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Interactive effects of genotype x environment on the live weight of GIFT Nile tilapias

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ABSTRACT

In this paper, the existence of a genotype x environment interaction for the average daily weight in GIFT Nile tilapia (*Oreochromis niloticus*) in different regions in the state of Paraná (Brazil) was analyzed. The heritability results were high in the uni-characteristic analysis: 0.71, 0.72 and 0.67 for the cities of Palotina (PL), Floriano (FL) and Diamond North (DN), respectively. Genetic correlations estimated in bivariate analyzes were weak with values between 0.12 for PL-FL, 0.06 for PL and 0.23 for DN-FL-DN. The Spearman correlation values were low, which indicated a change in ranking in the selection of animals in different environments in the study. There was heterogeneity in the phenotypic variance among the three regions and heterogeneity in the residual variance between PL and DN. The direct genetic gain was greater for the region with a DN value gain of 198.24 g/generation, followed by FL (98.73 g/generation) and finally PL (98.73 g/generation). The indirect genetic gains were lower than 0.37 and greater than 0.02 g/generation. The evidence of the genotype x environment interaction was verified, which indicated the phenotypic heterogeneity of the variances among the three regions, weak genetic correlation and modified rankings in the different environments.

Key words: *Oreochromis niloticus*, fish, genetic gain, heritability, genetic correlation.

INTRODUCTION

The projection by 2024 of world fishery production is 191 million tons, in which aquaculture will be the main responsible and that can reach production of 96 million tons, one of the productive sectors of accelerated growth, surpassing fishing in 2023 (OECD/FAO 2015). Nile tilapia, *Oreochromis niloticus*, is one of the most promising fish species for fish farming because it presents characteristics of zootechnical interest, it has tasty meat and great acceptance by the consumer market, its body growth

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is characterized by increased weight, length, height and circumference as a function of age (Rodrigues Filho et al. 2011).

According to data from the Brazilian Institute of Geography and Statistics (IBGE 2014), Brazil reached a production of more than 367 thousand tons of fish in 2014 and is one of the seven largest producers of tilapia in the world, being this species one of the between three most cultivated on the planet (ABPA 2014). Despite this commercial production potential, until a few years ago, there was no appropriate fish selection program. This fact can be led to intense national inbreeding because of the use of the small parental population that decreased the growth rate and the produce quality standards. In 2005, however, a partnership between the Universidade Estadual de Maringá and the WorldFish Center in Malaysia introduced approximately 600 breeder fish from a program based on 20 years of selection (Lupchinski et al. 2008).

Promising results were obtained in some of the fish breeding programs with the growth rate showing gains of up to 15% at every generation (Ponzoni et al. 2005). Is very important, when choosing the species, consider some background knowledge on fish production and reproduction and proper raising conditions, environmental conditions and market. However, for achieving high gains is establishing a base population for a genetic improvement program in aquaculture, possessing great genetic variability, which can be obtained from the use of various subpopulations (Hilsdorf et al. 2014).

The appropriate selection of the best animals for the population requires accurate estimates of the genetic parameters and components of covariance. Based on Resende (2007), estimates of the variance components are essential for achieving three goals: (i) the genetic control of the traits to design efficient breeding strategies, (ii) prediction of genetic values of the applicants to the selection program, and (iii) the sample size, the methods for estimating the genetic parameters and the selective accuracy.

In Brazil, the large territory and the various fish raising systems have made it necessary to evaluate the genotype x environment interaction because the phenotype is a consequence of the genotype under the influence of the environment, for this reason it is important to know if there is significant when there are several environments being tested (Ponzoni et al. 2008). Similar experiments were performed in Malaysia, where the responses from the GIFT tilapia were evaluated in ground ponds and net-cages (Khaw et al. 2009a); and in the Philippines under seven environmental conditions with different agro-climatic conditions and raising systems (Eknath et al. 2007).

The evaluation of this interaction is also important because it can promote genetic, phenotypic and environmental variations that affect the estimates of these parameters based on the environment where outstanding genotypes in one region cannot match the same ranking in another region. The genotype is assessed using several techniques and can interact with environmental factors that affect the responses and influences the animal phenotype (Baye et al. 2011). If this interaction is not considered, there will be modifications in the animal ranking selected under different environments (Cerón-Muñoz et al. 2004) with inefficient and biased selection when the aim of the genetic gain is not achieved. The current experiment was aimed at evaluating the effect of the genotype x environment interaction on the GIFT Nile tilapia live weight in three regions of the Paraná State (Brazil) using Bayesian inference.

