Original Article

Interactions Between Non-Allelic Loci and Their Effects on Categorized Meat Performance Traits in Ducks

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ABSTRACT

Traits associated with meat performance are characterized by a complex inheritance model, including the effects of non-allelic interactions. The aim of this study was to estimate the significance of non-allelic interactions between pairs of loci in each of two alternative groups based on four important performance traits of ducks: body weight (BW), carcass yield calculated as the ratio of carcass weight to body weight (CY), breast and leg muscle yield as a fraction of carcass weight (BL-CW), and skin weight and abdominal fat, again as a fraction of carcass weight (SF-CW). The experimental material was based on an F2 cross between two parental lines: A-55 (Polish Peking) and GL-30 (French Peking). In total, 368 individuals were recorded. All of the birds (including parents and F1) were genotyped for 23 polymorphic microsatellite loci. Entropy was taken as a measure of interaction between pairs of loci, and the chi-square test was used to verify significance. In total, 253 pairs of loci were analyzed in both categories of each of the four traits. Statistically significant interactions were obtained for each trait. However, it was observed that some of the loci showed a greater tendency to have significant opposite interactions for alternative categories of the same trait. The results indicate the dependence of the recombination rate within pairs of loci on the level of each of the four traits.

INTRODUCTION

Some performance traits of poultry of importance to both consumers and breeders can be classified as binary (for instance, satisfactory and not satisfactory). By definition, identified single loci are also categorized according to their genotypes. There are a number of reports on association studies of additive genetic effects of molecular markers with continuous animal performance traits (see e.g. Andersson *et al.*, 1994; Aulchenko *et al.*, 2007). On the other hand, it is well known that the genetic backgrounds of some traits are complex, including additive and non-additive effects between alleles vs. loci. Classical estimation of non-additive genetic effects (based on mixed model methodology) requires a very large data set with favorable pedigree structure, family size, many highly polymorphic loci, etc.

Pekin duck is becoming an increasingly popular poultry species among breeders not only in Asian countries, but also in Europe. Over recent years, a considerable upward trend in duck meat production has been recorded in some European countries. Godfray *et al.* (2018) reported that meat accounts for more than 30% of total food consumption around the world. The trend also corresponds with an increasingly diversified poultry meat market (Magdelaine *et al.*, 2008).

Unfortunately, in contrast to chicken and livestock mammals, the duck (*Anas platyrhynchos*) genome is still insufficiently known. There are several papers on the detection of genome regions determining important performance traits (Huang *et al.*, 2006, 2007a; Maak *et al.*, 2003; Mucha *et al.*, 2014; Dobek *et al.*, 2017; Zhang *et al.*, 2018). Huang *et al.* (2006) developed a genetic linkage map for the duck. In a later study (Huang *et al.*, 2007b) they identified some loci affecting body weight and conformation traits as well as carcass and meat quality traits in Beijing ducks. Also Mucha *et al.* (2014) found one highly significant QTL for skin weight at the beginning of the linkage group CAU1, as well as two significant QTLs for fatness of leg muscle and leg muscle electrical conductivity 24 hours post-slaughter. Recently, estimation of genomic variation in Pekin duck populations has been carried out (Zhang *et al.*, 2018; Zhu *et al.*, 2019).

To our knowledge, there are no existing reports on inter- and intralocus interactions in duck populations. However, these interactions may be perceived as good indicators of linkages in animal groups classified according to the level of studied traits.

The present study is a continuation of earlier work by Mucha *et al.* (2014), Moliński et al. (2015) and Dobek *et al.* (2017) with the same experimental material, based on a crossbreeding experiment. Today, studies on interlocus interactions are possible due to the advantages of statistical tools, such as the theory of information. This approach, especially entropy analysis, has been applied for human (e.g. Andrew *et al.*, 2006; Kang *et al.*, 2008) and livestock populations (e.g. Dobek *et al.*, 2012) to measure the uncertainty associated with the values of the traits. It is well known that productive traits are caused by multiple factors, namely locus main effects as well as locus–locus and locus–environment interaction. In this work we are most interested in the locus–locus interaction, being a form of epistasis. As entropy is commonly used to measure the uncertainty of random variables, we shall use an entropy-based test to establish the locus interactions. This approach has been applied in epidemiological studies by Kang *et al.* (2008). The so-called case-control design has been successfully employed in genetic association studies. To our knowledge there are no existing reports on the application of this methodology to livestock and poultry genetics.

The objective of this study was to examine the interactions between pairs of loci in two alternative groups of ducks defined according to trait levels.

MATERIAL AND METHODS

The experimental material was based on an F2 cross between two parental lines: A-55 (Polish Peking) and GL-30 (French Peking). In total, 390 individuals were recorded. More details on the crossbreeding experiment and housing and feeding management were given by Mucha *et al.* (2014). The experimental procedures were approved by the Local Ethics Committee for Animal Experiments in Poznań (Poland) by way of Resolution 60/2009. In the 11th week of life (before slaughtering), body weight was measured (using an AXIS B15S electronic balance with ± 5g accuracy) on live birds after 12 hours without access to feed but with permanent access to water. Slaughter and post-slaughter processing were performed in the same standard technological conditions. Dissection was performed using the method described by Ziołecki & Doruchowski (1989). Carcasses and their components were weighed with a RADWAG WPT 5C electronic balance with ± 0.2g accuracy. Body weight (BW), carcass yield (CY) calculated as the ratio of carcass weight to body weight, breast and leg muscle yield as a fraction of carcass weight (BL-CW), and skin weight and abdominal fat, again as a fraction of carcass weight (SF-CW) were recorded for each bird. A statistical description of the data is given in Table 1. The study included 23 loci, forming 253 pairs of loci. The primers for amplification of microsatellite sequences were chosen based on the literature (Huang *et al.*, 2005). A detailed description of the molecular methods applied in the present study was given by Mucha *et al.* (2014). The microsatellite markers used are presented in Table 2.

Table 1 – Statistical characteristics of analyzed traits (means and standard deviations).

Trait	Lower	Upper	Total
BW (g)	2878.83 (167.96)	3354.81 (165.42)	3122.00 (290.64)
CY (%)	73.09 (2.29)	76.72 (2.56)	75.02 (3.03)
BL-CW (%)	23.18 (1.09)	25.95 (1.15)	24.47 (1.78)
SF-CW (%)	28.33 (2.56)	33.44 (2.07)	31.78 (14.34)

BW- body weight, CY - carcass yield, BL-CW - breast and leg muscle yield as a fraction of carcass weight, SF-CW - skin weight and abdominal fat as a fraction of carcass weight.

