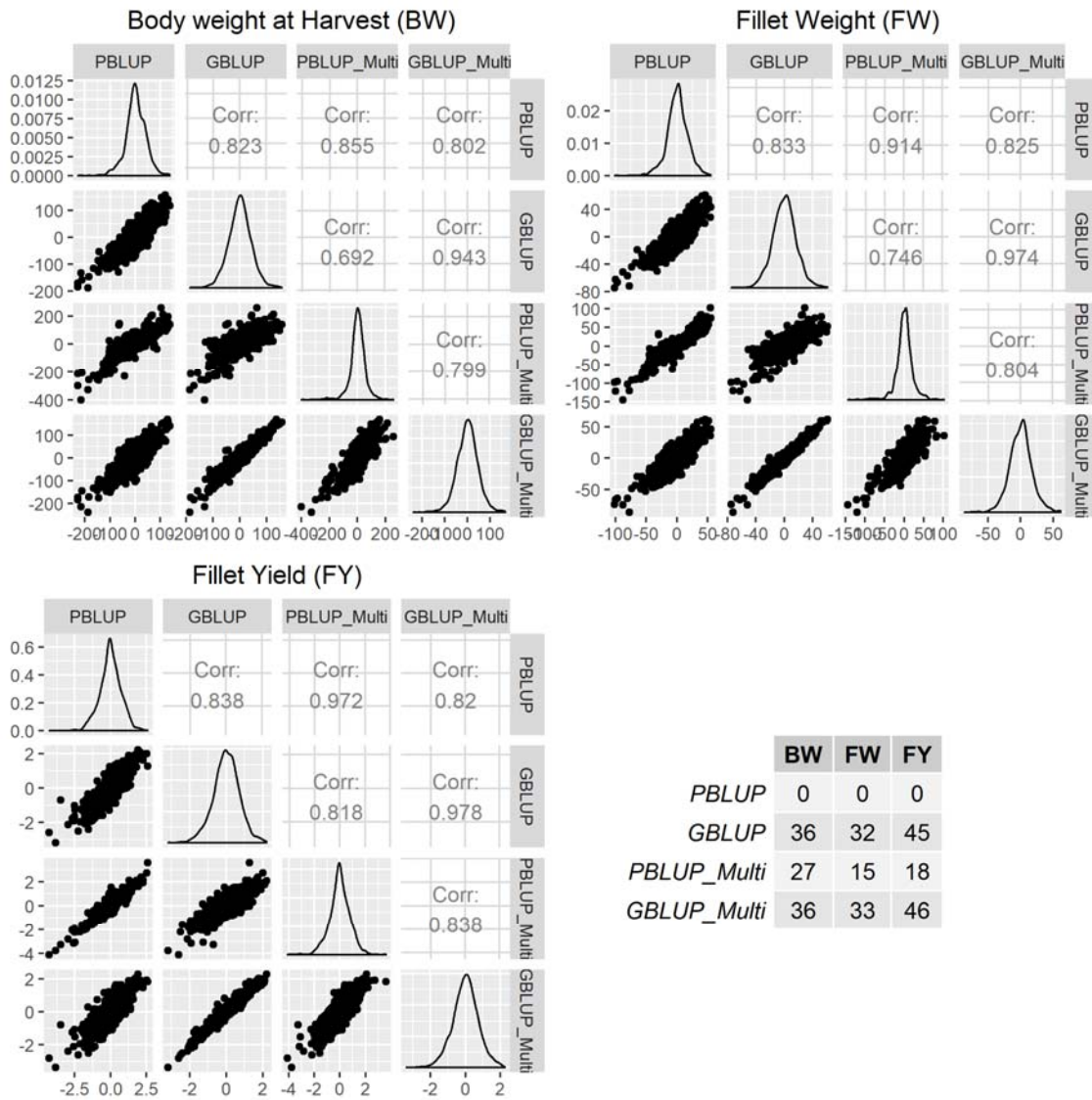
239 In general, the use of multivariate vs. univariate approaches affected the ranking of  
 240 the breeding values, with correlations between EBVs/GEBVs ranging 0.86 to 0.98.

