Netherlands Journal of Agricultural Science 42-1 (1994) 59-67

Between-animal variation in biological efficiency as related to residual feed consumption

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Received 27 December 1993; accepted 16 February 1994

Abstract

Production levels in livestock have been increased considerably, with a correlated increase in gross feed efficiency. However, mature body weight has also increased, leading to higher maintenance costs. Thus, net feed efficiency has not been improved much. Breeding for lower body weight has not been successful, but there exist possibilities for reduction of feed consumption independent of production and body weight (residual feed consumption). It is as yet uncertain to what extent animal stress susceptibility will be affected by changes in residual feed consumption.

Keywords: net feed efficiency, residual feed consumption, breeding, stress, pollution

Introduction

Production levels of all livestock species have increased considerably, not only as a result of improved nutrition and husbandry but also as a result of breeding. This increase in production has resulted mainly in a corresponding increase in feed consumption for production. This can be illustrated in laying hens; based on energy requirements the American National Research Council (NRC, 1984) described feed consumption in laying hens (for a diet containing 11.7 kJ g^{-1} metabolizable energy) as: 46.5 x average (body weight)$^{3/4}$ + 0.74 x egg mass production. It follows that an increase in egg mass production will result in a corresponding increase in feed consumption for production (0.74 x egg mass production). In addition, the part of feed consumption that is required for maintenance (46.5 x average (body weight)$^{3/4}$) will be divided over a larger amount of product (egg mass production). As a consequence, feed conversion - defined as total amount of feed divided by the total amount of product - has decreased in practice. Gross feed efficiency, being the reciprocal of feed conversion and an economically important parameter, is therefore increased.

Feed efficiency

The above relations hold for both juvenile slaughter animals and adult production animals (dairy cows, laying hens, etc.).

Juvenile slaughter animals

The effect of increased production on feed efficiency in species used for meat production consists not only of the above-mentioned dilution effect of maintenance feed over more product, but also of the effect of a physiologically lower age at a fixed slaughter weight. Selection for a fast growth rate at a fixed slaughter weight favours animals with a genetically larger mature size (Ogink, 1993). These larger-sized animals are physiologically less mature at equal slaughter weight, being at a lower proportion of their mature weight. Both lean proportion and feed efficiency tend to decrease as animals mature. Hence, this kind of selection leads to a higher lean proportion and feed efficiency at this fixed slaughter weight, only as a result of a lower degree of maturity at slaughter.

There are still two remarks to be made. In the first place, this effect will disappear when slaughter weights are increased (which is a common development). In the second place, the increased mature body size is expressed in the parental stock, which become very heavy and expensive to maintain. Hence, there is an antagonistic relation between increased production (expressed in juveniles) and maintenance costs of the population (expressed in adults). An attempt to overcome this antagonism has been the introduction of the sex-linked dwarf gene in broiler dam lines; however, this technique is not yet fully economically feasible.

Adult production animals

An antagonism between increased production and maintenance costs appears in adult production animals (dairy cows, laying hens, etc.) too. According to genetic size-scaling theory, an increase in (milk or egg) production inevitably leads to an increase in adult body weight, and hence in maintenance requirements (Taylor, 1985). Consequently, there is an antagonistic relation between increased production and maintenance costs, both expressed in adults. An attempt to overcome this antagonism has been selection for a low adult body weight (accompanying selection for a high egg production) in laying hens (Case 1); again, however, this technique is not yet fully economically feasible, and in addition the observed decrease in maintenance requirements has not been as large as expected from the realized reduction in body weight.

Feed consumption

In conclusion, one-sided genetic selection for high production will automatically lead to animals with increased maintenance requirements and, hence, to higher feed requirements, higher feed costs, less efficient usage of feed resources, higher heat production, higher CO_2 emission, higher manure production and higher environmental pollution. In animal breeding in the western world, the emphasis is gradually shifting from increasing production to increasing feed efficiency while keeping production levels constant. The antagonisms between production and maintenance costs appear to be difficult to overcome by using body weight reduction techniques. Accordingly, many breeders (in slaughter as well as egg production species) have started to select for low feed consumption or high feed efficiency in addition to selection for high production, even though measurement of feed consumption is difficult and expensive.