For each recorded trait, the observations were divided into two sets, the average value being the boundary. The sets were denoted as lower (L) and upper (U): BW-L, BW-U, CY-L, CY-U, BL-CW-L, BL-CW-U, SF-CW-L, SF-CW-U. Thus, eight data sets were analyzed separately. The interaction of loci was examined for the whole set of ducks as well as for the eight sets of observations. In total there were 2024 variants of

analysis. For each variant an incidence matrix was constructed based on the number of individuals with given genotypes.

Table 2 – Characteristics of analysed microsatellite loci.

Locus	GenBank accession	Primer sequences (5`-3`)
CAUD093	AY493338	AGAGCGGTGTGAGAGCAGAG GATATCGCTCGCAATTTTGG
CAUD112	AY587031	CAACTGACAGAGAGGCACG GACTGTGTTTCCAATGCTCC
CAUD086	AY493331	AACACAGCTTCACCCCACAG GCAGAGCGGTGTGAGAGCA
CAUD039	AY493284	GGGACATCTCTTGGAGCAAA AGTGAAAGCTGCTGCTGGAT
CAUD027	AY493272	AGAAGGCAGGCAAATCAGAG TCCACTCATAAAAACACCCACA
CAUD114	AY587033	GAAGCAAGGAAATCATCAGCC GGATGTGGGGTGGTTATGAC
CAUD066	AY493311	ACCGCCTGGGGAATAATG CGCTCTGTTGCTCTTGTAA
APH23	AJ515898	TCCTCTGCTCTAGTTGTGATGG CCTCAGCAGTCTTCCTCAGTG
CAUD018	AY493263	TTAGACAAATGAGGAAATAGTA GTCCAAACTAAATGCAGGC
CAUD074	AY493319	CAAGCCCTGGACCTATTCAG GAGATGGGAAGGGAGAGAGG
CAUD029	AY493274	GACCTCAAGAATTTACCAC ATTATTTTCTTCTGGCAGCA
CAUD107	AY587026	GCCATCTTAACCCCCTGAC TTTACGCTTCCCTGTGCTTG
SMO07	AJ427847	TTTCACCCAGTTCACTTCAGCC GATTCAAATTTGCCGCAGGATTA
CAUD023	AY493268	CACATTAACTACATTTCGGTCT CAGCCAAAGAGTTCAACAGG
CAUD095	AY493340	CGCAGCGAGTTTCCAGAC GTTCCCTTTCGCTCGTGTTA
CAUD031	AY493276	AGCATCTGGACTTTTTCTGGA CACCCCAGGCTCTGAGATAA
APH15	AJ515890	TGAATATGCGTGGCTGAA CAGTGAGGAATGTGTTTGAGTT
CAUD127	AY587046	CACTCATGGGACTACACTGT CAGATGAAAATAAACTCCAG
CAUD025	AY493270	AGTTCATCCCGATTTGTAGC AAATGCAGTGAGGTAAACCC
CAUD131	AY587050	CAGACTCCTGGAAACCTTCT TGGGTTTTTGAACACAGATA
CAUD020	AY493265	TAGGGTCAATAGTAAGAAACA TAACTGTGTGATAAGGGAGA
SMO06	AJ427846	GGGGTGGGAAAGAAGCAGTTTAG TCCTGGGACTTTGAAAGTGGCTC
CAUD103	AY587022	CATACTGGCATCATTCTGT CGTAATGAGTGGGGAAAGAC

To examine the interaction between loci in the context of a selected productive trait, the notion of entropy will be used. The Shannon entropy for a discrete random variable X is a function:

$$E(x) = -\sum_i p(x_i) \log p(x_i)$$

where $p(x_i)$ denotes the probability of X taking the value x_i. In the case of two loci, one with r genotypes and the other with c genotypes, the entropy takes the form

$$E_{obs} = -\sum_{i=1}^{r} \sum_{j=1}^{c} p_{ij} \log p_{ij}$$

where p_{ij} is the probability of the presence of an animal with the *i*-th genotype for the first locus and the *j*-th genotype for the second. If there is no interaction between loci, the entropy is equal to

$$E_{ind} = -\sum_{i=1}^{r} \sum_{j=1}^{c} p_{i.} p_{.j} \log p_{i.} p_{.j}$$

where $p_{i.} = \sum_{j=1}^{c} p_{ij}$ and $p_{.j} = \sum_{i=1}^{r} p_{ij}$.

It is known (Wilks, 1962) that the statistic $2n(E_{ind} - E_{obs})$, with *n* being the number of observations, follows a χ^2 distribution with $(r-1)(c-1)$ degrees of freedom. The rejection of this hypothesis indicates interaction between a pair of loci.

Additionally, the Pearson correlations among four variables were estimated. These computations were performed with the use of Statistical software (version 13.1, StatSoft, Tulsa).

RESULTS

The statistically significant interactions between the pairs of loci within two alternative categories of four recorded traits are given in Figures 1a–4b. In total, 253 pairs of 23 loci were analyzed. Relatively small Pearson correlation coefficients between the studied traits were obtained (Table 3). However, some of them were statistically significant (–0.124, –0.180 and –0.131 for BW and CY, CY and BL-CW, and BL-CW and SF-CW respectively).

Table 3 – Pearson's correlation coefficients between studied traits.