241 There was less reranking among GBLUP univariate and multivariate approaches,  
 242 compared with the PBLUP. Further, models within the same approach (i.e. PBLUP  
 243 and GBLUP models within univariate and multivariate approaches) for three different  
 244 traits revealed similar correlation in the range of 0.80 to 0.83. In overall, FY had

245 higher correlation between models and approaches and BW had lowest correlation  
246 between models and approaches. Thus, FY showed the least differences and BW  
247 showed the major differences in the genetic evaluation by the use of different models  
248 and approaches, based on correlation of the EBVs. A lower correlation may indicate  
249 that careful selection of the model and approach has to be done, so that the genetic  
250 gain can be maximised.

251 These differences in the estimated breeding values also brought the change in the  
252 ranking of the 100 best animals (see table in the bottom right axis in Figure 2). Using  
253 PBLUP univariate approach as the reference group, major changes in the top 100  
254 animals were observed using different models (PBLUP and GBLUP) and  
255 approaches (univariate and multivariate). GBLUP was less sensitive to  
256 univariate/multivariate modelling and the changes were more pronounced when  
257 going from PBLUP to GBLUP, which is consistent with the outcomes of the  
258 correlation of the breeding values. No major differences in the list of top 100 animals  
259 were observed using GBLUP univariate and GBLUP multivariate approaches, as  
260 these approaches also had the highest correlation of the estimated breeding values.  
261 These observations were similar across all the traits.





262

263 Figure 2: Impact of different models and approaches on the genetic evaluation. The  
 264 models with univariate approach are shown as PBLUP and GBLUP, whereas the  
 265 models with multivariate approaches have suffix “multi” in the models. The first three  
 266 figures show the scatterplot and correlation between the EBVs and GEBVs for 3  
 267 different traits. The table on the bottom right axis shows the impact of model choice  
 268 for the top 100 animals after ranking the animals based on EBVs or GEBVs. Since  
 269 the comparison is based on PBLUP model in univariate approach, the 0 for PBLUP  
 270 is by definition.

