

RESIDUAL FOOD CONSUMPTION AS A TOOL TO UNRAVEL GENETIC COMPONENTS OF FOOD INTAKE

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INTRODUCTION

The concept of residual food consumption (RFC) was first proposed by Byerly (1941) as an approach to limit food costs in the laying hen. The possibility to select on the fraction of total food intake which is not explained by maintenance requirements and production was, indeed, an appealing way to modify food efficiency without any change in production. This was first investigated in poultry, for the laying hen rather than for the broiler, and, later, in mammals. Extensive data have been obtained since 30 years on responses to selection on RFC in the laying hen, including metabolic studies, and, more recently, QTL detection. Sophisticated electronic devices are now available for larger farm animals, and genetic studies of RFC have been undertaken since 20 years in cattle, 10 years in pigs. Thus, this review will analyse the genetic components of food intake, as revealed by selection experiments on RFC in the laying hen, as well as more recent studies on RFC in beef cattle and pig. Furthermore, data are also available from mice selection experiments, with recent developments in QTL analysis.

DEFINITION OF RFC

Prediction equation. The classical prediction equation is a linear multiple regression of observed food intake (FI) on two types of components (1) body weight (BW) or metabolic body weight, corresponding to maintenance requirement, (2) body weight gain (BWG) which may be partitioned in 'protein gain' and 'fat gain', and/or 'exported' product such as egg output, corresponding to production needs. An intercept is generally included. Fixed effects may be added in addition to the covariables, in order to take into account effects of season, litter, or sex. Some options regarding this prediction equation need to be discussed.

Metabolic body weight is obtained as a power of body weight, the most frequently used value being 0.75. In the laying hen, the power value may vary in the range of 0.5 to 1 without affecting the efficiency of the prediction, and body weight has been shown to be an important source of variation in food intake (Hagger, 1991). In the growing pig, however, performance recording is often done at a fixed body weight, and in that case, metabolic body weight does not contribute significantly to variation in food intake (Mrode and Kennedy, 1993), but backfat thickness, and/or loin eye area have been considered as additional predictors of FI.

Another type of predictor to be added could be heat production. Indeed, from the point of view of bioenergetics, metabolizable energy is a function of (1) heat production, (2) energy retained as protein and (3) energy retained as fat (Webster, 1989). Thus, heat production is an obvious component of food efficiency. When heat production was added in the prediction equation of food intake in the laying hen, the residual variation was significantly decreased (Herremans *et al.*, 1989), and this decrease depended on the ambient temperature and on the feather cover of hens, which is also an important parameter for heat dissipation. The use of a direct

measurement of heat loss has been undertaken in a divergent selection experiment on adult male mice (Nielsen *et al.*, 1997a), the results of which will be discussed below. Predictors are most often phenotypic, but, as pointed out by Kennedy *et al.* (1993), the residual will be phenotypically independent from production traits but may not be genotypically independent from them, consequently, the residual may be better obtained from a regression model based on breeding values, assuming that genetic parameters are known. This was not the case, however, at the beginning of most selection experiments on RFC in poultry and beef cattle. It must be noticed that all poultry experiments showed a lack of correlated responses on egg production traits, whereas small variations in body weight were observed in a few cases. Most generally, the expected food intake, is derived from the regression on observed production and body weight. In beef cattle, the expected food intake has been derived also from standard feeding formula obtained from previous nutrition experiments (Arthur *et al.*, 2001). In this case, the prediction equation is fixed across batches or years.

Efficiency of the prediction equation. The residual variation in food intake which is not explained by variation in body weight and production level may represent from 10% to 50% or more of the total variation, according to species, breed, sex, age, and environment. Regression coefficients on the different predictors will vary according to the same factors.

Patterns of energy exchange during growth may be compared between species, using metabolic weight as a reference, for instance, maximal energetic efficiency was shown to be reached at 20% of mature body size for mammals, whereas this maximal value was sustained to a higher degree of maturity for broilers chickens or quails (Webster, 1989). This may have implications regarding the most suitable period to measure RFC during growth, according to species.