MATERIALS AND METHODS

Records from 1,132 fish (males and females) were collected from the data bank of the fifth generation (G5) of the tilapia breeding program at the Universidade Estadual de Maringá (UEM), Paraná

State, Brazil. First, the experiment started in the aquaculture system of the UEM, where fish from the fourth generation (G4) were mated to achieve the G5 generation and was responsible for raising siblings and half-siblings in the following regions of the Paraná State: Palotina, Floriano and Diamante do Norte counties. The mating proportion was two females to one male allotted in individual ground hapas measuring 1 m^3 under plastic film protection.

Every week, males and females were monitored to detect the ideal mating evidence: in males, an expanded urogenital opening and in females, a reddish urogenital opening with a swollen and soft ventral side that indicated the presence of eggs. Thus, males and females with the best characteristics were mated. Aggressive fish performance, hatching or any other improper fish performance in the hapas were always monitored to avoid progenitor losses and death during the reproduction season that lasted for approximately four months (from November 2011 to March 2012). Thereafter, the larvae stayed with the females during the entire reproductive season, and this period was proposed as the common environment of larvae culture (c). At the end of the reproduction season, all of the larvae were counted and kept apart. Shortly thereafter, groups (families) of siblings were divided and transferred into two hapas for raising the fingerlings that were randomly distributed to avoid bias within the pond. However, this procedure produced a common effect that was referred to as the "common effect of fingerlings" (w), which is the result of maintaining individuals from the same family from the reproductive season in the same hapas until transfer to the evaluation plots. When approximately 50 individuals of the same family had at least ten grams of live weight, they were numbered based on the passive integrated transponder (pit) tags in their visceral cavity. Seven days later, they were sent to the evaluation regions while maintaining the genetic connection among these three environmental conditions, where the brothers were distributed randomly getting representatives of each family in all evaluated environments.

A group of fish stayed in ground ponds with hapas measuring 200 m^3 in the Floriano Fisheries Experimental Station (UEM), where the average annual air temperature was approximately 21.9 °C. The second group was sent to Diamante do Norte County, where the average annual temperature was approximately 24 °C, and a third group of fish were grown in cage-nets measuring 600 m^3 set up in the watercourse of the Corvo River. Finally, the fourth group was sent to city of Palotina with the average annual air temperature was approximately 20.8 °C to grow in ground pond conditions.

A summary of the data set is reported in Table I. The quality of these data was monitored by the SAS® program (SAS Institute 2000), where outliers (less than 0.1%) were excluded to maintain the 1,132 fish. The live weight (g) and age (d) in the current experiment were collected from the fifth and last records taken from these animals.

TABLE I
Mean and standard deviation in every experimental region.

Region Counties		Animals number	Mean	SD
Floriano	LW	243	417.01	±137.18
Palotina		457	276.83	±90.51
Diamante		462	472.73	±214.03
Floriano	Age	243	333.37	±15.78
Palotina		427	320.84	±18.52
Diamante		462	337.13	±16.27

LW: Live weight (grams); age days.

The covariance components and genetic parameters for live weight (g) were estimated using Bayesian inferences with the Statistical program MTGSAM (Multiple Trait Gibbs Sampling in Animal Models) developed by Van Tassel and Van Vleck (1995). The animal model with fixed effects of sex, linear and quadratic effects of the covariate

age (d) was applied to the data set. Furthermore, additive genetic effects (a), common environmental effects of the larvae culture (c), common fingerlings environmental effects (w) and the residual effect were evaluated using the animal model for the uni-characteristic analysis as follows:

$$y = X\beta + Z_1 a + Z_2 c + Z_3 w + e,$$

in which y is the observation vector; X, Z_1, and Z_2, Z_3 are incidence matrices from the identified environmental effects; direct genetic effects; and the common environment of fingerlings and larvae culture, respectively. β is the sex effect vector, raising place, and age; *a, c, w* and *e* are, respectively, the vectors of the additive genetic effect, common environment of larvae culture, fingerlings and residual.