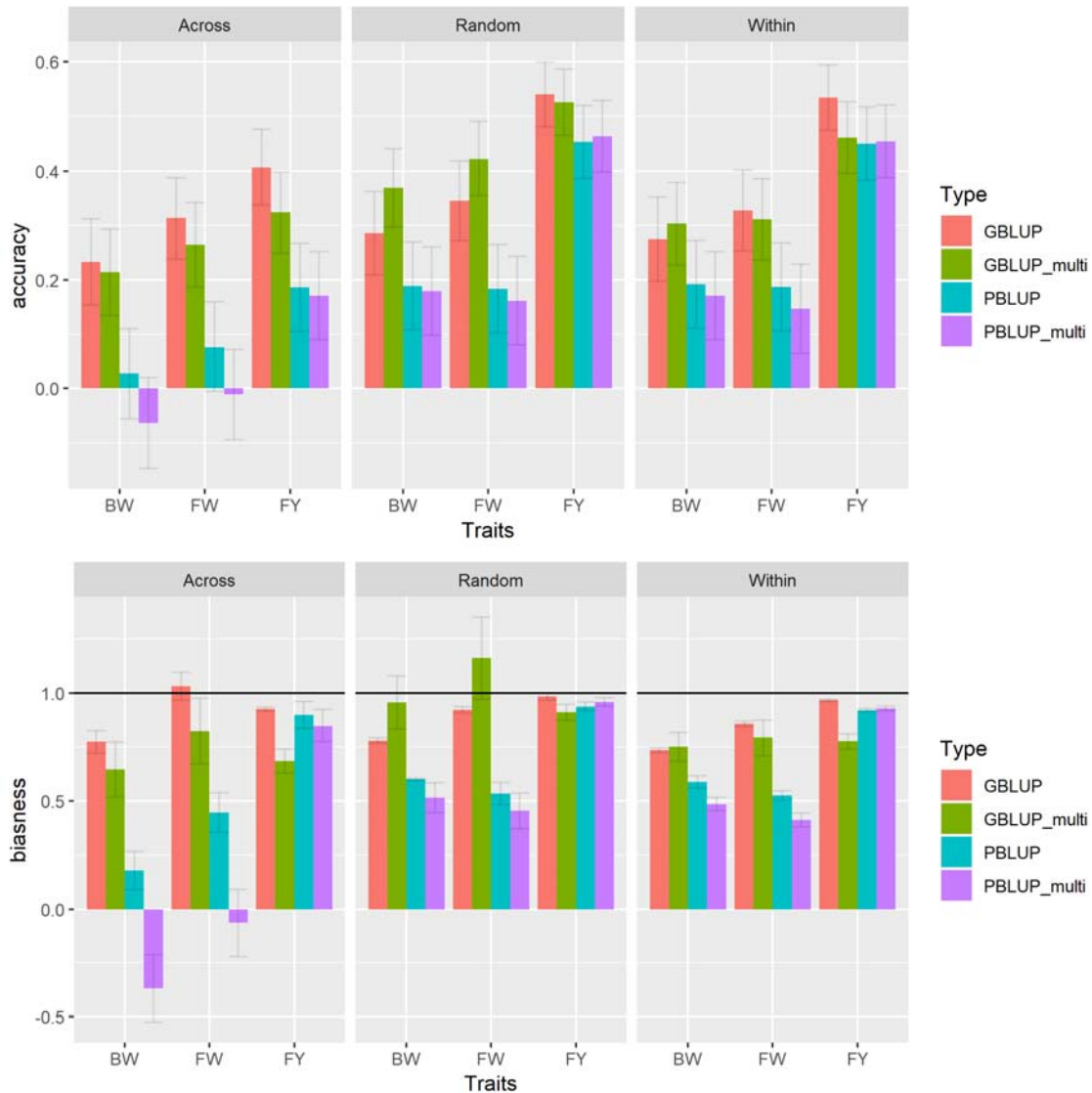
## 271 Prediction accuracy

272 Estimates for the prediction accuracy in different cross-validation methods are  
273 presented in Figure 3. As expected, prediction accuracy was lower in “across-family”  
274 and similar in “random” and “within family” cross validation methods, for all three  
275 traits. Prediction accuracies using PBLUP models in across-family cross validation  
276 methods were found to be very low, while GBLUP models increased the prediction  
277 accuracy by 119% for FY to as high as 759% for BW. This huge increase in  
278 accuracy is expected, as the PBLUP models have very limited potential for across-  
279 family prediction in this material (no half-sibs available). For both random and within-  
280 family cross-validation methods, GBLUP models were found to increase the  
281 prediction accuracy by ~20% for FY, >75% for FW and >43% for BW, compared to  
282 PBLUP models in univariate approach. Similar differences were found using PBLUP  
283 and GBLUP models in multivariate approach. In the majority of the cases (GBLUP  
284 and PBLUP), going from univariate to multivariate models did not improve prediction  
285 accuracy. However, for traits BW and FW in random cross-validation approach, a  
286 GBLUP multivariate model was found to slightly increase the prediction accuracy. In  
287 contrast, PBLUP multivariate models performed worse than univariate models, even  
288 giving negative prediction accuracy for BW and FY using the across-family cross  
289 validation method.

## 290 Prediction bias

291 Estimates for the prediction bias using PBLUP vs GBLUP models in different cross-  
292 validation methods are presented in Figure 3. Pedigree based models were found to  
293 inflate the estimated breeding values compared to GBLUP models. The prediction  
294 bias showed similar pattern to the prediction accuracy across all the models and  
295 methods. The PBLUP multivariate models were negatively biased for BW and FW in

296 the across model cross-validation method.



297

298 Figure 3: First figure showing accuracy of prediction and second one showing  
299 prediction bias. “Across family cross-validation” method is presented as “across”,  
300 “within family cross-validation” method as “within” and “random cross-validation”  
301 method as “random. The models with univariate approach are shown as PBLUP and  
302 GBLUP, whereas the models with multivariate approaches have suffix “multi” in the  
303 models. The lines in the bar charts represent  $\pm$  standard errors.