Within all species, RFC depends on the breed. Rhode-Island-Red (RIR) layers and White Leghorn (WL) layers showed different regression coefficients, explained by different maintenance requirements, RIR showed higher body weight, % body fat, and % yolk in the egg, resulting in a higher energy content in the egg mass (Bentsen 1983a, 1983b). Differences were also observed within breed between selected lines (Sabri *et al.*, 1991 ; Flock; 1998). In pigs, the Landrace breed was found to have a higher RFC as compared to Yorkshire and Duroc breeds (Mrode and Kennedy, 1993), or to Large White breed (Labroue *et al.*, 1999). In beef cattle, breed differences have been found in efficiency of maintenance, as reviewed by Archer *et al.* (1999). Crossbreeding effects on RFC are not well documented ; one study on laying hens, obtained from crossing high and low RFC lines, showed no reciprocal effect and a negative heterosis, moderate but significant (- 3.6%), on RFC (Bordas *et al.*, 1996).

The effect of sex has not been studied to the same extent across species. In pigs, data are generally obtained on boars only. In cattle, both sexes have been measured but data have generally been pooled to estimate genetic parameters. In the laying hen, selection has generally been done on female RFC records, but, in adult male chickens of a commercial white-egg laying strain, the regression on BW and BWG only, explained only 53% of total variation in FI, much less than that usually observed with a full model in females (Katie, 1991). In the single experiment where RFC was measured and selected independently in adults of each sex the genetic correlation between the male RFC and the female RFC was 0.19, not significantly different from zero (Tixier-Boichard *et al.*, 1995).

Age at measurement is a factor to be considered at two levels (1) time of measurement as compared to sexual maturity (2) length of recording period. Clearly, there can be a major

difference between RFC recorded either in the growing animal or in the adult. In chicken lines selected on RFC of the laying hen, a low phenotypic correlation (0.34) has been found between adult RFC and food efficiency of the growing chick (Kettle, 1991), and no difference was found between food efficiency of growing chicks from two lines divergently selected on adult RFC (Tixier *et al.*, 1988). In these lines, divergence on RFC was shown to take place precisely at the time of sexual maturity (Bordas and Minvielle, 1999). In beef cattle, RFC was not affected by age of the dam, and the genetic correlation between RFC measurements made at 15 or 19 months of age reached 0.90 (Arthur *et al.*, 2001). Independent studies of the length of recording period in the laying hen (Bordas and Mérat, 1975 ; Sabri *et al.*, 1991 ; Luiting, 1991) showed that a short period, such as 4 weeks, starting after the peak of lay, was a good compromise between accuracy of prediction and cost of measurement. A slight decrease in the regression coefficient on egg mass and a marked decrease of the coefficient on body weight gain were found with increasing age in laying hens (Luiting, 1991 ; Hagger, 1991).

The most relevant environmental factors to be considered for the efficiency of RFC estimation are temperature and food composition. High ambient temperature is known to decrease RFC in pigs for instance (Labroue *et al.*, 1999) and genotype x environment interactions are to be expected when lines with high or low RFC are compared at two temperatures, as shown in the laying hen (Bordas and Minvielle, 1997). A low energy diet has been shown to decrease RFC, (Luiting, 1991) and a high protein content is expected to decrease RFC. Differences between laying hens divergently selected on RFC were maintained when protein content of the diet was modified, but performance of high RFC hens was more affected by a lower protein content than performance of low RFC hens (Bordas and Mérat, 1991). Finally, food spillage must be avoided, obviously, to measure *ad lib.* food intake, but differences in feeding behaviour between lines or between individuals may cause some difficulty in the design of food recording systems, as noticed by Hastings *et al.* (1997) in mice.