Over the last 10 yr, Random Sample Test data of laying hens in The Netherlands and Germany have shown a steady improvement in feed conversion, accompanied by a large increase of egg mass production and a small decrease of body weight. Multiple regression of these feed conversion data on the corresponding egg mass production and body weight values showed that the variations in the latter traits accounted for 91% to 99% of the differences in feed conversion from 1980 to 1990 (Luiting, 1991). Feed consumption does not show a clear time trend in these data; the effects on feed consumption of a higher egg mass production and a lower body weight almost balance. These relations of feed conversion with egg mass production and body weight can also be found in the literature as estimated on individually measured hens, and as correlated responses for feed conversion in selection experiments for high egg mass production or low body weight. Most phenotypic and genetic correlation estimates of feed conversion with egg mass production are between -0.5 and -1; those with body weight are mostly between 0 and 0.5 (Luiting, 1991).

Net feed efficiency

In various livestock species, a considerable variation in voluntary feed consumption has been shown to exist among individuals with equal production and body weight levels. This implies that animals can be found with a high production level and at the same time low maintenance requirements. Selection programmes such as those mentioned above will only be successful if there exists genetic variation in feed consumption when production and body weight are kept constant, thus in net feed efficiency (being a biological parameter, in contrast to the economic parameter, gross feed efficiency). For example, in terms of the feed requirement equation given in the 'Introduction' (NRC, 1984), the 'constants' 46.5 and 0.74 are expected to vary among animals and this variation is expected to have a genetic background.

Residual feed consumption

Such variation in net conversion coefficients can be quantified by measuring it in individual animals only at great cost and with as yet unsolved experimental problems (Andersen, 1980; Damme, 1984; Luiting et al., 1992). An alternative would be to quantify the variation of feed consumption, adjusted for production and body weight levels by means of multiple regression techniques, making use of the residual. The

Table 1. Coefficients of determination (R^2) of the multiple regression models to estimate residual feed consumption, and its heritability (h^2) in various species (references in Korver, 1988; Luiting, 1991; De Haer et al., 1993).

Species	R^2 (%)	h^2 (%)
Pigs	32	45
Pigs	7-40	19-67
Beef cattle	34-52	28
Heifers	38	22
Poultry	22-77	10-45

determination of residual feed consumption as observed feed consumption, linearly adjusted for production and metabolic body weight levels, provides an indirect measurement of net maintenance requirements of an individual animal. It has been proven to be quite repeatable and heritable in various farm animal species (Table 1). On average over species, about 60% of the variance of feed consumption is not explained by multiple regression, and about 35% of this unexplained variation turns out to be genetic variation.

Genetic aspects

Most studies in the literature concerning residual feed consumption in laying hens, including our own studies in White Leghorns (Luiting, 1991), showed that egg mass production and body weight explain 60% to 80% of the feed consumption differences that can be observed between hens (R^2). This means that residual feed consumption is 20% to 40% of the variation of feed consumption. In our hens, measured over the whole laying period, this trait showed a standard deviation of 6 $g.d^{-1}$, a repeatability of 50%, and a heritability of 40%. Phenotypic and genetic correlations to egg mass production and body weight were found to be zero, as would be expected phenotypically because residual feed consumption has by definition been adjusted for these traits. We selected for a low and a high residual feed consumption for four generations, which has resulted in very clear selection responses in (residual) feed consumption (Figure 1), but not in egg mass production and body weight. Three other selection experiments on residual feed consumption in laying hens confirm this (Liuttula, 1989; Katle & Kolstad, 1991; Bordas et al., 1992). We conclude that residual feed consumption shows a considerable amount of systematic and permanent phenotypic and additive genetic variation.

