Quantitative genetics of feed efficiency in ducks

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Abstract

Given the worldwide diversity of duck production, genetics aspects of feed efficiency of ducks should be addressed depending on the production (broilers, layers, and “foie gras”) and on the genetic types (Muscovy duck, common duck, and their intergeneric cross mainly used in France for “foie gras” production after force-feeding, *i.e.* the mule duck). The two main criteria to characterize feed efficiency are the feed conversion ratio (FCR), computed as the ratio of food quantity divided by the output, and the residual feed intake (RFI) which is obtained through a multiple linear regression of feed intake by output and metabolic requirements. The former is a ratio, with undesirable statistic properties. In addition, it is uneasy to disentangle variations in net feed efficiency from variations in FCR due to production traits. The latter is supposed to be, at least phenotypically, independent from the constituent production traits. This is the reason why it gained popularity, even though it requires a thorough analysis of metabolic requirements, as in the overfed mule ducks, where the fat deposition capacity should not be impaired. In the literature, the values found for FCR depend on the genetic type and on the production: FCR≈2.5 at 12 wk. for male Muscovy and FCR >3.2 at 13 wk. for fatty mule ducks; FCR ≈ 1.9 at 42d for Pekin broilers; FCR ≈2.8 for layers. Usually RFI is moderately heritable ($h^2 \approx 0.25$ in layers; $0.3 < h^2 < 0.4$ in Pekin broilers) and slightly more heritable than FCR. RFI heritability of fattened mule ducks needs to be refined. Genetic correlations between FCR and RFI vary between studies, from moderate (ρ_G=+0.34) to high (ρ_G=+0.99). Reliable assessment of individual feed intake is an issue. Development of RFID based automatic feeders greatly helped the improvement of feed efficiency in duck breeding programs. Such devices open the field for new studies, as they give access to feeding behavioral traits. They also allow for the joint modeling of trajectories for feed intake and production traits. Finally, as a complex trait, selection for feed efficiency should benefit from the availability of molecular tools.

Introduction

Feed efficiency has become more and more important for all kinds of animal production, in response to rising feed cost and awareness of limited resources and environmental issues. Over the past decades, the combined effect of changes in management, a better formulation of diets to comply with each production period requirements, and an effective selection resulted in an improvement of feed efficiency in livestock and in poultry (Havenstein et al, 2003; Havenstein et al, 2007). As for any trait, implementation of an effective selection program to improve feed efficiency will require a proper individual measure of the involved traits and a relevant definition of the objective, based on estimated genetic parameters.

After a brief description of the variety of the worldwide duck production, the first part of this paper will thus discuss the feed efficiency concepts and definitions. In a second part, we will review some genetic parameters of feed efficiency, while the third and conclusive part will outline some prospects in the selection of feed efficiency in ducks.

A wide variety of productions and duck genetic types

When addressing feed efficiency, attention should be paid to the considered type of production (egg or meat) and to the genetic type of duck. The common duck (*Anas platyrhynchos*) is a domesticated bird derived from the wild Mallard. Some breeds have been selected for egg production (Khaki Campbell, Shan Ma, Tsaiya, Indian Runner…), some other for meat (Pekin) or dual purpose production (Orpington). The Muscovy duck (*Cairina moschata*) originates from Central and South America, is later maturing than common duck, with less fat and is mainly reared for meat. In Taiwan, a mule duck is obtained as the cross between a Muscovy drake and a Kaiya (common) female duck, and is favored for having good carcass composition with more meat and less fat than the Pekin type. In France, the mule duck is obtained by crossing a Muscovy drake and a Pekin female and now represents 95% of the "foie gras" (fatty liver) production, obtained through force-feeding. Genetic types of ducks used vary greatly from country to country.

As stated by Farrell (2015), unlike the chicken, the duck does not have a diverticulum and the crop is merely a widening of the esophagus, while it stands for a storage organ in fowl. In the duck, this organ controls movement of feed to the proventriculus and may be responsible for the rapid rate of digesta passing through their digestive tract, while gastric digestion occurs in the gizzard.

Even if a reasonable number of publications are available on the genetic aspects of feed efficiency in poultry, fewer studies were carried out specifically on ducks. In order to overview some key notions linked to feed efficiency, this review will thus also encompass chicken and turkey studies, despite the physiological differences between species and the special characteristics of ducks.