GENETIC VARIABILITY OF RFC

Many authors have studied heritability of RFC, a range of values will be given only (Table 1). Although estimates may not always be directly comparable, because of different models and different regression coefficients of the prediction equation, it appears clearly that selection on RFC is quite feasible. Heritability would appear, however, to be slightly lower for RFC measured in growing animals (broilers) than in adults (laying hen) within the same species. RFC is always positively correlated with total food intake, across species. Genetic correlations of RFC with its phenotypic predictors are of great interest : in laying hens, correlations between RFC and BW or egg mass are generally low, and in the desirable direction (Fairfull and Chambers, 1984). In broilers, RFC was not correlated with its predictors, start weight and weight gain (Van Bebber and Mercer, 1994). In cattle, genetic correlation between RFC and average daily gain varied between 0.32 to -0.10 according to breeds (Arthur *et al.*, 2001) and up to -0.54 when RFC was calculated as deviation of observed FI from standard food requirements (Arthur *et al.*, 2001). In pigs, correlations between RFC and production traits depended also on the breed and on the choice of predictors. Genetic correlations between RFC and average daily gain, or backfat, ranged from 0.06 to 0.49, or 0.02 to 0.67, respectively (Mrode and Kennedy, 1993; Johnson *et al.*, 1999; Labroue *et al.*, 1999).

Table 1. Range in heritability estimates for RFC across species

Species	Range	Average	References
Laying hen	0.15 to 0.50	0.30	Wing and Nordskog (1982); Bentsen (1983b); Luiting (1991) ; Katle (1991) ; Tixier-Boichard <i>et al.</i> (1995) ; Schulman <i>et al.</i> (1994)
Broiler	0.21	0.21	Van Bebber and Mercer (1994)
Beef cattle	0.14 to 0.44	0.26	Archer <i>et al.</i> (1999) ; Arthur <i>et al.</i> (2001)
Dairy cattle	0.08 to 0.36	0.20	as reviewed by Archer <i>et al.</i> (1999)
Pig	0.10 to 0.38	0.21	Labroue <i>et al.</i> (1999); Johnson <i>et al.</i> (1999)
Mouse:young	0.11	0.11	Hastings <i>et al.</i> (1997)
adult	0.35	0.35	

CORRELATED RESPONSES TO SELECTION ON RFC

These have been investigated extensively in the laying hen, where 4 selection experiments were undertaken independently (1) in France on RIR layers (Bordas *et al.*, 1992) (2) in Norway (Katle, 1991), (3) in Finland (Schulman *et al.*, 1994) and (4) in the Netherlands (Luiting *et al.*, 1991) on White Leghorns. In each experiment, the prediction equation was calculated again at each generation and coefficients could fluctuate between generations.

Heat production (HP). Anatomical measurements related to heat dissipation, such as shank and wattle length in the laying hen, were modified by selection on RFC (Bordas *et al.*, 1992). In experiments (1) (2) and (4), chickens were measured in respiration chambers. Significant differences were always found between high and low RFC lines, representing a 23% increase of total HP for females (Katle, 1991) and a 29% increase, respectively 32%, of total HP in males, respectively females, in a fed state (Gabarrou *et al.*, 1997 ; 1998). Sampling White Leghorn hens on extremely high or low RFC, in a single generation, revealed a difference ranging from 10 to 30% in total HP across two replicates (Luiting, 1991). The main component of the difference in HP was found to be Diet-Induced Thermogenesis (DIT) and not basal metabolic rate in exp. (1). In White Leghorns of exp. (2) and (4), 30 to 50 % of the difference in HP was due to activity-related HP, which suggested that 50 to 70% of it could represent differences in maintenance requirements (Luiting, 1994) and/or in DIT.

Conversely, mice divergently selected on HP differed also on food intake per unit of metabolic body weight, with a higher intake in the high HP line, and a 20.6% difference between lines after 15 generations of selection (Nielsen *et al.*, 1997b). Mice divergently selected on food intake corrected for body weight near sexual maturity showed a trend for a higher HP in high intake lines (+ 14%), but the difference was not significant, and the DIT was very variable among replicated sublines, with no significant difference (Hastings *et al.*, 1997). In this experiment also, no difference was found in digestibility.