Biological aspects

From statistical and especially from experimental results of work in respiration chambers studying the partitioning of feed energy over the biological processes in the body (Luiting, 1991; Luiting et al., 1991), it can be concluded that the variation in residual feed consumption in laying hens is mainly caused by variation in maintenance requirements of hens with similar egg mass production and body weight. In a

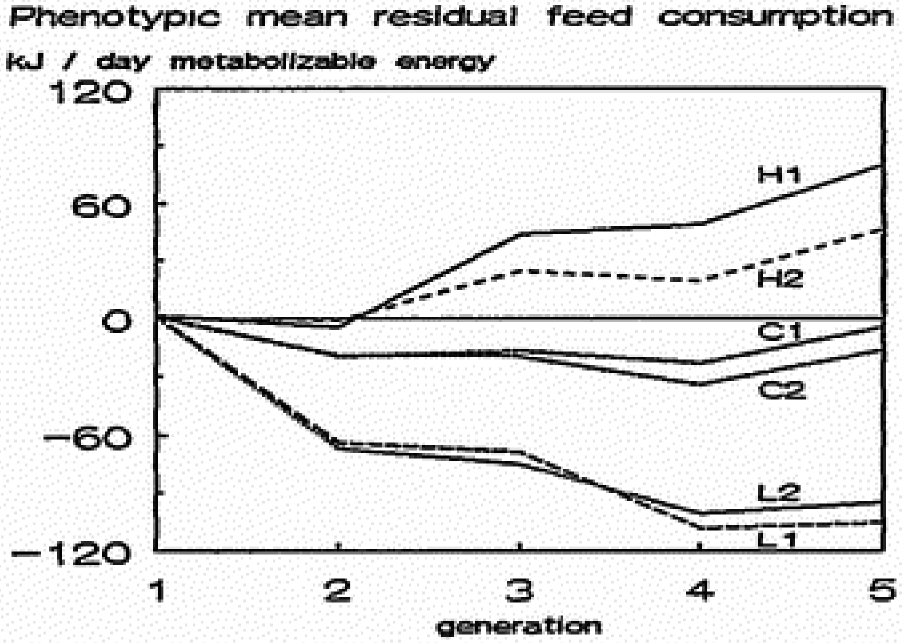

Figure 1. Results of a selection experiment in laying hens for low (L) or high (H) residual feed consumption in duplo on two diets (1, 2) with different energy content. C: control lines (Luiting, 1992).

quantitative sense, the most important sources of this variation seemed to be differences in physical activity, in the energetic requirement for sustaining body temperature and in basal metabolic rate. Hens with a lower residual feed consumption are less active (Figure 2), have smaller unfeathered body areas through which they can lose energy, tend to be slightly better feathered, and have a lower basal metabolic rate. Differences in digestibility and metabolizability of feed energy and differences in the heat increment of production (e.g. differences in composition of eggs and deposited body mass) turn out to play an unimportant role. The results about digestibility and activity have been confirmed by De Haer et al. (1993) in growing pigs.