Definition and measure of feed efficiency

As reviewed by Willems et al (2013a), the two main measures of feed efficiency are food conversion ratio (**FCR**) and residual feed intake (**RFI**). Alternative measures such as residual maintenance energy (**RME$_m$**), residual gain (**RG**) and residual intake and gain (**RIG**) have been proposed. All these notions will be presented below.

Feed Conversion Ratio

In science, efficiency is defined as the ratio of the total output to the total input, and is usually expressed as a percentage. Here, feed efficiency (**FE**) is defined as the ratio of production weight (**PW**) (body gain or egg mass) to feed intake (**FI**). The most widely used criterion is feed conversion ratio (**FCR**), namely the inverse of **FE**, the latter being only occasionally used in the literature (Dransfield and Sosnicki, 1999). **FCR** is an economic indicator of the production efficiency at the animal level. From a nutritional point of view, Carré et al (2008) derived **FCR** as a function of:

- the duration of the considered period, which implies that economic relevant **FCR** values should account for the productive life length of animals, longer in Muscovy than in fast growing Pekin broilers.
- the mean metabolic weight, to account for basal metabolism requirements. Skinner-Noble and Teeter (2003) suggested that body temperature could be used to assess basal metabolic rate in chicken.
- the lipid and protein concentrations of the diet. Sørensen et al (1983) evidenced a genotype by environment (**GxE**) interaction for growth on chicken broilers selected for growth rate and fed with high or low protein content diets. Large differences exist between Asian countries known for the mass-scale, integrated, extensive production systems, and Europe and Northern America, where the selection of poultry is mainly based on intensive systems. Therefore, potentially unfavorable **GxE** interactions may arise. More recently the effect of diet dilution with rice hulls was also noted by Wu et al (2012) on the growth and **FCR** of Pekin ducks.
- the metabolisable energy of the diet (**ME**), which was long considered insensitive to selection (Pym et al, 1984; Fairfull and Chambers, 1984). This hypothesis now needs to be modified, as it was shown that the heritability of **ME** value can be rather high, as in growing chicken fed wheat-based diets (Mignon-Grasteau et al., 2004).
- and obviously the output **PW**.

Being a ratio of grams of feed to grams of output, **FCR** is dimensionless. However, in order to account for the energy content and metabolizability of the diet, and to allow for the comparison between studies, some authors (Romero et al, 2009) advocate the expression of **FI** in kilocalories of **ME** instead of grams of feed.

In comparison with other poultry industries, ducks, and in particular mule ducks, have a high **FCR** during growth. Huang et al (2007) gave a **FCR**=3.09, between 0-10 weeks in 1986 for mule ducks bred for meat and obtained from crossbreeding white male Muscovy with Kaiya female. It was>3.2 kg of feed per kg of **BW** from 28 to 84 d old for mule ducks bred for fatty liver and prepared to enter force feeding (Guy et al., 1995). In the marketed broilers strains, the alleged **FCR** values at slaughter age are **FCR**≈2.5 at 12 wk for male Muscovy duck, while **FCR** ≈ 1.9 at 42d for Pekin broilers.

Huang et al (2012) reported a **FCR** of 2.72 in laying Brown Tsaiya ducks in 2009 (while it used to be 6.72 in 1964). In meat-type birds, **FCR** is dependent on considered periods for, as underlined by Pingel (1999), ducks have a remarkably rapid growth during the first weeks of life. At slaughter age, both Pekin, Muscovy and mule ducks reach 70 to 80 % of adult weight, while chicken broilers have a slaughter weight less than 40 % of adult weight. Since birth, common ducks have a high percentage of skin with subcutaneous fat for protection against cold water, which leads to higher values of **FCR**, compared to chickens. The late intensive growth of the breast muscle is related to the growth of wings to become able to fly. Therefore, indirect improvement of **FCR** uniquely by decreasing age at slaughter holds little promise because of the late growth of breast muscle, resulting in poor carcass quality (Pingel, 1999). Since Wilson and Obsourn (1960) demonstrated the phenomenon of compensatory growth in poultry, early feed restriction was found as another way for improving feed efficiency and decrease production costs in broilers. Tan and Ohtani (2000) carried out an experiment to compare the effect of different feed restriction regimes between 8 to 14 days of age on performance, carcass composition, and lipid metabolism of male Pekin ducks and concluded that early feed restriction could be used to improve the growth performance and carcass traits of meat-type ducks.

Numerous studies have demonstrated that **FCR** is moderately heritable in poultry and livestock species. However, because **FCR** is strongly correlated with production (*e.g.*, growth) and influenced by maturity pattern, it is difficult to distinguish **FCR** variation related to level of production from variation related to non-productive functions. For instance, selection for a lower FCR in Pekin ducks (Pingel, 2011) resulted in responses in breast meat thickness (measured by a needle probe). The authors concluded that selection for **FE** should better account for a criterion independent of production traits.