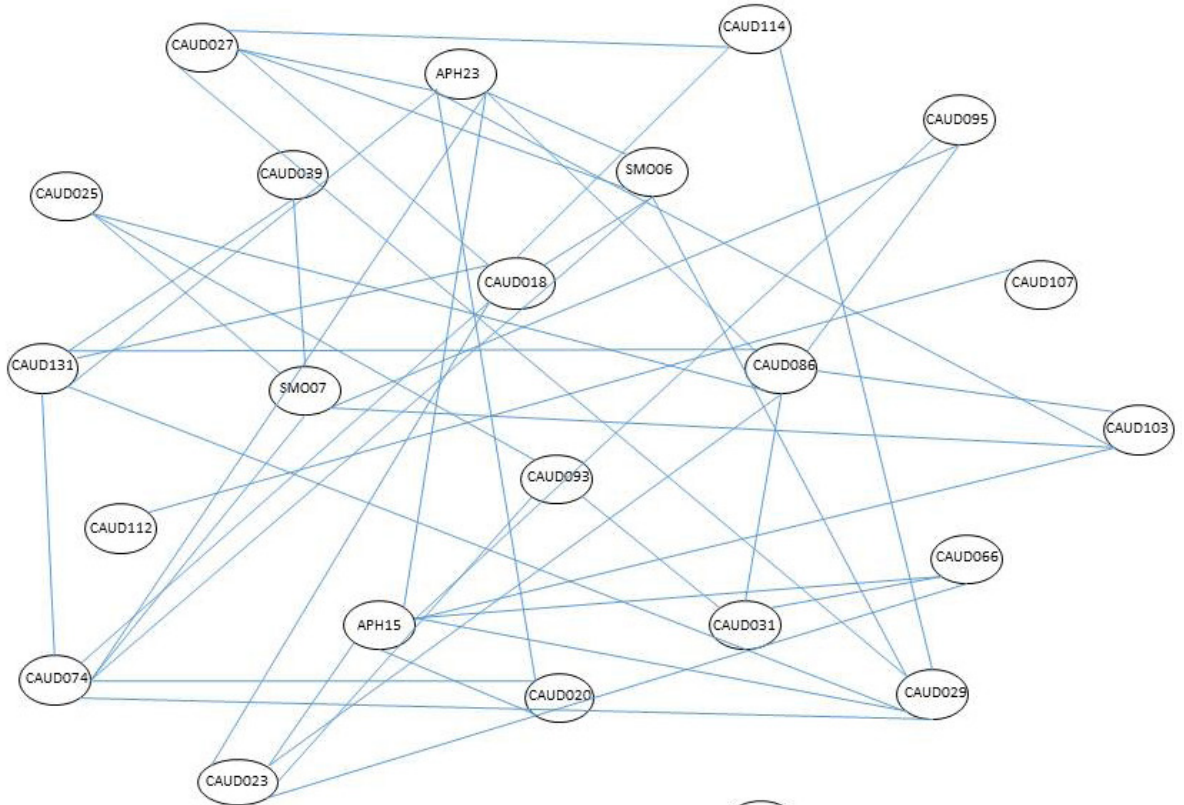|	CY	BL-CW	SF-CW
BW	-0.124*	-0.033	0.0168
CY		-0.180*	0.077
BL-CW			-0.131*

*/ p < 0.05

Body weight

The results for both body weight classes are given in Figures 1a–b. In the class of heavier birds (BW-L) four loci (CAUD018, CAUD131, CAUD074, SMO07) did not display interactions, whereas in the second class (BW-U) only one locus (CAUD127) is non-interactive. Hence,
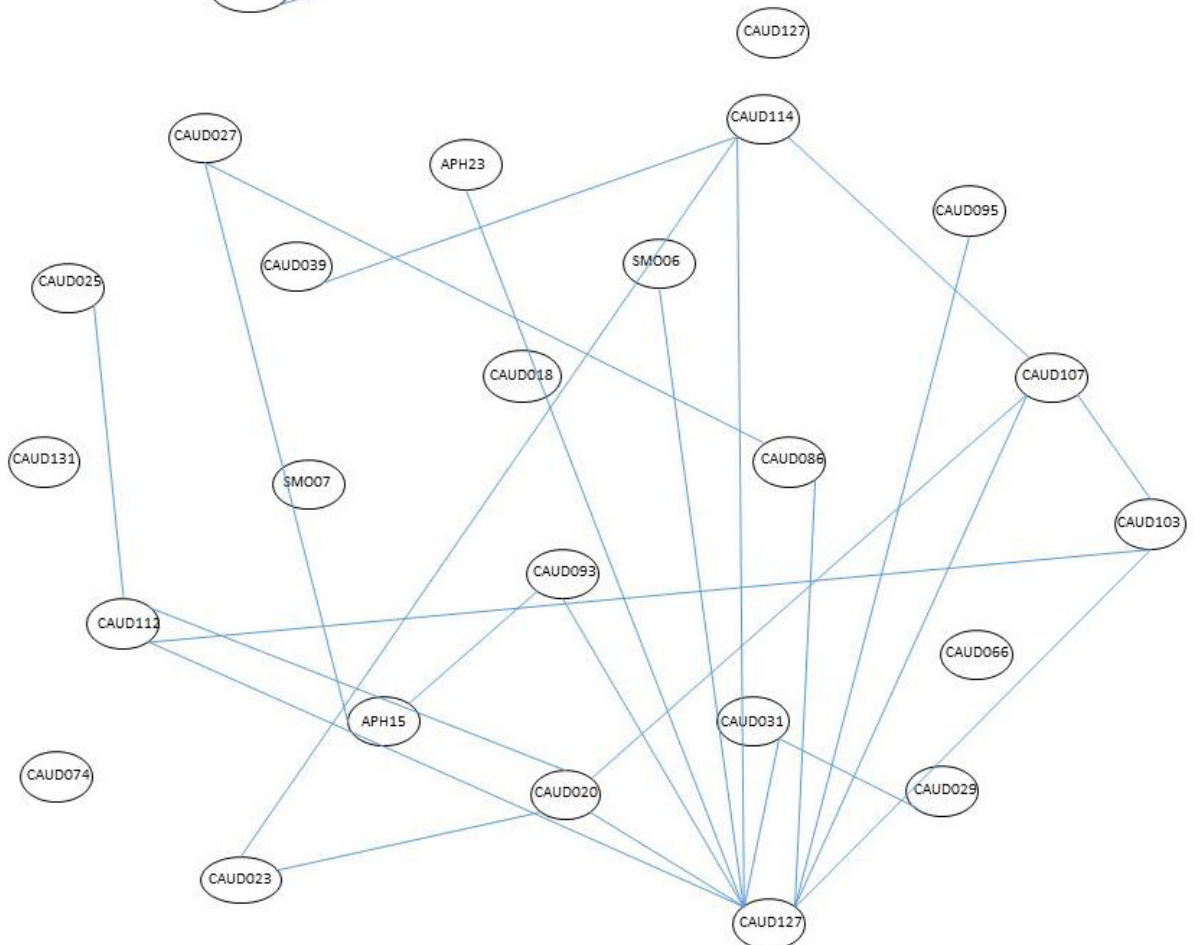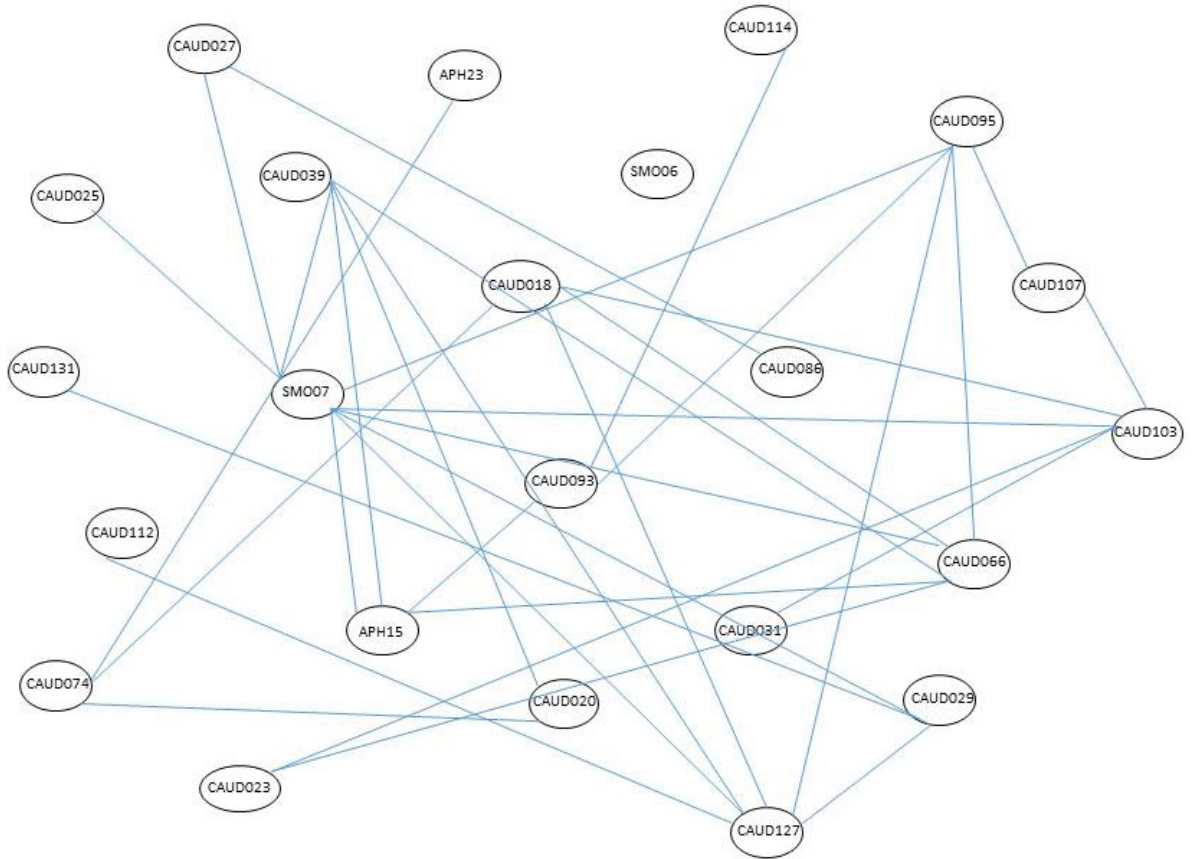
BW-U