Behaviour. High and low RFC chicken lines from exp. (2) differed for a range of behavioural traits, such as walking, pacing, or aggressivity, and hens from the low RFC line were always more quiet and spent more time resting and sleeping (Katle, 1991). Total activity was also lower in hens of the low RFC line from exp (4), which showed also less 'frustration' behaviour (Luiting, 1994), it was suggested, however, that efficient hens may still be susceptible to stress but may exhibit less behavioural possibilities to cope with stress. The study of food intake

pattern in exp. (1) showed a higher number of food access periods for high RFC hens but no difference in the total time spent eating, similarly, high RFC males spent the same time eating than low RFC males, but ate bigger meals, particularly just at the onset of light (Gabarrou *et al.*, 1998). High RFC hens were particularly susceptible to food deprivation at moulting (Bordas, unpublished data). In the pig, young Landrace boars were found to have a higher RFC than Large White boars, and to make also a smaller number of bigger meals, (Labroue *et al.*, 1999) as found in high RFC cocks of exp (1). Different results were obtained with Landrace and Yorkshire growing pigs, where RFC was positively correlated to total time spent eating per day, but not correlated with time per meal (de Haer *et al.*, 1993 ; Von Felde *et al.*, 1996)

Body composition. The 4 selection experiments which were conducted on adult chickens, as well as the selection experiments done on adult mice for heat loss (Nielsen *et al.*, 1997b) or for adjusted food intake (Hastings *et al.*, 1997) showed a lower body fatness in the high RFC lines. The relative difference in fatness between lines could vary from 3 to 100 % of the mean fatness level, highest relative differences were found between mice selected for adjusted food intake and between high and low lines of RIR chickens from exp. (1) (El Kazzi *et al.*, 1995). It must be noticed however, that fatness of the low RFC, high efficient line, could not be considered generally as excessive, but rather at a normal level, whereas fatness of the high RFC line was really abnormally low. Expression of lipogenesis genes was also found to differ between high and low RFC lines (Lagarrigue *et al.*, 2000). Furthermore, fatness was also found to be lower in young chicks from the RIR lines selected at the adult stage (Tixier *et al.*, 1988). In view of the very low level of fat in the high RFC line of exp. (1) it may be suggested also that fat tissue could be used as a substrate for heat production.

Opposite results have been obtained in beef cattle selected for lower RFC, which appeared to be leaner (Richardson, unpublished data) and negative genetic correlations between RFC and lean % have been reported in british Hereford and Charolais young bulls (Herd and Bishop, 2000 ; Renand and Krauss, this congress). In the pig, genetic correlations between backfat thickness and RFC also suggested that selection for decreased RFC should decrease fatness.

Differences observed between studies on beef or pigs, and studies on chickens or mice, could be due to different ages or to different species. Performance recorded on beef and pigs involved growing animals, for which protein synthesis is more efficient than fat deposition, whereas, in the adult, maintenance requirements are higher for protein than for fat, for a similar liveweight. Regarding protein turnover, however, muscle proteins may be distinguished from visceral proteins, because visceral organs are known to have a high metabolic activity (Archer *et al.*, 1999). Indeed, Angus steers differing in RFC differed also in intestinal weight, proportionally higher in less efficient animals (Richardson, unpublished data). Interestingly, in chickens, the high RFC line of exp. (1) showed a higher proportion of viscera in females only, with a significant line x sex interaction (El-Kazzi *et al.*, 1995). Thus, a variable proportion of visceral proteins as compared to muscle proteins could be a source of RFC variation, particularly in ruminants characterized by a large visceral mass. This would explain why selecting for lower RFC may result in a relatively higher % muscle proteins, to the contrary of the observations made in adult chickens or mice.

Reproduction and fertility. Few data are available on these traits, which are not consistent between species : in the chicken, fertility and hatchability were significantly decreased in the

high RFC line of exp. (1) as compared to low RFC line (Bordas and Mérat, 1993), whereas in mice, litter size was decreased in the line selected for low HP, mainly because of a change in ovulation rate (Nielsen *et al.*, 1997b). Further investigations on male fertility in chicken lines of exp. (1) revealed a lower % of normal sperm cells, and a lower motility, which could be explained by a lower overall mitochondrial activity (Morisson *et al.*, 1997). This result suggested an altered production of energy at the cellular level.