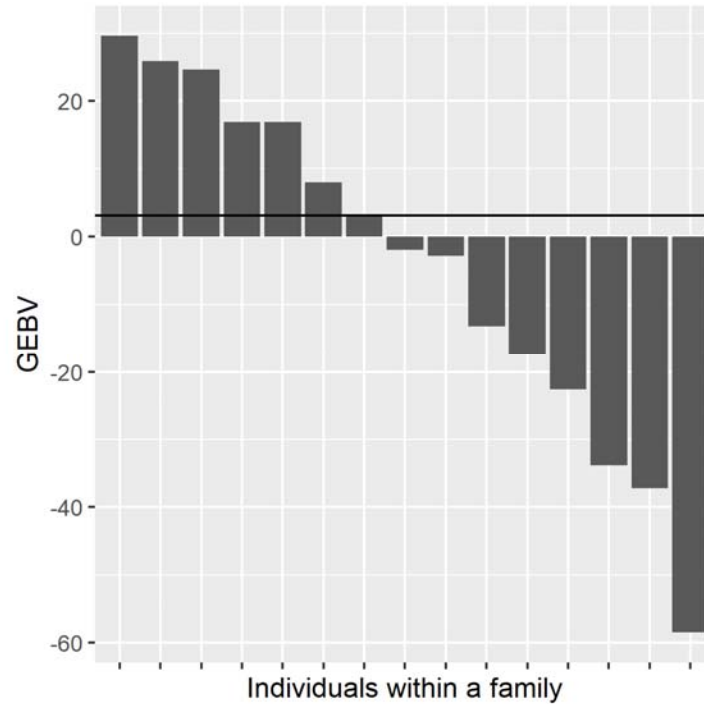
304

## 305 Discussion

306 Genomic heritabilities have previously been reported for the commercial traits in Nile  
307 tilapia [26,27], but these studies fail to report the predictive abilities of the genomic  
308 and pedigree based models. In another study, increase in prediction accuracies was  
309 indeed reported for Nile tilapia [28], based on univariate single-step GBLUP models.  
310 Thus, to the best of our knowledge this is the first report comparing prediction  
311 accuracy using both univariate and multivariate approaches with GBLUP models and  
312 pedigree-based models in Nile tilapia. Thereby, these are the first reports on  
313 heritabilities and correlations using multivariate genomic models.

## 314 Genomic selection increases prediction accuracy in Nile tilapia

315 The increase in the prediction accuracy using GBLUP models, is due to the more  
316 accurate construction of the relationship matrices with better estimation of the  
317 Mendelian sampling effects using genomics (Figure 4). Using PBLUP models all full-  
318 sibs (without own phenotype) have identical EBVs, which is the parental average.  
319 Whereas, GBLUP can capture the Mendelian segregation among the full-sibs and  
320 the putatively best (unphenotyped) candidates within a full-sib family can be  
321 identified. This explains the very low accuracy (near to 0) in across-family cross-  
322 validation methods using PBLUP. Thus, the benefit of using genomics to predict the  
323 breeding values is very significant for invasive traits, where the breeding values of  
324 the animals in different full-sib families might have to be predicted based on  
325 phenotypes on other full-sib families. For example, disease challenge test in a  
326 handful of full-sib families due to expensive phenotype measurement.



327

328 Figure 4: Distribution of GEBVs (g) for BW in a family with 15 offspring. The cross-  
329 validation using PBLUP predicted only one breeding value (shown as a horizontal  
330 line) for all the full-sibs. Whereas the GBLUP predicted different breeding values for  
331 all the full-sibs based on Mendelian segregation.

332 The lower prediction accuracy for the traits BW and FW, compared to FY across all  
333 the models and approaches may be related to the heritability and the genetic  
334 architecture of the trait [29,30]. The expected accuracy of prediction has been given  
335 as [31,32]:

$$r^2 = \frac{Nh^2}{Nh^2 + 4N_eL}$$

336 where, r is the accuracy of prediction, N is the number of animals in the training set,  
337  $h^2$  is the heritability,  $N_e$  is the effective population size and L is the genome size in  
338 Morgan. Given the same training set and phenotypes being measured in the same  
339 animals, accuracy of prediction decreases with the decrease in heritability [33]. Joshi

340 et al. [19,34] have shown the substantial contribution of non-additive genetic effects  
341 and maternal effects for BW and substantial contribution of maternal effects for FW  
342 in Nile tilapia. Thus, for BW and FW, maternal effect and non-additive genetic effects  
343 are part of the genetic architecture, but the model used cannot separate these  
344 effects in our data, which may affect predictive ability. Whereas, the trait FY was  
345 shown to favor simple additive model, like the model we have used in this study.  
346 Hence using the model corresponding to its genetic architecture might have  
347 increased the prediction accuracy for FY, compared to BW and FW. The mating  
348 design used in the current study made it impossible to fit complicated models to  
349 separate non-additive and maternal effects.

