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Genetic variability of FCR with suboptimal food and prospects for selection

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Feed cost represents a high part of production cost in chickens. So, feed efficiency is a key factor of poultry production profitability. Genetic selection of standard broiler chickens has resulted in a huge decrease in feed conversion ratio. Nowadays, as high quality feedstuffs price and human population both increase, there is a growing interest in improving efficiency of birds on alternative diets, for economical and ethical reasons. These diets could include low cost feedstuffs or by products of agriculture that are not consumed by humans. However, these alternative diets often show low and variable quality. Moreover, this approach is a kind of challenge since selection is usually made on high quality diets in order to express the growth genetic potential of modern genotypes. This review aims at evaluating the potential interest in using alternative and lower quality diets in a selection for feed efficiency, keeping in mind that the diet quality may interact with the selection criteria used to reach this goal.

Introduction

Feed cost represents the highest part of the production cost of meat-type chickens, from 55 to 65 % depending on the production type (Riffard *et al.*, 2011). Therefore, feed efficiency is a key factor in the profitability of poultry rearing. The selection of rapid growing broilers for 3 decades resulted in a continuous decrease of feed conversion ratio in these birds, as shown in **Figure 1**. The "certified chickens" that result from a cross between a standard broiler sire and a slow-growing dam also show such a tendency (**Figure 1**). However, no decrease in feed conversion ratio is observed for slow growing "label rouge" chickens (**Figure 1**) (Riffard *et al.*, 2011).

Nowadays, the importance of feed efficiency has been reinforced for economic and ethical reasons. Feed price, especially for the high quality diets required for modern genotypes, is still increasing. For example, in France in 2010, feed price was 9.1% and 30.9% than in 2009 and 2006, respectively (Riffard *et al.*, 2011). These prices become limiting for the development of production in developing countries which have to import these feedstuffs and cannot achieve maximum performances due to environmental constraints as hot and humid climate (Farrell, 2005). Simultaneously, the increase of human population leads to an increased demand for poultry products, which in turn increases the demand for the high quality feedstuffs used in poultry diets. From an ethical point of view, it is important to be able to reduce the pressure of

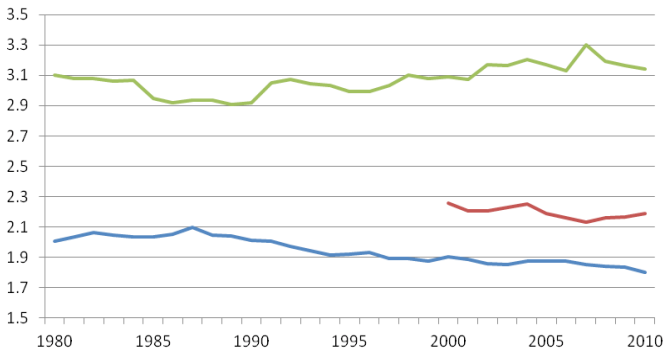


Figure 1 - Evolution of feed conversion ratio of broilers (blue curve), certified chickens (red curve) and "label rouge" chickens (green curve) in France since 1980 (Riffard *et al.*, 2011).

animals on cultivated surfaces, as 80% of cultivated surfaces are used to provide resources to animals and only 20% to humans (Steinfeld *et al*., 2006). To reach this goal, it would be interesting to replace part of the high quality feedstuffs used in poultry diets by other feedstuffs, especially those that cannot be consumed directly by humans. However, these products often show a poor and variable quality, and may not be adapted to modern genotypes. Thus, it would be needed to select for chickens that would be adapted to such suboptimal diets.

Composition of feed efficiency traits

Feed conversion ratio (FCR) (feed intake / weight gain) is a composite trait depending on compositions of feed and body growth. It can be modeled as follows (Carré *et al*., 2008a; Carré and Mignon-Grasteau, 2009):

$$FCR = \frac{119\ D\ \frac{MBW}{PW} + 9.36 C_L + 5.6\ C_P}{0.8\ AMEn}$$

Where D is the duration of production, MBW the mean metabolic weight (i.e. mean body weight raised to the power 0.70), PW the production weight, C_L and C_P the lipid and protein concentrations of production, and AMEn the apparent metabolizable energy value of diet, corrected to zero nitrogen retention.