BW-L

Figure 1a-b – Significiant interactions between non-allelic loci for alternative classes of body weight - upper (BW-U) and low (BW-L).
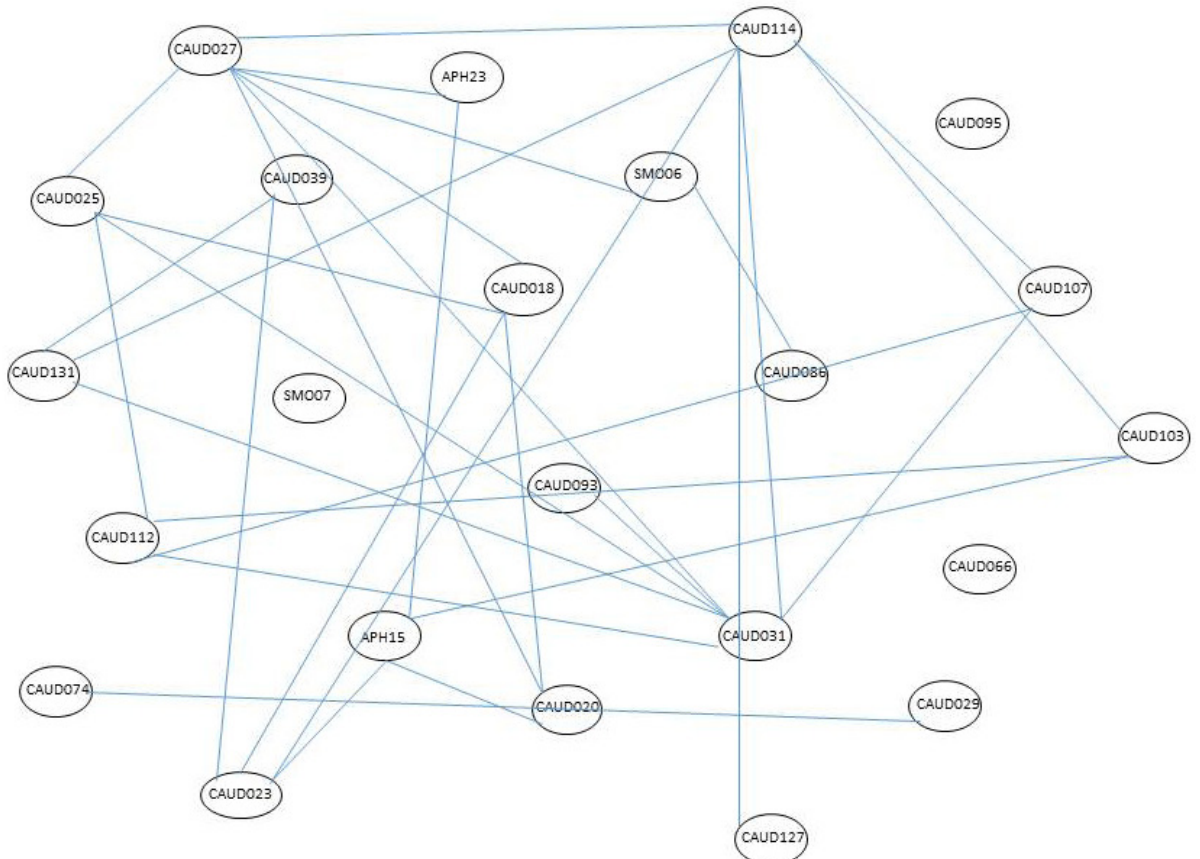
CY-U