Finally, the use of ratio-based traits in breeding programs can also result in erratic selection responses due to their poor statistical properties (Gunsett, 1984). For all these reasons, alternative expressions of **FE** have been investigated.

Residual Feed Intake

Residual feed intake (**RFI**) was originally proposed by Byerly (1941) and used by Koch et al. (1963) in beef cattle, and in poultry by Bordas and Mérat (1981). **RFI** is defined as the difference between actual **FI** and **FI** predicted from requirements for production and maintenance. Studies across multiple species have found that 60-80% of the inter-animal variation in feed intake is accounted for by differences in body weight and the level of production, leaving **RFI** to potentially account for the remaining 20-40% of unexplained variation (Bottje and Carstens, 2009). **RFI** is usually obtained as the residual of the multiple regression of observed feed intake on indicators of production (*e.g.* body weight gain for broilers and egg mass laid for layers) and of maintenance (metabolic body weight). Statistically, the mean RFI within a population is zero, and is phenotypically independent from the constituent production traits (Kennedy et al., 1993). A more efficient bird (low **RFI**) should have a negative value for **RFI**, indicating that it uses less energy than predicted for its production and maintenance. Additional indicators of production requirements have been proposed, for instance when the variability of the production composition in terms of lipids versus proteins affects feed intake. The choice of the components to be introduced in the regression model is crucial. In the case of fattened mule ducks, Drouilhet et al (2014) corrected **FI** for the TOtal Body Electrical Conductivity (**TOBEC**, Cornuez et al, 2013; Forthun-Lamothe et al, 2002) score of each animal, in order to account for the lipid mass variability in animal's body. This strategy aimed at improving feed efficiency without impairing fat deposition and correlatively foie gras production.

Following the resource allocation theory (Beilharz et al., 1993), it is hypothesized that the extra energy intake of high **RFI** birds, which is not used for production processes, is a buffer available for other resource-demanding functions or life traits. This theory states that in an environmentally limiting situation, animals have a package of finite resources. Resources used by one function are no longer available for other functions, meaning that animals have to make a trade-off between allocations of resources toward life traits to obtain maximal fitness. In a situation of limited resources, low **RFI** animals would thus be less flexible to put resources into maintenance processes, whereas high **RFI** birds would have resources remaining. Evidences of this theory have been provided in poultry essentially: for instance Van Erden et al (2004) found that high **RFI** birds (growing layer hens) were able to keep their metabolism at a higher level (higher heart and liver weights), compared to low **RFI** birds after a *Salmonella enteritidis* infection.

Alternatives measures of FE

As reviewed by Willems et al (2013a), three alternatives measures of feed efficiency have been proposed in the last decade. The residual maintenance energy (**RME_m**) (Romero et al., 2009), unlike **RFI** or **FCR**, aims to measure energetic efficiency through the computation of

ME (expressed in kcal) instead of plain quantity of feed intake (expressed in grams). Non-linear methods were used to estimate the maintenance energy requirement (**ME_m**) of each individual bird. Subsequently a linear regression between **ME_m** and feed intake was performed, the residuals representing **RME_m**. In the case of growing animals, residual gain (**RG**) is defined as the residual from the linear regression of average daily gain (**ADG**) on both **FI** and **BW**. Improved **RG** is, on average, associated with faster growth rates but not with differences in feed intake (Berry and Crowley, 2012). Residual intake and gain (**RIG**) combines the beneficial characteristics of both **RFI** and **RG** such that **RIG** is independent of body weight, but when used for selection it can increase weight gain and reduce feed intake simultaneously. This concept was first developed in cattle, but also introduced in poultry by Willems et al (2013b). They concluded that both **RG** and **RIG** traits have characteristics that make them appealing for inclusion in a multiple trait selection index but similar results could be reached by applying appropriate coefficients on their component traits in a selection index. Van der Werf (2004) postulated the very same remarks about **RFI**, which makes it relevant to review now the genetic parameters of **FE** traits.

Genetic parameters of FE traits in ducks

The questions of interest are whether the **FE** traits are sufficiently heritable to provide significant gain in genetic selection and whether they are favorably (or not) correlated with other economic traits. As lower values of **RFI** or **FCR** are praised, negative values of genetic correlations with economic traits are favorable, unless mentioned otherwise.