This equation illustrates why rapid growth and body composition have often been used as selection criteria to improve feed efficiency. Direct selection has also been performed but more scarcely, as it implies to measure individual feed intake, i.e. to place animals in individual cages. Fairfull and Chambers (1984) estimated that 65% of the differences in FCR originated from differences in weight, growth rate and body composition.

Selection for improved FCR

Direct selection for FCR

Direct selection on FCR is possible as this trait present a moderate to high heritability (Pym, 1990). It has been confirmed by selection experiments on this trait. Leenstra and Pit (1987) and Sutedjo *et al*. (2001) showed that direct selection on FCR was more efficient to reduce FCR than selection on fatness or growth and that this selection also led to leaner birds. However, all these experiments have been done using standard diets in order to allow birds to express their genetic potential for growth, and did not try to show adaptability to poorer quality diets.

Indirect selection on growth under suboptimal environment

Godfrey (1968), Neisheim (1975), Sorensen (1980) and Marks (1978) selected broilers or quails for growth under normal or 30% reduced protein rate, or low arginine or lysine content. Marks (1987) selected quails for growth under normal or high salt diet (0.4 vs 1.6%). Finally, Leenstra and Pit (1987) selected chickens for growth under ad libitum or feed restricted conditions.

All these studies found that the response to selection for growth was lower in the suboptimal environment than in the normal environment. In the feed restricted environment, Leenstra and Pit (1987) had to apply a selection pressure twice as high as in the ad libitum environment to obtain similar responses in both environments. Without no difference in selection intensity, Sorensen (1980) found lower response to selection for body weight at 40 d in the line selected on low protein diet (LP) than in the line selected on normal protein diet (NP) after 7 generations of selection (+ 80 g *vs* +250 g). When both lines were fed the normal protein diet, the NP line was 75 g heavier than the LP line (Sorensen, 1985). At the opposite, when fed with reduced protein content, the LP line was 180 g heavier than the NP line. So, this strategy did not improve adaptability to suboptimal diets, but adaptation to a special diet. Moreover, when the protein rate decreased too much, the line selected on low protein content became extremely variable.

These results are consistent with the fact that heritability of growth traits is 0.05 to 0.10 points lower in the unfavorable environments than in the favorable environments (Godfrey, 1968; Marks, 1986, 1987).

Finally, this selection on growth in unfavorable environment had a negative effect on body composition and on efficiency. Indeed, as protein but not energy content was modified, birds increased their feed consumption to meet their protein requirements. For example, the quail line selected on growth with a low lysine diet consumed 11 to 13% more than the line selected on adequate

lysine content when fed a diet with low lysine content (Godfrey, 1968), but the difference of feed intake vanished when they were both fed an adequate diet. The excess of energy consumption is deposited as fat, which could be deduced from equation [1] (Carré *et al.*, 2008a). So, the LP line had 17% more total fat and 37% more abdominal fat than the NP line when both lines were fed a standard commercial diet, 25% more total fat and 60% more abdominal fat when they were fed a restricted protein diet (Sorensen, 1980). When fed a normal diet, the LP line had a higher FCR (+0.05), lower digestibility of dry matter (-1.3%) and a lower proportion of nitrogen retention (-6.4%, Sorensen *et al.*, 1983).

Indirect selection on digestive efficiency

It has long been argued that digestive efficiency was not controlled by genetics as differences between breeds were low and as birds were already very efficient (Neishem, 1975; Pym, 1990). However, Carré *et al.* (2002) compared different varieties of wheat used in poultry diets, and observed that the variability of metabolizable energy of diets was much lower between wheat varieties (around 300 kcal.kg^{-1} DM) than between animals within a variety (around 900 kcal.kg^{-1} DM) (cf. **Figure 2**). More recently, Bandengan *et al.* (2009) also stated that the variability of ileal digestibility of proteins and amino acids was much higher between animals than between diets, even when using highly variable feedstuffs such as DDGS. For instance, the proportion of total variability of amino acids digestibility explained by the diet was ranging between 4.9% for phenylalanine to 24.1% for lysine (9.2% for total crude proteins), whereas variability due to animals within a diet represented respectively 95.1%, 75.9%, and 90.8% for phenylalanine, lysine and total crude proteins.