CY-L

Figure 2a-b – Significant interactions between non-allelic loci for alternative classes of carcass yield - upper (CY-U) and low (CY-L).

interlocus interactions were detected for 19 and 22 loci in the two alternative data sets. However, the numbers of interactions with particular loci are very diverse in each of the two body weight classes. In the BW-L group, the most statistically significant interactions (11 interacting loci) were observed for the CAUD127 locus (with the following loci: APH23, CAUD020, CAUD031, CAUD086, CAUD093, CAUD095, CAUD103, CAUD107, CAUD112, CAUD114, SMO06). In this group, four loci (CAUD020, CAUD114, CAUD107, CAUD112) displayed four significant interactions, and locus CAUD103 had three interactions. Generally, the distribution of interactions in the second class of ducks (heavier individuals) is quite different compared with the first class. The most interacting locus (with eight significant interactions) was APH23, whereas for three loci (CAUD131, CAUD029, APH15) six significant interactions were estimated. Each of the five loci (CAUD018, CAUD023, CAUD027, CAUD086, SMO06) displayed five interactions. As already mentioned, there was a large variation between the groups for some loci. Extreme confirmation of this is provided by the locus that has no significant interactions for BW-L, but a large number of interactions for BW-U.

Carcass yield

The bi-locus interactions in both alternative classes of carcass yield are visualized in Figures 2a–b. The most important interacting loci in the CY-L group (each with seven interaction pairs) were CAUD027, CAUD031 and CAUD114. In the case of five loci, four interactions were statistically significant. In the case of the second group (CY-U) the largest interactive ability was demonstrated by the locus SMO07 (with nine loci: APH15, CAUD025, CAUD027, CAUD029, CAUD039, CAUD066, CAUD095, CAUD103 and CAUD127), followed by two loci (CAUD066, CAUD127) with six interactions. It should be noted that three loci (CAUD066, CAUD095 and SMO07) were interacting for CY-U, although in the case of CY-L they produced no statistically significant interactions. Antagonistic bi-locus interactions were detected for both categories of carcass yield, especially for the markers SMO07, CAUD127, CAUD031 and CAUD066.

Breast and leg muscle yield as a fraction of carcass weight

As presented in Figures 3a–b, there were three non-interacting loci in each of the alternative groups (APH23, CAUD039 and CAUD093 for BW-CW-L, and SMO06, CAUD066 and CAUD103 for BL-CW-U). However, the remaining markers displayed different

degrees of interaction between loci (from 1 to 6). For instance, for CAUD031, seven bi-locus interactions were registered in the BL-CW-L group, but only one in the alternative group (BL-CW-U). The opposite position was obtained for CAUD031, with interaction with six loci (CAUD095, CAUD107, CAUD074, CAUD127, CAUD086, CAUD093) in the BL-CW-U group, whereas the same locus in the alternative group (BL-CW-L) displayed interaction with one locus only. Considerable disproportion in the two categories was observed for CAUD029. In the case of BL-CW-L, this locus displayed interaction with seven microsatellite markers (CAUD027, CAUD114, SMO06, CAUD074, CAUD066, CAUD086, CAUD018), but in the alternative category (BL-CW-U) only one interaction (with CAUD112) was registered.

Skin weight and abdominal fat as a fraction of carcass weight

Generally, the number of interactive loci varied between the two categories based on this trait. The number of interactions for SF-CW-L was considerably smaller than for SF-CW-U. In the case of SF-CW-L (Figure 4a-b), seven loci (CAUD020, CAUD066, CAUD086, CAUD093, CAUD095, CAUD103, SMO06) did not interact, and for six other loci (APH23, CAUD025, CAUD029, CAUD031, CAUD074, CAUD131) only single interactions were detected. The largest numbers of interactions (in this category) were obtained for CAUD112 (six) and for APH15 (five bi-locus interactions).

As already mentioned, in the case of the SF-CW-U data, the density of interactions was considerably larger than in the case of SF-CW-L. Here only one non-interacting locus (CAUD025) was detected. For two loci, CAUD029 and CAUD103, the numbers of significant interactions were eleven (APH15, CAUD066, CAUD074, CAUD086, CAUD093, CAUD095, CAUD103, CAUD114, CAUD131, SMO06, SMO07) and ten (APH15, APH23, CAUD018, CAUD023, CAUD029, CAUD031, CAUD074, CAUD107, CAUD112, SMO07) respectively.