The model in the analysis of bi-characteristics was:

$$Y = \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Z_{1_1} & 0 \\ 0 & Z_{1_2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{2_1} & 0 \\ 0 & Z_{2_2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} Z_{3_1} & 0 \\ 0 & Z_{3_2} \end{bmatrix} \begin{bmatrix} w_1 \\ w_2 \end{bmatrix} = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \end{bmatrix},$$

where y1, y2 are observational vectors of live weight and the indices 1 and 2 are the experimental regions. X1 and X2 are the incidence matrices of sex and age effects in the vectors β1 and β2, correspondent to every region. Z_{1_1} and Z_{1_2} are incidence matrices from the additive genetic effects in the vectors a1 and a2. Z_{1_2} and Z_{2_2} are incidence matrices from common environmental effect of larvae culture in the vectors c1 and c2. Next, the matrices Z_{3_1} and Z_{3_2} are the incidence effects of common environment of fingerlings in the vectors w1 and w2. Finally, ε_1 and ε_2 are random error vectors associated with the vectors y1 and y2.

Based on *y, a, c, w* and *e* with conjunct multivariate normal distribution as

$$\begin{bmatrix} y \\ a \\ c \\ w \\ e \end{bmatrix} \sim NMV \left\{ \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}; \begin{bmatrix} V & Z_1 G & Z_2 C & Z_3 W & I_n \sigma_e^2 \\ GZ_1' & G & \varphi & \varphi & \varphi \\ CZ_2' & \varphi & C & \varphi & \varphi \\ CZ_3' & \varphi & \varphi & W & \varphi \\ I_n \sigma_e^2 & \varphi & \varphi & \varphi & I_n \sigma_e^2 \end{bmatrix} \right\};$$

where $V = Z_1 G Z_1' + Z_2 C Z_2' + Z_3 W Z_3' + R$, so that, for the bi-characteristics analysis $G = G_* \otimes A$,
where
A: is the parentage matrix; $\otimes$: is the Kronecker product; G: is the additive genetic covariance matrix:

$$G_* = \begin{bmatrix} \sigma_{a_1}^2 & \sigma_{a_1 a_2} \\ \sigma_{a_2 a_1} & \sigma_{a_2}^2 \end{bmatrix};$$

$$C = I_l \otimes C_*,$$

where
I_l is the identity matrix, with rank equal to the group of siblings number.
C_* is the covariance matrix from the common environmental effect of larvae culture (c), as

$$C_* = \begin{bmatrix} \sigma_{c1}^2 & 0 \\ 0 & \sigma_{c2}^2 \end{bmatrix};$$

$W = I_m \otimes W_*$, where

I_m is the identity matrix of rank equal to the hapas number of the fingerlings structure used every year.
W_* is the covariance matrix of the common environmental effect of fingerlings (w) as

$$W_* = \begin{bmatrix} \sigma_{w1}^2 & 0 \\ 0 & \sigma_{w2}^2 \end{bmatrix};$$

$$R = Ie \otimes R$$

I_e is the identity matrix with rank equal to the hapas number in the fingerlings structure used every year.
R is the covariance matrix of the residual effect:

$$R_* = \begin{bmatrix} \sigma_{e1}^2 & 0 \\ 0 & \sigma_{e2}^2 \end{bmatrix};$$

Uni- and bi-characteristics were analyzed combining the live weight from every region as distinct characteristics. Based on the diagnosis test described by Heidelberg and Welch (1983), the entire generating chain achieved convergence. The selection intensity was the same for males and females with approximate genetic gain in every generation of fish selection. The direct genetic gain was based on

$$\Delta G_{dir} = \frac{\overline{a_m} - \overline{a_f}}{2};$$

where

$\overline{a_m}$: genetic average of males; and $\overline{a_f}$: genetic average of females; The indirect gain was based on

$$\Delta G_{ind} = \frac{\sigma_{a1a2}}{\sigma_{a1}} . \Delta G_{dir}$$

where σ_{a1a2} = genetic covariance of characteristics of the environment 1 and 2; and σ_{a1} = additive genetic standard deviation of one characteristic in the environment 1.

The gain percentage (%) was calculated to identify the rate at which the indirect selection has participated in the direct selection:

$$\%Gains = \frac{\Delta G_{ind}}{\Delta G_{dir}}$$

The Spearman correlation were the estimates that were used to verify the animal ranking based on the genetic values predicted in bi-characteristic analysis thus to monitor the different ranks of the animals in every region (Palotina, Floriano and Diamante do Norte), and the Pearson correlation evaluated the level of association among the environments. These correlations were calculated from the predicted genetic values in the bi-characteristics analyses.