Mignon-Grasteau *et al.* (2004) showed that digestive efficiency of broilers was heritable when birds were fed a challenging diet containing 50% wheat from the Rialto variety, which is especially difficult to be digested because of its hardness and its high viscosity (Carré *et al.*, 2002). The genetic basis of digestibility was confirmed by a divergent selection experiment on AMEn using this challenging diet. After 8 generations of selection, AMEn of the Rialto wheat diet differed by 35 to 40% between the high (D+) and low (D-) line (Mignon-Grasteau *et al.*, 2010; de Verdal *et al.*, 2010, 2011a). This AMEn divergence was associated with a much lower excretion of nitrogen and phosphorus in D+ than in D- birds (de Verdal *et al.*, 2011b). On the 7th generation with the same diet, digestibilities of starch, proteins and lipids were also 42%, 15%, and 50 % higher in D+ than in D- line (Carré *et al.*, 2008b). D+ birds also had 6.2 to 8.7 % higher AMEn and a 17.6% lower excretion rate of nitrogen and phosphorus when compared to commercial broiler genotypes on wheat (Carré *et al.*, 2008a; de Verdal, 2011). When birds were fed diets easier to digest (i.e. based on corn and soybean), differences were still observed between D+ and either D- or commercial broiler birds, but were largely reduced, ranging between 2.5 and 5 % for AMEn (Carré *et al.*, 2008a; Mignon-Grasteau *et al.*, 2010). These differences in digestive efficiency were associated with a smaller intestine, a bigger gizzard (Garcia *et al.*, 2007; Rougière *et al.*, 2009; de Verdal *et al.*, 2010, 2011a), and a longer gizzard retention time (Rougière and Carré, 2010) in D+ than in D- birds. So, gizzard physiology seems to be involved in the differences between D+ and D- lines, as reported by a study on gizzard motility showing a higher responsiveness of gizzard to environment variations in D+ than in D- birds (Rougière *et al.*, 2012). In agreement with this statement, genetic correlations between AMEn

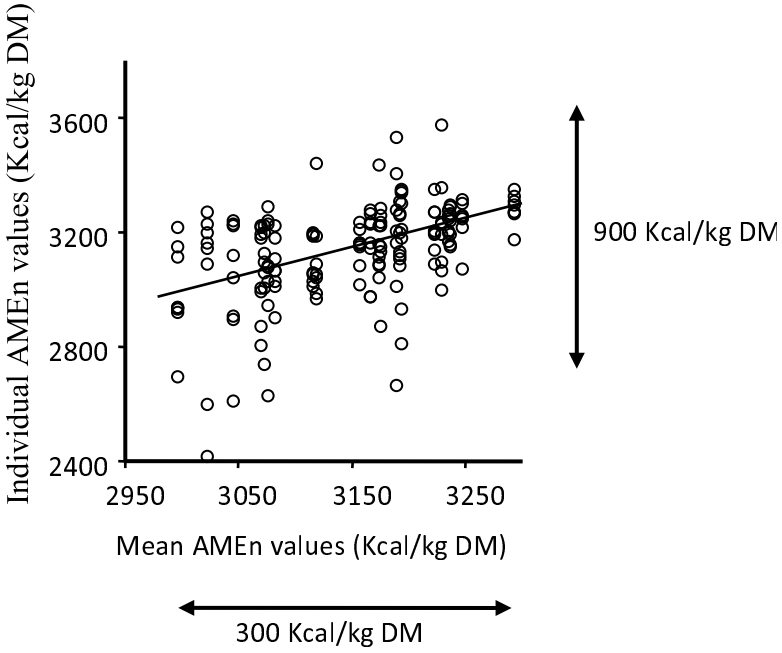


Figure 2 - Variability of AMEn of wheat diets between wheat varieties and between animals within a wheat variety (after Carré *et al.*, 2002).

and relative weights of gizzard and proventriculus were observed to be rather high (0.43 and 0.59, respectively) (de Verdal *et al*., 2011a).

Various studies performed on these birds indicated that performances of D+ birds depended less on characteristics of diets than D- birds (Carré *et al*., 2008a; Rougière *et al*., 2009) and that, in contrast with a selection on growth in suboptimal environment, selection on AMEn led to more adaptable birds. These results are consistent with the strong and positive genetic correlations obtained between digestibility traits on corn or on wheat diets, which ranged from 0.67 for digestibility of starch to 0.88 for digestibility of proteins. This implies that selection on digestive efficiency on one diet would also improve performances on the other diet. However, progress would be more efficient if selection was made on wheat, as, except for starch, heritability of digestibility is much higher with wheat that with corn diet: respectively 0.32 and 0.15 for AMEn, 0.28 and 0.26 for starch, 0.25 and 0.04 for lipids, 0.29 and 0.09 for proteins (Mignon-Grasteau *et al*., 2010). Again, at the opposite to selection on growth in suboptimal environment, the D+ and D- lines did not show significant differences in fatness at market age (de Verdal, 2011).