DISCUSSION

Over recent decades, population scale sequencing projects have made large progress in documenting genetic structure in a number of species, including ducks. Also, current advances in molecular genetics and genomics have generated new opportunities for genetic improvement programs due to the association of chromosomal regions with productive traits. However, the genetic backgrounds of numerous traits
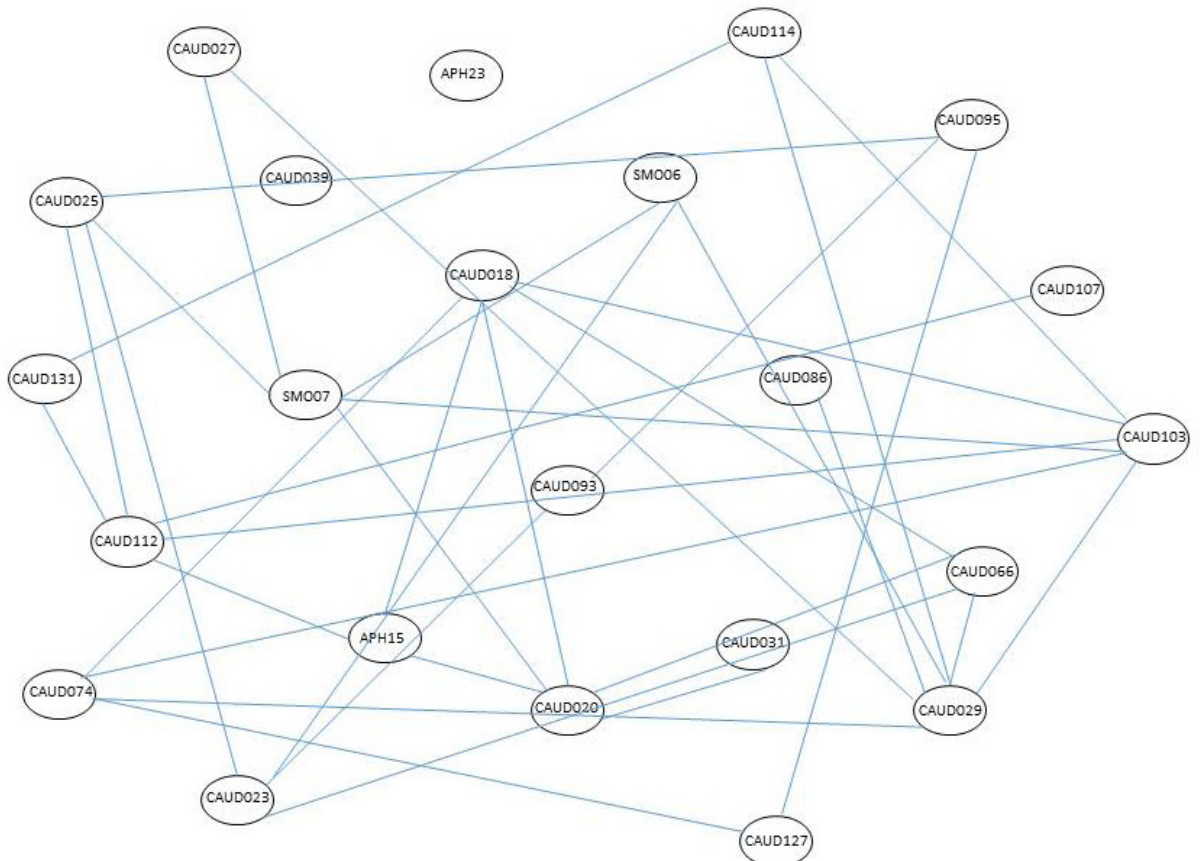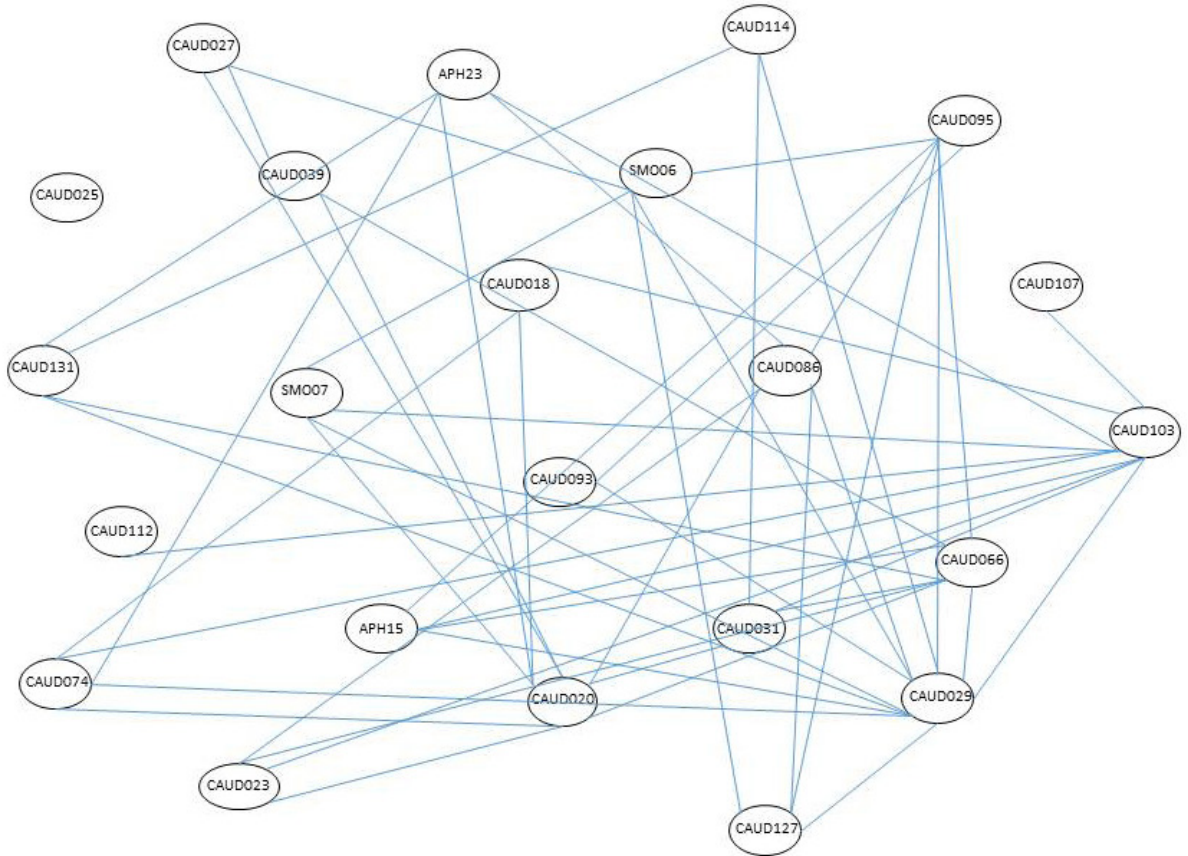
BL-CW-U
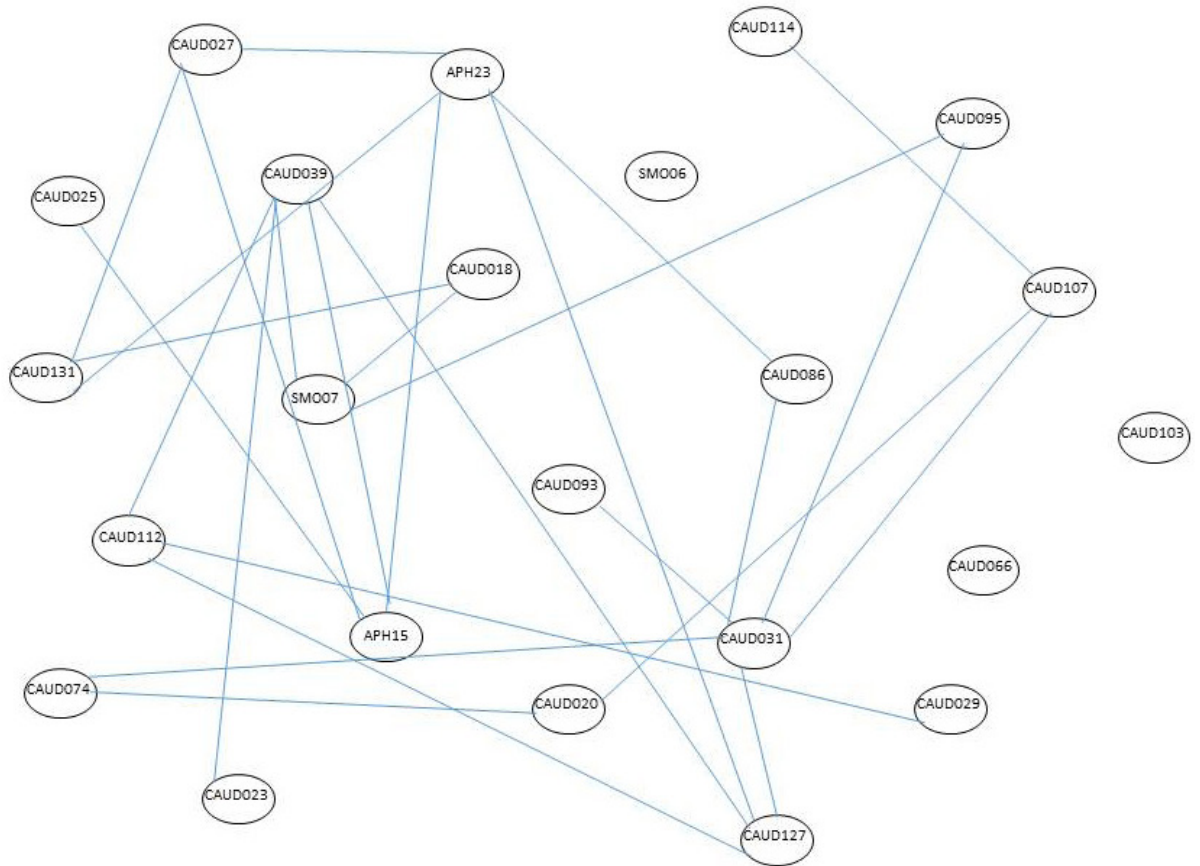
BL-CW-L