RESULTS AND DISCUSSION

Estimates with their credibility intervals (ICr) and the high-density regions (HPD) for the variance components of live weight (g) in three sites are shown in Table II. Heritability estimates (h^2) and genetic participation in phenotype expression from common environment to larvae culture (c^2) and fingerlings (w^2) are shown in Table III, both from the uni-characteristic analyses.

The bi-characteristics analyses in Table IV had posteriori means for the additive genetic variances and genetic correlation, residual and phenotypic with the credibility intervals and high-density region (all values were positive) for all three regions. The results in Table V indicate the values of heritability, credibility intervals and high-density regions.

The highest genetic variation of 37.629 was found in Diamante do Norte (DN), and the lowest of 6.244 was found in Palotina (PL) (Table II). Knowing that in both environments exist the same genetic representation, we can understand the greater genetic variation in DN environment as the environment that most favored the expression of the genetic potential of the animals. Rutten et al. (2005) reported an additive genetic variance from 1.481 to 2.778 from GIFT tilapia mated with other lines. Charo-Karisa et al. (2007) reported low estimates for additive genetic variation with weight of 782.8 g at the harvesting period. These results show the great genetic progress because of outstanding animals, and the genetic variation suggests continual weight gain (Ponzoni et al. 2005).

The differences in the "a posteriori" means for all of the parameters (Table II) were significant ($p < 0.05$) in all of the regions based on the analyses of Bayesian contrasts. These results show that the genetic expression among the several environments are different, and they indicate a genotype x environment interaction, being that the evaluated environments, presented variations on the production system (land farmed and network tank) and also management, each system kept the usually adopted routines (feed, number and times

TABLE II
Estimates of the variance components for live weight (g) from uni-characteristic analyses.

Site	Parameters	Means	ICr		HPD	
			Lower	Upper	Lower	Upper
PL	σ_a^2	6,244	2,616	9,203	2,790	9,350
	σ_c^2	280	74	836	48	678
	σ_w^2	241	76	580	51	502
	σ_e^2	1,892	624	3,717	508	3,536
	σ_y^2	8,657	6,553	10,720	6,508	10,650
FL	σ_a^2	13,679	6,454	20,500	6,281	20,245
	σ_c^2	634	171	1,88	114	1,527
	σ_w^2	585	169	1,594	114	1,329
	σ_e^2	3,942	1,347	7,740	1,080	7,278
	σ_y^2	18,841	14,26	24,040	14,053	23,801
DN	σ_a^2	37,629	14,24	61,360	13,569	60,553
	σ_c^2	1,519	418	4,524	289	3,679
	σ_w^2	1,438	433	3,591	280	3,07
	σ_e^2	14,968	4,237	27,420	3,736	26,653
	σ_y^2	55,556	42,09	70,650	41,019	69,382

Credibility intervals (ICr) and high-density region (HPD), $\boldsymbol{\sigma}_a^2$: additive genetic variance; $\boldsymbol{\sigma}_c^2$: environmental variance common to larvae culture; $\boldsymbol{\sigma}_w^2$: environmental variance common to fingerlings; $\boldsymbol{\sigma}_e^2$: residual variance; $\boldsymbol{\sigma}_y^2$: phenotypic variance.

TABLE III
Heritability estimates (h^2), participation of common environment of larvae culture (c^2) and common environment of fingerlings (w^2) in the phenotypic uni-characteristic analyses.

Region	Parameters	Means	ICr		HPD	
			Lower	Upper	Lower	Upper
PL	h^2	0.71	0.38	0.89	0.4	0.9
	c^2	0.03	0.01	0.09	0.01	0.07
	w^2	0.03	0.01	0.06	0.01	0.05
FL	h^2	0.72	0.42	0.89	0.4	0.9
	c^2	0.03	0.01	0.09	0.01	0.07
	w^2	0.03	0.01	0.08	0.01	0.05
DN	h^2	0.67	0.32	0.89	0.3	0.9
	c^2	0.03	0.01	0.07	0.004	0.06
	w^2	0.03	0.01	0.06	0.01	0.05

TABLE IV
Estimates from bi-characteristic analyses.