Genomic data on FCR

QTL detection

Despite the importance of FCR for poultry production, very few QTLs have been detected on FCR. In pigs for example, Rotschild *et al*. (2007) stated that on 1675 QTL that had been detected, only 8 were detected on feed efficiency, as compared to 16, 224, and 404 for feed intake, growth and fatness. Similarly, on 2736 QTL detected until now in poultry (laying hens and growing chickens), only 25 are related to feed efficiency traits (cf. **Figure 3**), coming from 5 studies, among which none detailed the diet used in the experiment (de Koning *et al*., 2003, 2004; Parsanejad *et al*., 2004; Hansen *et al*., 2005; Ewald *et al*., 2007). Most studies that were looking for QTL on populations differing by their feed efficiency finally found QTL on components of feed efficiency, mainly feed intake and body composition (Hocking, 2005, Abasht *et al*., 2006). None of them were performed on a challenging diet.

Regarding performances on low quality diet, a QTL detection program has been initiated using a F2 cross between the D+ and D- lines fed a diet including 55% of Rialto wheat. A total of 945 animals have been genotyped on 6000 SNPs and the 864 F2 birds were measured for digestibility, performances and anatomy. The first analyses show the existence of several QTLs, which in most cases co-localized for AMEn, digestibility of dry matter, starch and proteins.

Candidates genes and expression data

Parsanejad *et al*. (2002, 2004)) proposed that PEPCK-C and ornithine decarboxylase 1 may be involved in residual feed intake of adult laying hens. The former is part of the process of glucose generation from non-sugar carbon substrates. The latter is implied on efficiency of nutrient absorption including calcium. More recently, studies found in broilers that FCR was correlated with SNP variations in genes regulating metabolism and energy partitioning (growth hormone receptor or neuropeptide Y, Sherman *et al*., 2008), genes implied in thermogenesis and proton leak (avian uncoupling protein, Sharma *et al*., 2008, Bottje *et al*., 2009) or in energy homeostasis and feeding behaviour (melanocortin 3 receptor, Sharma *et al*., 2008). By comparing expression of genes between high and low FCR chickens, differences have been detected in genes implied in the regulation of mitochondrial energy metabolism (Ojano-Dirain *et*

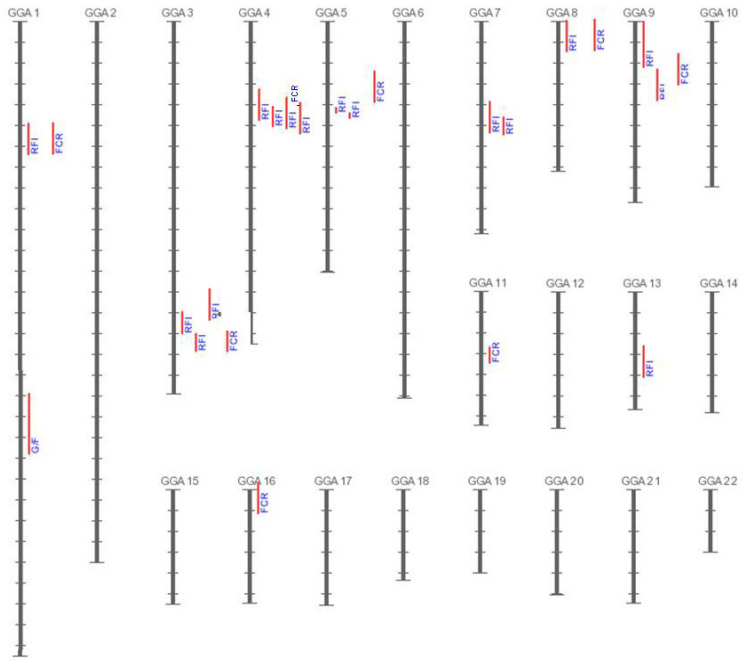


Figure 3 - QTL detected on feed efficiency (FE), feed conversion ratio (FCR) and residual feed intake(RFI) in chickens and laying hens (www.animalgenome.org/cgi-bin/QTLdb, 02/25/2012).

al., 2007), and in heat shock protein involved in oxidative stress (Kong *et al*., 2011).