First, estimates for **FE** measured in layers are reported. For Pekin layers housed in cages, Basso et al (2012) estimated and heritability of 0.24±0.11 for **RFI**, and a high genetic correlation with **FI** (ρ =+0.89±0.07). Zeng et al (2016) obtained similar heritability estimates for **RFI** (h^2=0.26), moderately correlated with **FI** (ρ=+0.67) and even less with **FCR** (ρ=+0.34). Liu et al (2012) computed weekly **RFI** of brown Tsaiya layers and estimated genetic parameters. Heritability of **RFI** ranged from 0.30 to 0.43 and genetic correlations between whole and partial (4 wk.) laying periods were high (above +0.93).

Second, estimates for meat-type production will be reviewed. In meat-type Pekin ducks, Thiele (2016) estimated genetic parameters in a male and in a female broiler line. **RFI** was assessed on growing birds, accounting for metabolic body weight and body weight gain. In both lines, **RFI** was moderately heritable (h^2=0.39 in the male line and h^2=0.33 in the female line). Genetic correlation with body weight, breast thickness and conformation where positive (*i.e.* unfavorable) but low (below 0.10). **RFI** was not correlated to laying performances of female breeders, except with egg weight (ρ=-0.40), which is favorable. In the female line, **RFI** was also unfavorably correlated with liveability (ρ=+0.37). This antagonism was in accordance with the above-mentioned resource allocation theory, but liveability was not

precisely defined in this paper and exhibited a low heritability (h^2=0.05). **RFI** during growth thus appeared as a trait of choice to improve **FE** in Pekin broilers, with no adverse effect on reproduction. In two lines of Pekin broilers, Alletru and Thiele (2016) also estimated genetic parameters for **FE** traits. In both lines, **FCR** was moderately heritable (h^2=0.32 and h^2=0.37), with slightly lower estimates than for **RFI** (h^2=0.39 and h^2=0.40). The genetic correlations were high between these two traits in both lines ($\rho=+0.93$ and ρ=+0.95). Finally, using a sire-dam model on a purebred population of growing Pekin ducks housed in metabolic cages, Zhang et al (2017), estimated an heritability of 0.41± 0.18 for **RFI**, similar to h^2=0.38± 0.15, obtained for **FCR**, the two traits being only moderately correlated (ρ=+0.54±0.05).
Estimates can also be obtained from selection experiments applied to a single trait of interest. In the divergent selection for **RFI** of fattened mule duck progeny of Muscovy drakes (Drouilhet et al, 2014), paternal half sibs growing mules were housed in the same pen, and **FI** was measured on a familial basis. This resulted in a probably overestimated value for **RFI** heritability (h^2=0.83±0.42), higher than for **FCR** (h^2=0.41± 0.18). As in Thiele (2016), the genetic correlation between **FCR** and **RFI** was very high (ρ =+0.99). Despite an expected phenotypic negligible correlation between **RFI** and **TOBEC** derived lipid quantity, these two traits were moderately correlated (ρ=0.33±0.38) at the genetic level but the magnitude of the confidence interval was too high to conclude about possible impacts of selection for a reduced RFI on fatness. Further studies were carried out on the same selected lines, and Drouilhet et al (2016) concluded that selection for **RFI** had no effect on liver weight and quality, and a slightly deleterious impact on meat quality (decreased drip loss and meat color of the "magret" muscle). This latter study benefited from individual measures of **FI** of animals reared in groups, which leads us to the final part of this review, dealing with prospects in data analysis of **FE** traits.

Prospects in the selection for FE in ducks

Clearly, one of the largest improvements in the commercial realized **FCR** has come from developments of new technology in measurement of individual feed intake in groups of animals, coupled with radio frequency identification (**RFID)**. Testing in a group environment is associated with the following benefits (compared to testing in individual pens or metabolic cages):

- The environment is closer to that applied commercially and is thus a more relevant trait to the poultry industry, which helps reducing **GxE** interactions.
- It allows for social interactions between animals that impact feeding behavior, competition and activity.
- It provides a better welfare for the animals.
- Dynamics of feed intake and efficiencies can be studied.

- Compared to metabolic cages, a substantially larger proportion of animals can be tested (sires and dam included), leading to a possible higher genetic gain and a more accurate estimation of genetic parameters.
- Test periods can be extended to cover a larger part of the bird life, optimizing the coverage of periods of highest importance for each product category. Ideally, the control of only a few days considered as sufficiently informative in the rearing period could allow for a higher turn-over of the flocks and a more efficient use of the buildings.
- It provides plenty of information on feeding behavior, which can be split in many elementary traits (*e.g.* number of visits, number of meals, feeding rate…). These traits may be more heritable than plain **FCR** or **RFI**. They can also provide a better understanding of **FE** mechanisms.