	Parameters	Means	ICr		HPD	
			Lower	Upper	Lower	Upper
FL-PL	σ_{a1}^2	13.641	6.384	20.400	6.341	20.356
	σ_{a2}^2	6.171	2.393	-9.314	2.507	9.409
	cov_{a12}	1.035	-4.887	6.770	-4.826	6.823
	r_{a12}	0.12	-0.5	0.6	-0.4	0.7
	r_{y12}	0.08	-0.37	0.5	-0.35	0.5
PL-DN	σ_{a1}^2	8.065	3.855	10.530	4.304	10.774
	σ_{a3}^2	46.170	18.490	67.610	19.243	68.205
	cov_{a13}	1.320	-11.860	14.380	-11.765	14.436
	r_{a13}	0.06	-0.5	0.6	-0.5	0.6
	r_{y13}	0.05	-0.4	0.5	-0.4	0.5
FL-DN	σ_{a2}^2	14.203	6.761	20.780	7.048	21.001
	σ_{a3}^2	37.564	14.180	61.490	14.553	61.813
	cov_{a23}	5.152	-10.480	20.060	-9.905	20.481
	r_{a13}	0.23	-0.5	0.7	-0.3	0.7
	r_{y13}	0.11	-0.3	0.5	-0.2	0.5

Variance genetic: σa^2; covariance genetic: cov_a; genetic correlation: $r_{a;}$ residual correlation: r_y; credibility intervals ICr and high density regions: HPD.

of treatment, care and water quality fertilizer tanks - when necessary).

In all of the environments, the participation of the common environment for fingerlings σ_c^2, 280(PL), 634(FL), and 1,519(DN), and fingerlings σ_w^2, 241(PL), 585(FL), and 1,438(DN), were similarly and relatively lower than reported by Santos et al. (2011), who found σ_c^2 = 1,147.64 in cage-nets where the common fingerling environment was a motherhood effect. The residual variation was 1,892(PL) and 3,942(FL), which were also lower than the values reported by Santos et al. (2011), σ_e^2 = 5,965.53 in contrast to DN, where the variation was higher (14,968) than reported in the literature. The phenotypic variance among the regions, 8,657(PL), 18,841(FL) and 55,556(DN), and it performed similarly to the genetic (relatively low).

The "a posteriori" distribution of all parameters was symmetric based on the closeness of the credibility interval and the high-density region. Because either the mean or the median could be used to represent the distribution, the current option was the mean "a posteriori".

Based on the credibility intervals (Table II), we found residual heterogeneity of variance in the Palotina x Diamante environment and phenotypic heterogeneity variance in the Palotina x Floriano environment. Heterogeneity occurs when the credibility interval of a parameter in one region is not contained in the other region interval. In Table II, the Palotina interval (ICr = 624 – 3,717) is not contained in the ICr of Diamante do Norte (ICr = 4,237 – 27,420) and phenotypic heterogeneity of variance in Palotina (ICr = 6,553 – 10,720) x Diamante do Norte (ICr = 42,090 – 70,650) also exists as in Floriano (ICr = 14,260 – 24,040) x Diamante do Norte (ICr = 42,090 – 70,650) because of the genotype x environment interaction.

These heterogeneities can occur because the differences in local management, stress, farming system (ground pound or cage-nets) and conditions, water and feed quality, daily serving, weather

sanitary conditions can affect the animal responses in every experimental condition. Variance differences with subclass (regions) can reduce the accuracy of predicting parent values with an inadequate selection of fish in different environments and can consequently reduce the genetic progress (Weigel and Gianola 1993). Without residual heterogeneity, the results can overwhelm the data from animals raised in large environments.

The heritability values were higher from all of the regions (Table III) with 0.71 in Palotina, 0.72 in Floriano and 0.67 in Diamante do Norte of than authors working with previous generations, in this same lineage as presents Oliveira (2011) when the estimates of h^2 for live weight were 0.15 using Bayesian Inference and Santos et al. (2011), with a heritability of 0.39 for live weight at the harvesting time using frequentist inference. The increase in heritability results can be seen as a response to the selection that has occurred over the years in this tilapia (fifth generation - G5) strain in Paraná, which favors increased genetic and yield performance with each generation. Ponzoni et al. (2005) found h^2=0.34 for live weight, similar to Nguyen et al. (2007), who reported an average of 0.35. The closest result to this current report was described by Charo-Karisa et al. (2006, 2007), who found a heritability of the live weight of 0.60 at harvesting time.