Perspectives for selection with suboptimal diets

Variability of feedstuffs

Variability in the quality of feedstuffs may be a problem in estimating the potential of genetic improvement of feed efficiency on alternative diets as it does not allow a reproducible selection environment. It is especially the case of byproducts such as bran or DDGS, that highly depend on the raw material composition and technological process (drying, milling, addition of solubles). For instance, Ravindran and Blair (1991) highlighted that the machinery used for milling rice affects the proportion of hulls in the rice bran, which fiber and fat contents can vary respectively from 12.6% to 30.9% and from 6.6 to 31.6%. Bandegan *et al*. (2009) also showed that depending on feedstuff sample, apparent ileal digestibility of essential amino acids as lysine and threonine varied from 24.4 to 45.7% and from 48.2 to 60.9%, respectively.

It is often claimed that selection efficiency is decreased when environment, including diet, is suboptimal, because variance due to the environment increases and heritability, and thus possibilities of selection, decreases. Indeed, if selection is done on maximum growth, the animal needs an optimized environment to fully express its genetic potential for growth. This is especially true for modern genotypes, since their rapid growth and high protein deposition rate require a high quality diet. However, if the criterion of interest is the robustness of animals in a difficult environment, it is precisely in a difficult environment that the capacity of animals to cope with difficulty will be expressed. The high positive genetic correlations found between capacities to digest wheat and corn diets (Mignon-Grasteau *et al*., 2010) show that improving performances in a difficult (wheat) environment would also improve performances in a more favorable (corn) environment. Sorensen (1980) found a much lower genetic correlation (0.30) between broiler growth obtained on a normal or a low protein diet, but in their case, the low protein diet was really out of requirement, which could partly explain this very low correlation.

Criterion of selection

Criterion of selection has to be chosen carefully when selecting on improved feed efficiency on low quality diets. Results from Sorensen *et al*. (1980, 1983) showed that selection for growth of birds fed diets with low protein contents would lead to increased feed consumption and fatness, whereas selection on digestive efficiency with a wheat diet does not increase neither feed consumption nor fatness in the high line (Mignon-Grasteau *et al*., 2004, 2010). Thus, when suboptimal diets are considered, selection criteria such as digestive efficiency (AMEn or digestibility of dry matter) seems to be more appropriate than the growth criteria. Attention has also to be given to age at selection. Indeed, the development of gastrointestinal tract is strong in the first weeks of age, which increases the chances of success when selecting at this age. Birds of D+ and D- lines were selected at 3 weeks of age. The differences between both lines for development of gastrointestinal tract and for digestive efficiency appear after one week, are maximal at 3 weeks and decrease or disappear at 8 weeks (de Verdal, 2011).

Homogeneity of results

When selection is performed in a difficult environment, attention has also to be given to homogeneity of performances in addition to the mean value. Data collected on several generations of D+ and D- lines showed that the coefficients of variation of AMEn, coefficients of digestibility of starch and proteins were diet dependent in D- line but not in D+ line. Coefficient of variation of lipid digestibility was diet dependent in both lines (cf. **Table 1**, Mignon-Grasteau *et al*., 2010).