Figure 3a-b – Significiant interactions between non-allelic loci for alternative classes of breast and leg muscle as a fraction of carcass weight- upper (BL-CW-U) and low (BL-CW-L).
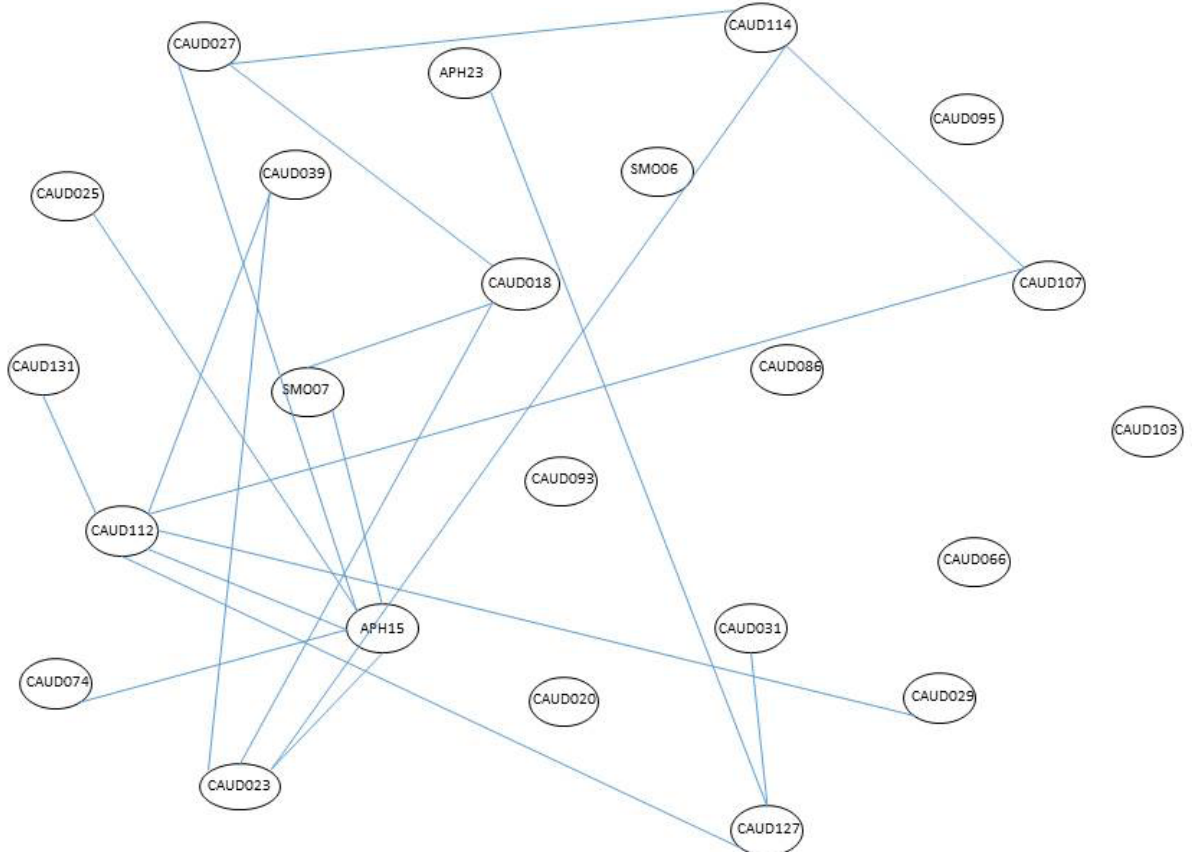
SF-CW-U

SF-CW-L

Figure 4a-b – Significant interactions between non-allelic loci for alternative classes of skin weight and abdominal fat as a fraction of carcass weight - upper (SF-CW-U) and low (SF-CW-L).

are very complex, including not only additive effects of loci, but also intra- and interlocus interactions. Kang *et al.* (2008) reported that identifying gene interactions using molecular tools is time-consuming and expensive in comparison with statistical methods, which may be perceived as an efficient alternative approach for elucidating the interaction mechanisms.