With high estimates of heritability, the emphasis of the selection must be centered at the individual level, which means that the best individuals are chosen as the reproducers. However, based on the average to low estimates of h^2, the best choice is based on families. Individual selection exhibits fast responses in genetic gain/generation but the variability in small group is reduced in less time than the selection within the family.

Works with previous generations, show that participation in the genetic variation of the common environment of larvae production and fingerlings were close to zero, as reported by Oliveira (2011), and lower than reported by Santos (2009) from 0.20 to 0.05 for σ_c^2 (common maternal environment = common larvae production environment). The explanation for such high heritability values is that of all of the fish participated in the genetic selection process and the current fifth generation and that the selection criterion is daily weight gain highly correlated with live weight (0.99) (Porto et al. 2015).

The close estimates of the credibility intervals (ICr) and HPD confirm the symmetrical "a posteriori" distributions (Table III). The small interval of credibility for all of the parameters indicate high accuracy in the estimates. The bi-characteristic estimates are similar to the uni-characteristic estimates (Tables II and IV), thus strengthening all of the results of genotype x environment interaction (variance heterogeneity) and indicating that the uni-characteristic analyses are sufficient to explain the current genetic parameters.

The genetic and phenotype correlation were very low (Table IV), which indicated the interference of the region in the genetic and phenotypic variation of the live weight in all of the animals. Several experiments with tilapias were performed in Asian countries. In Malaysia, the values of genetic correlation for live weight with the GIFT variety were 0.70 (Khaw et al. 2009b) in two environments (ground pond and cage-net), and from 0.36 to 0.99 in the Philippines, also with the GIFT variety in seven environments (Eknath et al. 2007). Therefore, similar environments as ground pounds exhibit high correlations from 0.76 to 0.99 and cage-nets of 0.99, in contrast to the results obtained from these distinct environments, where the correlations tend to be lower, from 0.36 to 0.86. Similarly, these types of responses were found in Brazil (Santos 2009), where a genetic correlation of 0.89 was reported for similar environments (cage-net), which showed no genotype x environment interaction, in contrast with a distinct

environment, where the estimates from 0.58 to 0.65 were responses to this interaction. In Vietnam, the genetic correlation of weight at harvesting time from animals farmed in brackish and fresh water was 0.45 (Luan et al. 2008).

A genetic correlation higher than 0.8 can discharge the genotype x environment correlation (Robertson 1959), but with estimates lower than 0.8-0.7, the fully genetic gain can only be achieved when the animals are selected and farmed in the same environment (Mulder et al. 2006) because a correlation lower than 0.7 indicates the presence of interaction, as we found in the current experiment.

The estimates from the uni-characteristic analyses were close to the bi-characteristic analyses (Tables II and V), thus sustaining the results for high heritability. The credibility intervals for bi-characteristic were lower, and they showed high precision in the results

The Spearman correlation from the uni-characteristic analysis was low (Table VI), where the highest was for Diamante do Norte x Floriano at 0.30 and the lowest was for Floriano x Diamante at 0.08. These values are lower than those reported by Santos (2009), who reported correlations from 0.75 to 0.84 (ground pound and cage-net) and 0.96 (cage net). The low values in the current experiment indicate interaction in the animal ranking. The same was observed with the genetic association from the Pearson correlation lower than 0.22 from Palotina x Diamante to 0.01 in Floriano x Diamante. These results indicate that after selecting animals from one region, they will not occupy the same rank in another location, which is strongly indicative of the interaction.

TABLE V
Estimates using the bi-characteristic analyses.

Regions	Parameters	Mean	ICr	
			Lower	Upper
FL-PL	h_1^2	0.71	0.4	0.8
	h_2^2	0.70	0.3	0.8
	c_1^2	0.03	0.01	0.1
	c_2^2	0.03	0.01	0.1
	w_1^2	0.03	0.01	0.1
	w_2^2	0.03	0.01	0.1
PL-DN	h_1^2	0.73	0.4	0.8
	h_2^2	0.66	0.3	0.8
	c_1^2	0.03	0.01	0.1
	c_2^2	0.03	0.01	0.1
	w_1^2	0.03	0.01	0.1
	w_2^2	0.03	0.01	0.1
FL-DN	h_2^2	0.71	0.4	0.8
	h_3^2	0.70	0.3	0.8
	c_2^2	0.03	0.01	0.1
	c_3^2	0.03	0.01	0.1
	w_2^2	0.03	0.01	0.1
	w_3^2	0.03	0.01	0.1

h^2: heritability; c^2: common environment larvae culture participation; w^2: common environment of fingerlings.