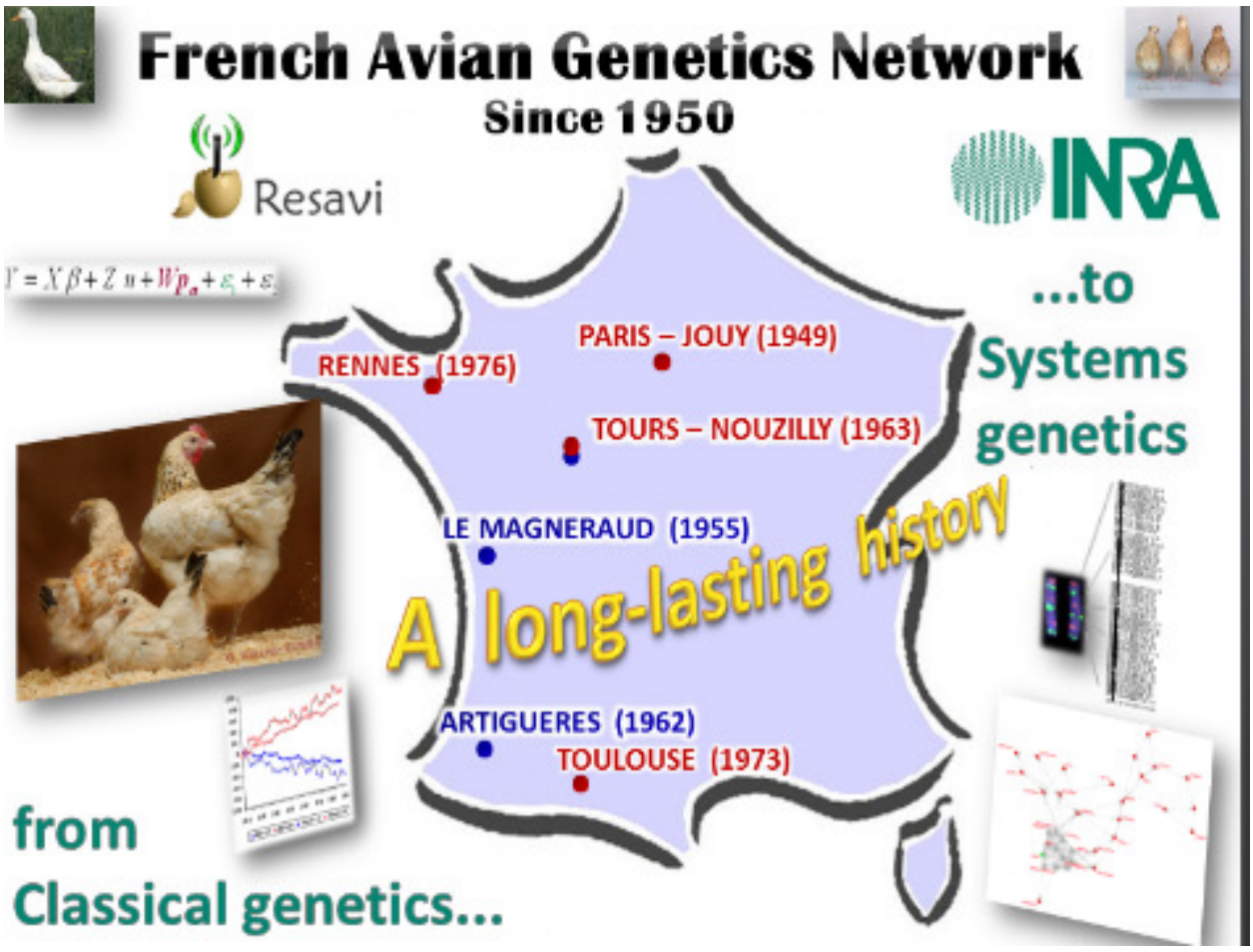
Table 1 - Effect of the diet on mean value and on homogeneity of digestive performances in D+ and D- lines.

	Corn diets				Wheat diets			
	D+		D-		D+		D-	
	mean	CV (%)	mean	CV (%)	mean	CV (%)	mean	CV (%)
AMEn (kcal.kg^{-1} DM)	3298	6.6	3063	7.3	3247	8.6	2411	26.5
Digestibility of lipids (%)	90.9	3.1	84.6	11.2	83.0	12.0	68.6	26.2
Digestibility of starch (%)	97.9	0.9	96.8	2.0	96.1	3.6	87.4	14.2
Digestibility of proteins (%)	83.1	4.8	78.6	6.7	77.4	6.0	68.1	11.7

However, it is worthy to note that, in most studies on digestibility or feed efficiency using suboptimal or alternative diets, only the global standard error of the mean is given in studies, which does not allow to see whether variance is modified in each treatment.

Conclusions

This review shows that selection for improved feed gain ratio using challenging or alternative diets is efficient, provided that conditions, age, and especially criterion of selection are appropriate. It is especially obvious that, in suboptimal conditions, a selection on growth is less suitable than a selection on digestive efficiency. Finally, in addition to an improved average value in selected populations, another goal that has to be reached for selection in such environments is homogeneity of population, which is a major factor of profitability of poultry breeding.



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