From a methodological point of view, due to the relatively large genetic and phenotypic variabilities, a crossbreed population appears to be suitable for the estimation of interlocus interaction. This is the case with the data studied in the present paper. Let us recall that the recorded and genotyped individuals originated from generation F2 of a crossbreeding experiment. On the other hand, as reported by Mucha *et al.* (2014), the polymorphism and, in consequence, heterozygosity of the genotyped loci are different. The polymorphism information content (PIC) of the studied microsatellite loci ranged from 0.29 (APH15) to 0.70 (CAUD131). Coefficients of observed and expected heterozygosity as well as polymorphism information content for this population (estimated by Mucha *et al.*, 2014) are presented in Table 4. Baratti *et al.* (2015) observed a gametic disequilibrium for the APH15 and APH10 microsatellite loci in a mallard population in Italy.

Table 4 – Estimated parameters of expected (H$_E$xp) and observed (H$_O$bs) heterozygosity as well as polymorphism information content (PIC) of the studied loci (Mucha *et al.*, 2014).

Locus	HObs	HExp	PIC
CAUD029	0.48	0.46	0.35
CAUD086	0.19	0.67	0.59
CAUD107	0.50	0.66	0.58
CAUD114	0.57	0.47	0.41
CAUD066	0.68	0.70	0.64
APH23	0.46	0.43	0.33
CAUD027	0.72	0.61	0.54
CAUD112	0.36	0.40	0.37
CAUD074	0.67	0.61	0.53
CAUD093	0.74	0.71	0.66
CAUD039	0.79	0.68	0.61
CAUD018	0.15	0.46	0.36
CAUD023	0.45	0.50	0.47
CAUD095	0.32	0.52	0.48
SMO07	0.37	0.34	0.32
CAUD031	0.75	0.67	0.60
APH15	0.35	0.35	0.29
CAUD127	0.34	0.35	0.31
CAUD103	0.32	0.34	0.30
CAUD025	0.53	0.47	0.36
CAUD131	0.79	0.74	0.70
CAUD020	0.28	0.26	0.22
SMO06	0.66	0.60	0.53

In the present study, the number of statistically significant interactions varies between alternative trait classes. The largest number (12) of interactions in one subclass (SF-CW-U) was recorded for locus CAUD029, characterized by relatively low polymorphism (PIC=0.35). Mucha *et al.* (2014), in a study on the same population, indicated locus CAUD029 as the flanking marker for fatness of leg muscle by sensory evaluation. According to those authors, CAUD029 explained 3.2% of the phenotypic variance of this trait. This may emphasize even more the role of the locus. Incidentally, the marker CAUD029 was indicated as being associated with the uniformity of basic performance traits in the analyzed population (Dobek *et al.*, 2017). It should be noted that some other studied loci have also been indicated as important. Huang *et al.* (2007b) reported the microsatellite loci CAUD117, CAUD126 as flanking markers for body weight of Beijing ducks. In the analysis of breast muscle weight, one peak was obtained at 394 cM (flanking markers: CAUD103 and CAUD025). This region was not in the neighborhood of the QTL reported by Huang *et al.* (2007a). In an earlier study (Moliński *et al.*, 2015) performed on the same population, some of the most antagonistic interacting loci (CAUD086, 2CAUD093 and CAUD018) had discriminative properties. Also in the SF-CW-U subclass, ten significant interactions were observed for CAUD103. As with the previous locus, the polymorphism of this marker was small (PIC=0.30). In an earlier study (Mucha *et al.*, 2014) CAUD103 was detected as a flanking marker for breast muscle weight.

The results obtained suggest that gametic equilibrium can be determined by the level of certain traits. It is well recognized that locus–locus interactions, also known as epistasis, may be one of the potential mechanisms implicating some traits. Definition of the phenomenon is not always clear. Epistasis is usually considered for a given trait (Ruiz-Larranaga *et al.*, 2017). However, some authors (e.g. Kang *et al.*, 2008) suggest the approach adopted in the present study, whereby gene–gene interactions are estimated for classes of traits.

The results of the present study call into question the random process of interactions between the studied loci. This is evidenced by the different numbers of interactions within alternative classes of all four recorded traits. As already noted, the numbers of interacting loci are relatively large. However, they were considerably differentiated across two classes of a single trait. On the other hand, in the case of some microsatellite markers, the numbers of most

interacting loci are usually similar for alternative classes of different traits. This is mainly a consequence of correlations between the traits studied.

It is well known that the effectiveness of statistical inference is determined by the size of the subclasses. Therefore, in the case of highly polymorphic loci with a small number of subclasses, some interactions may not have been detected. Although there is not necessarily a direct relation between statistical and biological interactions, genetic interaction analyses can provide relevant information regarding the biological mechanism which might underlie the performance traits recorded (Kang *et al.*, 2008).

To our knowledge, this is the first application of such an approach in poultry. As noted by Kang *et al.* (2008), the methodology has several advantages, such as the fact that the interactions among multiple loci can be characterized by the entropy of a locus system, and the possibility of evaluating associations of multiple loci with a binary expression of recorded traits. Let us recall that the categorization of performance traits is also very useful from a practical point of view.

It should be recalled that microsatellite loci are genetic markers (of the second class) not localized at any coding genome regions. Hence, only indirect associations (without physiological pathways) of these loci with performance traits can be considered. However, it is well known that they are widely applied to evaluate the genetic structure of a population (including its variation among populations and over time) and, in consequence, to study relationships with characteristics. However, apart from the above considerations, the results obtained in this work clearly indicate the rearrangements of microsatellite loci (alleles) within subgroups of birds. This may have larger implications for other genome regions, including those where coding areas (genes) are located.

In conclusion, the studies conducted provide some arguments for a complex inheritance model for the most important performance traits in ducks. This was confirmed by the number of opposite interactions between pairs of loci in each of two alternative groups of individual ducks classified according to the level of analyzed traits. The results suggest some non-random biological backgrounds of gametic disequilibrium.

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DECLARATION OF INTEREST

There is no conflict of interest with other works.

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