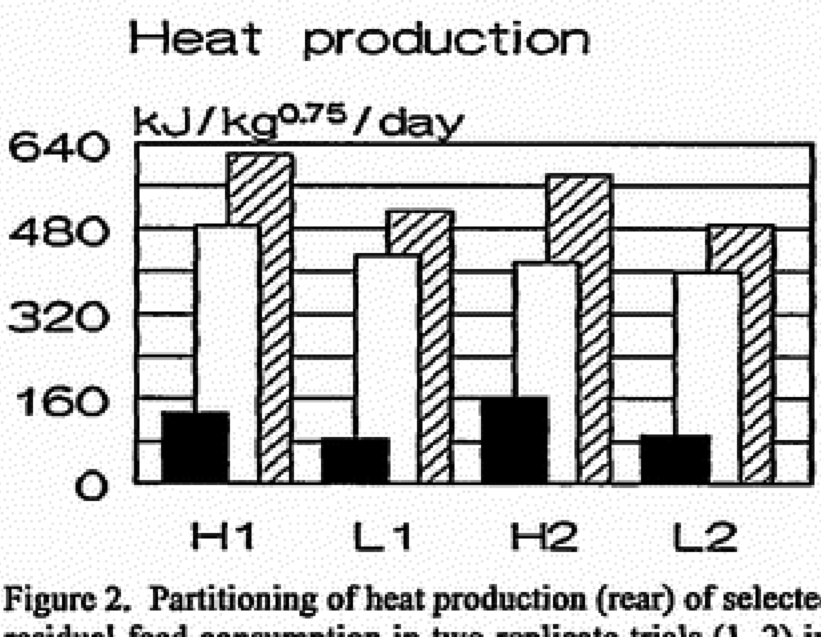

Figure 2. Partitioning of heat production (rear) of selected hens with a high (H) or a low (L) residual feed consumption in two replicate trials (1, 2) into a zero-activity (middle) and an activity related part (front) (Luiting et al., 1991).