Physiological indicators. In chickens, body temperature differed significantly for males only in exp. (1), being higher in the high RFC line ; in exp. (2) a trend was observed for a higher body temperature in females. Comb temperatures were also higher in high RFC males and females from exp. (1) and in females of exp. (2). In cattle (Richardson *et al.*, 1996) as in chickens (El-Kazzi *et al.*, 1995), differences were found on blood volumes. Few data are available on hormonal or biochemical parameters. Plasma levels of uric acid and proteins increased in high RFC line (El-Kazzi *et al.*, 1995). In chickens of exp. (1), the administration of propranolol decreased HP, suggesting a β -adrenergic control of HP. Higher plasma levels of thyroid hormones and lower levels of insulin were found in high RFC males in a fed state, which could account for their higher HP and increased leanness (Gabarrou *et al.*, 2000).

In view of the increased thermogenesis in adult chickens selected on high RFC, together with the abnormal mitochondrial activity in sperm cells, recent studies focused on the uncoupling protein (UCP), which shows different forms, UCP1 specific to brown adipose tissue (BAT), and UCP2 or UCP3 expressed in other tissues such as muscle. The avian homologue of UCP2 and UCP3 was cloned, and because the chicken is devoided of BAT, UCP expression was studied in muscle and was found to differ significantly between the high and low RFC lines of exp. (1) (Raimbault *et al.*, 2001). This result could suggest a mechanism able to explain probably most of the differences in HP found between the divergently selected lines.

QTL DETECTION

Complementary to the physiological approach just presented with the UCP study, studies have also been undertaken in order to identify QTL regions controlling the variability of RFC, HP or other traits differing between lines divergently selected in chickens and in mice. In both cases, F2 design were set up. In chicken lines, a rather high level of inbreeding limited the informativity of microsatellite markers, but a few regions have been identified : in particular chromosome 10 was shown to carry a QTL affecting shank length in males but not in females, (Tixier-Boichard *et al.*, 1998) as well as a QTL affecting RFC in females, whereas another QTL affecting total FI in females was identified on chromosome 11 (Pitel *et al.*, 2001). More QTLs have been suggested in males, that will have to be confirmed, and additional chromosomes are being studied in females. In mice, F2 crosses were set up in order to detect QTL between high and low HP lines (LH cross), as well as between the high HP line and an unrelated inbred line (HB cross). Five QTL regions were associated to a significant effect on variability of heat loss, some of them affecting also BAT weight, additional QTL regions were identified for fat %, body weight, liver % and heart % (Moody *et al.*, 1999). Search for candidate genes in the most significant regions may indicate future ways for research ; interestingly enough, UCP2 and UCP3 genes were located in one QTL region on mouse chromosome 5 affecting heat loss and total fat %. The study of chicken chromosomal regions homologous to mice QTL regions was attempted in the F2 cross between high and low RFC

lines, but lack of informative microsatellite markers limited this approach. From these studies, it can be expected that, soon, new tools will be available to monitor genetic variability in heat production independently from production traits.

CONCLUSIONS

This review was not aimed at a general discussion of selection for food efficiency, but rather at investigating the information brought by using RFC. In the laying hen, RFC has been used in the selection of commercial lines since many years. The main difference to be expected from selecting on RFC as compared to food conversion ratio involves the correlated response in BW, in layers as well as in broilers (Flock, 1998 ; van Bebber and Mercer, 1994). Correlated responses to single-trait selection RFC clearly underlined the importance of heat production and body composition and did not reveal useful variation in feed digestibility. The main sources of variation of HP appeared to be diet-induced thermogenesis and activity, rather than basal metabolic rate. Regarding environmental issues, low RFC lines may have more difficulties to adapt to high ambient temperature, because of limited heat dissipation, which is of importance for heat tolerance and adaptation to tropical climate. High RFC lines will maintain a higher FI and a better production level, whatever the temperature, but are expected to produce more manure, rich in proteins. Regarding body composition, species may react differently to selection on RFC : RFC appears a promising tool to monitor body composition in beef cattle, but the importance of age at selection relative to sexual maturity must be kept in mind. Finally, the QTL approach is expected to bring new data on the genetic control of appetite and HP, with potential applications in animal breeding but also in medicine.

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