Bley and Bessei (2008) first published a description of feeding patterns of Pekin ducks split in groups upon their number of meals. However, the statistical analysis of automatic feeder data owes a lot to the pioneering work of Howie et al (2009), where they describe a method to split feeding behavior into meals, which allows for reliable comparison between animals kept in different husbandry systems. Using this methodology, Howie et al (2010) found out that short-term feeding behaviors have a similar structure in broilers, turkeys and ducks. After Howie et al (2011), who estimated genetic parameters of feeding behavior on a wide range of chicken broiler lines, Le Mignon and Chapuis (2017) performed a similar study on Pekin broilers. Except average daily feed intake (**ADFI**), feeding behavior traits were moderately to highly heritable (0.30 – 0.70) without a strong genetic link with economic traits. Despite these low correlations, which make it easier to introduce these traits in a breeding objective, the cumulative information brought by the measures of nine feeding behavior traits led to an increase in accuracy of **RFI** breeding values for selection candidates.

Thiele (2016) also used data obtained with an automatic feeder, and estimated genetic parameter of feeding behavior traits in the two Pekin broiler lines. Heritabilities were in the same range as Le Mignon and Chapuis (2017): 0.43 and 0.60 for number of meals, 0.49 and 0.57 for duration of feed intake per day, 0.47 and 0.28 for average daily feed intake, 0.49 and 0.42 for meal duration and finally 0.43 and 0.62 for feeding rate, in the two lines.

Validation of the obtained data is a key step (Cobo et al, 2017a), in order to find out an optimal animal density (Cobo et al, 2017b) to allow for reliable results at reasonable cost. Feeding behavior of mule ducks was first deciphered by Basso et al (2014), while Cobo et al (2017c) compared the feeding pattern of the mule duck and its two parental strains. They evidenced that mule duck had intermediate **ADG** and **FCR** compared to the two parental species. The hybrid mule was characterized by feeding behaviors close to the Pekin duck, and production performance approaching the Muscovy duck. Muscovy ducks ate only twice as more as mule or Pekin duck, during visits that were roughly six times longer. Therefore, feeding rate for Muscovy was three time lower than for mule and Pekin.

As stated above, automatic feeders allow for the computation of trajectories and new modeling of feed ingestion. After Jaffrézic et al (2004), David et al (2015), analyzed the pattern of mule duck feed intake across time using structured antedependence models (**SAD**). Such models seem more apt than random regression models to describe the correlation between performances, as the time gap increases. Multivariate **SAD** models (David et al, 2017) now allow for simultaneous analysis of growth and **FI**, and a better deciphering of **FE** data. Simultaneously analyzing longitudinal feeding and growth data permits a new approach of **RFI**, as proposed by Strathe et al (2014) who directly computed the genetic parameters related to **RFI** from a bivariate analysis of **FI** and **BW**.

In addition to accurate measures of **FI**, estimating **FE** via **RFI** usually requires a quantification of body or carcass composition. The **TOBEC** approach has been used in some studies, with limits related to the accuracy of the predicting equation and the bird size. This measure remains a critical point to select animals that are more efficient, without affecting their body composition. In other species, image based approaches have been proposed, and first evaluations of ultrasound measurements in mule duck showed promising results.

Finally, this review on prospects of selection of **FE** traits in duck could not omit the possible advantages of new molecular genomic tools for the improvement of **FE** traits. Marie-Etancelin et al (2014) first presented a detection of genomic regions involved in **FE** traits. These promising results should be refined and extended with the expected forthcoming availability of HD SNP chips, in order to either identify genomic variants with large effects affecting **FE**, or propose genomic selection based approaches enhancing the power of future selection for **FE**.

LIST OF ABBREVIATIONS:

ADFI: average daily feed intake; **ADG**: average daily gain**; BW**: body weight; **FCR**: feed conversion ratio; **FE**: feed efficiency; **FI**: feed intake; **ME**: metabolisable energy; **ME_m**: maintenance energy requirements; **PW:** production weight; **RFI**: residual feed intake; **RFID**: radio frequency identification; **RG**: residual gain; **RIG**: residual intake and gain; **RME_m**: residual maintenance energy; **SAD**: structured antedependance; **TOBEC**: total body electrical conductivity

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