TABLE VI

Spearman correlation above the diagonal and the Pearson below the diagonal from the uni-characteristic analyses.

Regions	PL	FL	DN
PL	1	0.30	0.15
FL	0.16	1	0.08
DN	0.22	0.01	1

Based on the environment, the animal ranking was modified, and no single species exhibited similar records in all of the regions (Table VII). This fact also sustains the interaction for daily mean weight because of the numerous environmental factors such as weather conditions, management and farming systems.

Additional evidence of interaction was the direct gains with values higher than the indirect gains (Table VIII). This was the primary data obtained for fish breeding because when farming occurs under similar selection conditions, the fish can reach their

TABLE VII

Fish ranking within the families based on high genetic values for live weight (g) from 1-10, intermediate genetic values from 11-20 and lower genetic values from 21-30 in the uni-characteristic analyses.

Animals	PL*	FL*	DN*
1	29434	608452	28096
2	27916	453960	26684
3	27034	617198	27400
4	27586	783030	26396
5	28904	394902	28140
6	27334	643694	26368
7	29368	463342	26802
8	27542	681374	29338
9	29584	404818	26606
10	26466	382628	27462
11	629846	27420	788162
12	628512	27382	737586
13	617066	27356	729932
14	616766	27348	729366
15	612106	27276	728194
16	610114	27240	675966
17	484180	27016	670974
18	466206	26936	659210
19	465854	26916	648460
20	456676	26876	640496
21	26854	724550	25636
22	27578	642532	25680
23	27932	24628	27250
24	28834	477780	26810
25	25776	692706	27808
26	26852	672762	27438
27	29706	609290	25290
28	26692	837096	26700
29	28282	627940	26364
30	26766	477778	27566

*number microchip.

full genetic potential with higher gains compared with farming in distinct environments. This result can guide future decisions about selection. Selecting cores and farming conditions in Brazil could intensify the results of breeding programs. Such decisions, however, require high initial investments that may hamper such work, but the incipient results (Table VIII) from the indirect selection show genetic gains because there were no situations with negative values, which indicate losses. In a situation where direct selection for weather and management is not possible, the indirect selection with lower genetic gains can increase productivity (Hulata 2001, Reis Neto et al. 2014).

The highest genetic gain was observed in Diamante do Norte (281.35 g/generation) (Table VIII) because previous generations were selected in net-cages and the cumulative genetic gain can benefit the current generation with positive effects. The values from Floriano (198.24 g/generation) and Palotina (98.74 g/generation) are distinct because 100 g is a significant difference for two similar ground pond environments. Therefore, this difference may be the result of different management approaches, such as feed quality, water quality, or pond fertilization, which could affect the quantity of phytoplankton because tilapias are omnivorous filter fish that can use this resource when it is available.

TABLE VIII
Direct gain (g/selection generation) in the main diagonal and indirect gains (g/selection generation) above and below this diagonal.

Gain	PL	FL	DN
PL	98.74	16.38	16.43
FL	15.01	198.24	74.66
DN	7.77	38.52	281.35

The differences between Palotina and Floriano were highlighted when the animals were selected in Diamante do Norte and evaluated in Palotina. The lower genetic gain of 7.77 g/generation was incipient compared with the animals selected in Floriano and evaluated in Diamante do Norte, whose gains were 74.66 g/generation (Table VIII).

The low participation of indirect genetic gains on the direct ones is evidence of the interaction. The lower participation was in Diamante do Norte with Palotina, where the gain was 0.0276 g/generation, and the highest was 0.3766 g/generation in Floriano with Diamante do Norte (Table IX).

TABLE IX
Percentage of indirect participation in the direct gain in the three regions.

Gains (%)	PL	FL	DN
PL	1	16.58	16.63
FL	7.57	1	37.66
DN	2.76	13.69	1

CONCLUSIONS

The evidence of the genotype x environment interaction was verified by the results of the uni- and bi-characteristic analyses, which indicated the phenotypic heterogeneity of the variances among the three regions, weak genetic correlation, modified rankings in the different environments based on the higher levels of direct genetic gains compared with indirect gains, and the lower participation (%) of the indirect gains in the direct gains. Such results can guide further fish breeding programs.

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