350 Further, the prediction accuracy for these commercial traits is somewhat lower than  
351 that have been reported in Nile tilapia [28] and other species [5,6]. One of the  
352 reasons for this might be our data structure. In the study we have 20 full-sib families  
353 with only one observation per family and a few more families with only 2 or 3 animals  
354 per family. Prediction of the phenotypes for the individuals in these families based on  
355 the information from other families gives lower accuracy, which might have affected  
356 our overall value of the prediction accuracy. Another reason for overall lower  
357 prediction accuracy might be the sample size. It has been stated that  $2NeL$  number  
358 of animals are required to achieve accuracies higher than 0.88 [33], and the  
359 accuracy decreases with the decrease in the sample size and vice versa. In GST®  
360 strain of Nile tilapia, this suggests that we need at least 2304 animals ( $Ne= 83$   
361 (unpublished result) and  $L= 14.70$  [14]) in training set for higher prediction accuracy,  
362 but this study uses 1444 samples.

363 [Multivariate approaches were not found to increase the prediction accuracy in Nile](#)  
364 [tilapia](#)

365 Multivariate approaches account for the genetic and phenotypic correlation between  
366 the traits and are supposed to increase the prediction accuracy and decrease the  
367 bias [35] depending on the genetic correlation between the traits. On one hand,  
368 various studies have shown an increase in prediction accuracy for traits with low  
369 heritabilities, when used together with a correlated trait of higher heritability [36]. On  
370 the other hand, it has also been shown that when the genetic correlation between  
371 the traits is low (like BW and FY in our case), there is no improvement in accuracy  
372 using multivariate approaches over univariate approaches [37,38]. No consistent  
373 differences in the prediction accuracy was found between univariate and multivariate  
374 GBLUP models which might also be related to the types of traits used in this study.  
375 The three traits studied are not independent, as FW is a part of BW, while FY is a  
376 ratio of the two former traits.

377 The obvious question now is; which method is the best and should be used in the  
378 evaluation in the current Nile tilapia breeding program. Theoretically, the models  
379 giving best prediction value, minimising mean-squared error and giving unbiased  
380 estimates of the EBVs should be used [42,43], whereas practically this also depends  
381 on the selection schemes, for example the selection among the single generation of  
382 individuals, like in Nile tilapia, depends only in the prediction accuracy, as they share  
383 the common mean and bias is not concern. Whereas, it is strongly recommended to  
384 consider bias in the selection of the prediction model, if the aim is to compare  
385 between multiple generations and to predict the genetic potential of the young  
386 animals [39].



### 387 [Estimates of variance components and heritabilities](#)

388 Our study showed moderate heritabilities for BW, FW and FY, which have also been  
389 reported in previous studies [19,26,28,34,44–46]. Similarly, the genetic and  
390 phenotypic correlations between the traits are similar to what has been published  
391 earlier [47], but there are some studies indicating a positive genetic correlation  
392 between BW and FY [44,46], while our estimates are negative. Negative genetic  
393 correlation between BW and FY suggests a relatively larger increase in head, gut  
394 and/or skeleton tissues with increasing body size, which is undesirable. Few studies  
395 recognize that the variance parameters and the corresponding heritabilities obtained  
396 using different relationship matrices, for example numerator and genomic  
397 relationship matrices in PBLUP and GBLUP models in our study, are different  
398 estimates for different base population. Hence, re-scaling of the relationship matrices  
399 to the same base population [25] is necessary to make sense of the comparison as it  
400 has been shown that the large differences in the pedigree and genomic based  
401 heritabilities can be accounted for by this difference [25,34,48]. Hence, it will not be  
402 wise to compare our estimates of heritabilities with the published estimates without  
403 converting them to the same base (these kinds of estimates are difficult to come by  
404 for Nile tilapia).

405 The difference in heritabilities using PBLUP and GBLUP models were high in the  
406 univariate approach compared to the multivariate approach. Comparing the  
407 heritabilities based on different approaches, FY gave similar heritabilities for both  
408 multivariate and univariate approaches, given the same model. For BW and FW,  
409 multivariate models gave slightly higher (but not significantly different) heritabilities  
410 compared to univariate models, whereas PBLUP models gave generally higher  
411 heritabilities compared to GBLUP models. This suggests that the markers used in



412 GBLUP was not able to capture all genetic variance (especially if the family structure  
413 is not that strong).

414 An earlier study [34] has also shown the higher pedigree based heritabilities  
415 compared to genomics for these three traits (which were scaled to the same base)  
416 for the population out-crossed from generation 22 of the GST® strain (in this study  
417 we are using generation 27 of the GST® strain). Comparing the value of the  
418 estimates, heritabilities obtained using GBLUP models in our study were similar to  
419 theirs, whereas the heritabilities using PBLUP in our study was lower than theirs.