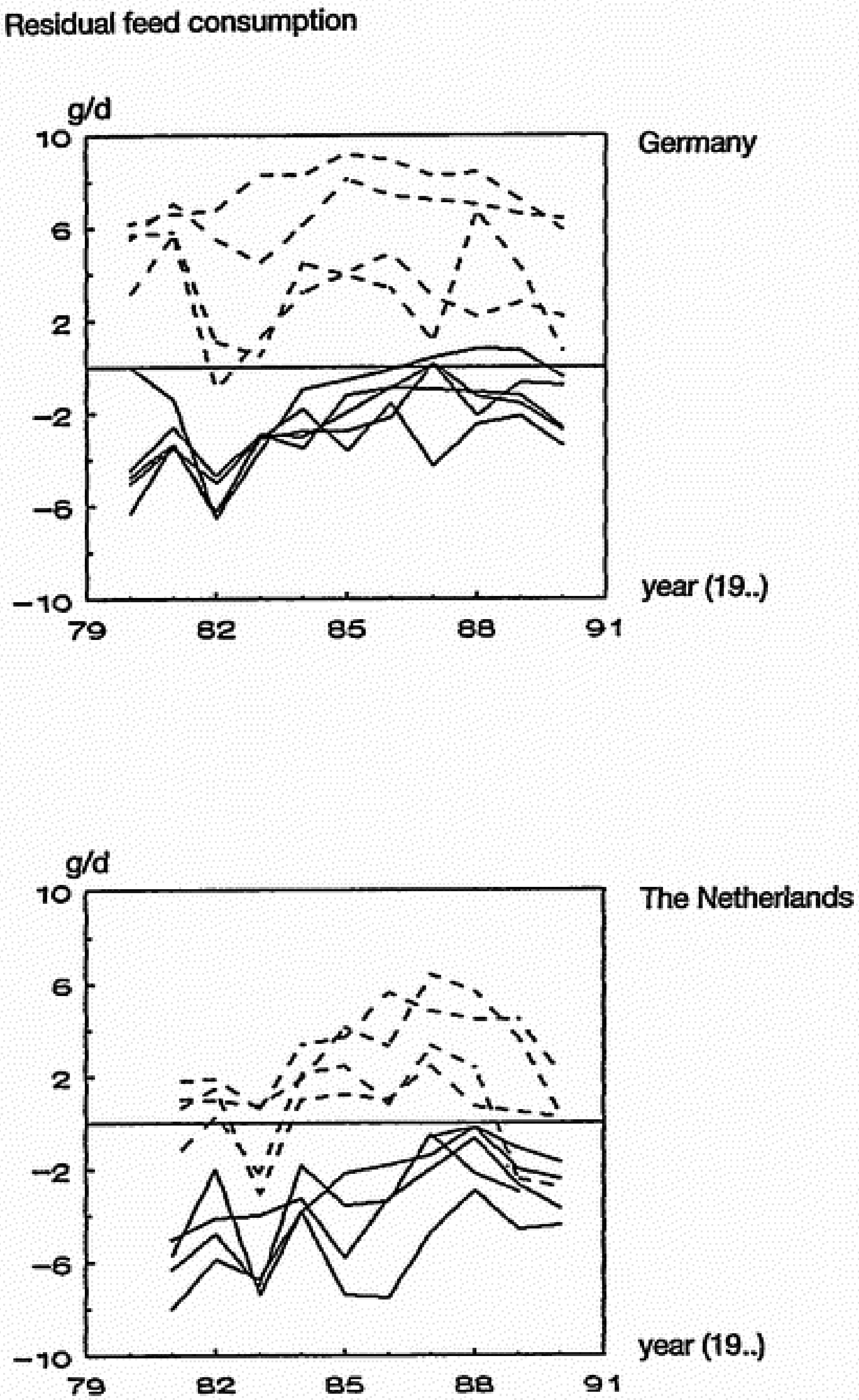

Figure 3. Time trends of residual feed consumption in German and Dutch Random Sample Test data. Solid lines: brown hens; dotted lines: white hens (Luiting, 1992).

Practical selection up to now

It would be a challenge for animal breeding to exploit this evident variation among animals which would eliminate the supposed automatism of genetic progress in production being accompanied by increased maintenance requirements with its accompanying undesirable effects for the environment.

As can be seen in Figure 3, residual feed consumption (calculated by means of the feed requirement equation given in the 'Introduction'; NRC, 1984) does not show a clear time trend in the white hen lines in the German Random Sample Tests nor in the Dutch ones (Luiting, 1992). The residual feed consumption of some of the brown hen lines seems even to increase over time (on average annually by 0.4 and 0.3 g d^{-1} in Germany and The Netherlands, respectively). The white lines, with a body weight around 1.7 kg, naturally have a higher gross feed efficiency than the brown ones, with a body weight around 2.2 kg, but not to the extent that would be expected from their body weight difference; Figure 3 shows that the net feed efficiency in the white lines is worse (i.e. higher residual feed consumption). The absence of a time trend in hens that lay white eggs reveals that the selection activities over the past 10 year have not exploited the variation in residual feed consumption and, therefore, did not achieve a clear improvement in net feed efficiency. The increase over time seen in some brown hen lines means that the selection that has been practised has even reduced net efficiency, although gross feed efficiency has generally been improved.

Susceptibility to stress

However, apart from the favourable effects of a reduction of feed consumption for the environment, some possible side effects for the animals themselves need more study. Present knowledge indicates that genetic selection for a low residual feed consumption will lead to less active animals; in our own selection experiment, 80% of the genetic difference in residual feed consumption between the divergent lines could be related to a difference in physical activity. This is in line with the behaviour studies in the Norwegian selection experiment for residual feed consumption in white laying hens (Braastad & Katle, 1989). When animals with low and high residual feed consumption (efficient versus inefficient feed utilization) were compared, those with low residual feed consumption were found to show less 'frustration' behaviour (which is connected to long-term stress from an ethological point of view), e.g. less aggressive behaviour, less flight behaviour, less pre-laying pacing, and less standing with head movements. This leads to the conclusion that animals with low residual feed consumption may be less sensitive to stress. In a similar French selection experiment (using brown hens), the animals with low residual feed consumption showed lower blood corticosterone levels after being handled at a young age, which again suggests lower susceptibility to stress.

However, when old hens from our own selection lines were transferred to respiration chambers, animals with low residual feed consumption showed more moulting, more weak egg shells and a longer adaptation period to the respiration chambers (which are regarded as symptoms of stress). This would lead to the opposite conclusion: animals with low residual feed consumption may be more sensitive to stress.

In species for meat production, selection for a fast growth rate in combination with a high feed efficiency generally leads to heavy animals with a large proportion of glycolytic fast-twitch muscle fibres and a low physical activity level. The proportional increase of this muscle fibre type may result in an increased susceptibility to stress, which in these species is expressed primarily in terms of transport losses and deteriorated meat quality (Henckel, 1992).

A clear question arising from these findings, and still to be answered, is: are animals with a high net feed efficiency less or more sensitive to stress? The reduced activity may be regarded as a development towards less susceptibility to stress, but it is also possible that these animals have fewer (behavioural) possibilities to cope with stress. It is clear that such issues can only be solved by an interdisciplinary research approach to rediscover the biological basis for animal production as a first step to new sustainable animal production systems.

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