#### 420 **CONCLUSION:**

421 Genomic selection is beneficial to the Nile tilapia breeding program as it increases  
422 prediction accuracy and gives more unbiased estimates of the breeding values  
423 compared to the pedigree. It is recommended to use an univariate GBLUP approach  
424 in the routine genetic evaluation for the commercial traits in Nile tilapia.

425

426 **List of abbreviations**

**Acronym Full Form**

<b>BW</b>	Body Weight at Harvest
<b>FW</b>	Fillet Weight
<b>FY</b>	Fillet Yield
<b>GBLUP</b>	Genomic Best Linear Unbiased Prediction
<b>GST</b>	GenoMar Supreme Tilapia
<b>G(EBVs)</b>	(Genomic) Estimated Breeding Values
<b>PBLUP</b>	Pedigree Best Linear Unbiased Prediction

427 **Declarations**

428 **Ethics approval and consent to participate:** Not applicable

429 **Consent for publication:** Not applicable

430 **Availability of data and material**

431 The data used in the study are from commercial family material. This information  
432 may be made available to non-competitive interests under conditions specified in a  
433 Data Transfer Agreement. Requests to access these datasets should be directed to  
434 Alejandro Tola Alvarez: alex@genomar.com.

435 **Competing interests**

436 The authors declare that they have no competing interests.

437 **Funding:** Not applicable

438 **Authors' contributions**

439 RJ did the statistical analysis and wrote the initial draft of the paper, AS contributed  
440 to the draft and was responsible for genotyping and microsatellite-based pedigree

441 construction, MDV supervised the experiments, phenotyping and collection of fin  
442 samples in the farm, ATA conceived the study, JØ supported in the statistical  
443 analysis and all authors contributed to the discussion of the results and writing of the  
444 final version of the paper.

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446

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448

449

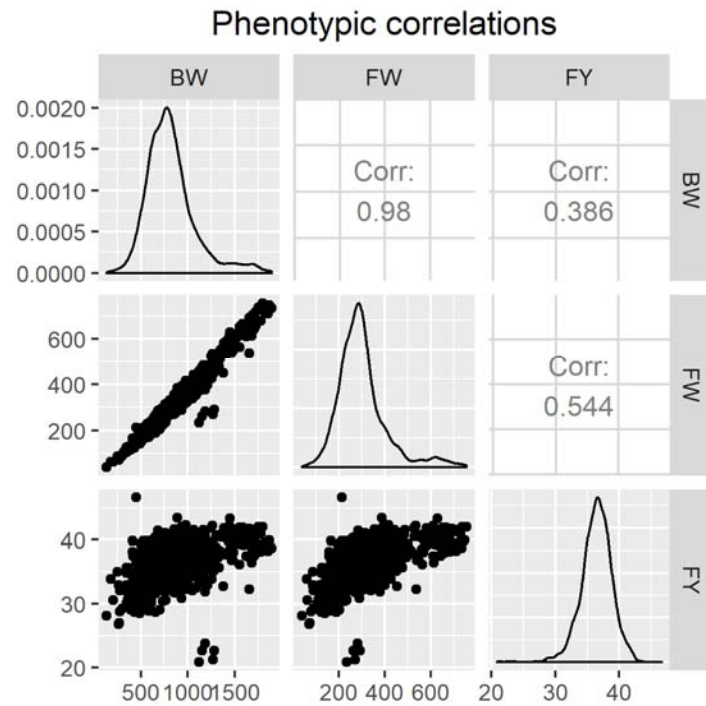
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- 576
- 577

578 **Supplementary**



579

580 Figure S1: Scatterplots and correlation between different phenotypes. Phenotypic  
581 correlation between the traits is not corrected for fixed effects in the plot. Table 3  
582 shows the phenotypic correlation corrected for fixed effects.