

## DOES SELECTION FOR HIGH PRODUCTION AFFECT PROTEIN TURNOVER RATE?

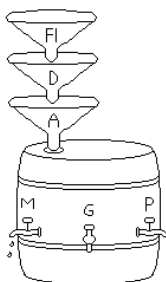
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### INTRODUCTION

Rauw *et al.* (1998) have shown that genetic selection of livestock species for high production is often compromised by physiological and immunological problems. For example, a faster growth rate in broiler chickens runs parallel with an increased incidence of ascites (Scheele, 1996). Breeding for high lean tissue growth rate in pigs prolongs in many cases the weaning to farrowing interval (Ten Napel, 1996). In general, high producing dairy cows are bred later, show more days open and require more services per conception than low producing cows (*e. g.*, Berger *et al.*, 1981). These undesirable side effects of selection may result from an unbalanced resource situation. Resources come from food intake or body reserves. Input constraints (food intake, digestion and absorption) are engaged in series whereas outputs (maintenance, growth and production) are parallel (Figure 1). If the sum of output rates does not match the input, the balance is buffered by body reserves. In the long run, however, energy expenditure must balance energy intake (Weiner, 1992). When 'genetically forced' to produce highly, disproportionally many resources may be (re)allocated towards the production trait, leaving the animal lacking in ability to respond to other demands (Beilharz *et al.*, 1993; Rauw *et al.*, 1999). When resources are limited, the body may be economising on the level of protein turnover, because this is a very expensive metabolical process.



**Figure 1. The barrel model of an organism's energy balance (after Weiner, 1992). The first spigot always leaks (basal metabolic rate). FI = food intake; D = digestion; A = absorption; M = maintenance; G = growth; P = production**

The objective of this paper is to discuss the possible relationship between high production, changes in resource allocation patterns and changes in protein turnover rates. First, results are presented on experiments done in mice that show how selection for high litter size has changed resource allocation patterns (Rauw, 2001). The second part will discuss the effect that selection for high production may have on protein turnover rate.

## **SELECTION FOR LITTER SIZE CHANGES RESOURCE ALLOCATION PATTERNS**

In a series of studies, Rauw *et al.* (*e. g.*, 1999, 2002) investigated changes in resource allocation patterns with long-term selection for litter size using a mouse model. It was hypothesised that animals selected for high litter size allocate a larger amount of resources to the trait selected for, leaving less resources to respond to other demands. The females used for the studies originated from two lines of the Norwegian mouse selection experiment: a line selected for more than 90 generations for high litter size at birth (S-line; about 20 pups born per litter) and an unselected control line (C-line; about 10 pups born per litter).

Estimates of mature virgin body weight and mature virgin daily food intake were higher in the S-line than in the C-line (38.7 vs. 28.8, and 6.14 vs. 4.66; Rauw *et al.*, 2002). Virgin residual food intake (RFI-Virgin) at maturity, which is defined as the difference between the food that actually is consumed by the animal and its predicted consumption from observed body weight and growth, was also higher in the S-line (0.927 g/d more) than in the C-line. RFI-Virgin is an estimate of food intake that is independent of differences in body weight and growth and is suggested to be an estimate of the amount of 'buffer' resources that are available for, *e.g.*, physical activity and the ability to cope with unexpected stressors (Rauw *et al.*, 1999).

The larger amount of food resources available to non-reproductive mature S-line females for processes other than maintenance and growth may be intended for the highly increased resource-demanding processes of pregnancy and especially lactation. Therefore, resource allocation patterns and the consequences for pup development were investigated in lactating females of both lines. Residual food intake from farrowing to peak lactation (0 to 2 weeks in lactation) and from peak lactation to weaning (2 to 3 weeks in lactation; RFI-Lactation) was lower in S-line females (1.69 and 0.75 g/d less, respectively) than in C-line females. RFI-Lactation is an estimate of food intake that is independent of differences in body weight, growth of dam and litter, and of litter size, which indicates that S-line females allocate more resources to the processes that support milk production and have consequently fewer resources left to respond to other demands. Furthermore, pre-weaning mortality rate was higher in S-line litters (35.6%) than in C-line litters (18.1%) and degree of maturity (*i. e.*, body weight as a percentage of mature body weight) from birth to weaning was about 25% higher in C-line pups than in S-line pups. These results show that the higher amount of available resources at maturity were not sufficient to buffer the highly increased resource demand without compromising other processes. Therefore, these animals, while supporting the genetically highly increased litter size, may be more at risk to behavioural, physiological and immunological problems. Although S-line females allocated a particularly large amount of resources towards lactation, this was insufficient to provide the offspring with an adequate amount of resources, resulting in reduced pup development and increased pre-weaning mortality rates (Rauw *et al.*, 2002).

## **SELECTION FOR HIGH PRODUCTION MAY CHANGE PROTEIN TURNOVER RATE**

The metabolic basis for the inverse relationship between high levels of production and health and welfare of high producing animals can be investigated by studying the protein turnover

rate. Protein turnover is defined as the continuous breakdown and replacement of cellular proteins. Protein turnover is essential for life since it provides the flux that is necessary for metabolic regulation and adaptation. It enables the metabolic adjustments that are required for reproduction and development, the repair of damaged tissue, combating infection, and during or following changes either in the environment or in the nutritional/physiological status (Hawkins, 1991). Furthermore, Pirlet and Arthur-Goettig (1999) suggest that specific degradation of defective, old, damaged, denatured protein molecules forces the selection of structurally superior proteins.

Protein turnover is essential for life, but is also expensive. Because of the positive relation between protein synthesis and metabolic rate, protein turnover represents a general index of the energy requirements for maintenance, with a minimal estimate of about 20% for the contribution of protein synthesis to maintenance metabolic expenditure (Hawkins *et al.*, 1989). Therefore, when the body economises on protein turnover rate, a considerable amount of energy may become available for other processes (Hawkins, 1991). Likewise, when in a limited resource situation more resources are allocated towards high production values, the body may be economising on the level of protein turnover.

This hypothesis is supported by several studies, especially those in fish and shellfish: a higher growth efficiency by adopting a lower protein turnover strategy has been shown in ratfish (Carter *et al.*, 1998), catfish (Conceicao *et al.*, 1997), rainbow trout (McCarthy *et al.*, 1994) and in mussels (Hawkins and Day, 1996). Bates and Millward (1981), Tomas *et al.* (1991) and Oddy *et al.* (1995) reported that breeding programmes have resulted in slower protein turnover in rats, chickens and lambs selected for increased growth rate, leading to lower energy expenditure and higher growth efficiencies.

Similar results may be found in animals that are selected for high litter size or other production traits. According to Bauman and Currie (1980), the functions of pregnancy and lactation have a very high priority over other functions, which allows them to proceed at the expense of other metabolic processes even to the point that a disease state is created. In case net protein production for lactation has the highest priority, the body may have to economise on the level of protein turnover. Indeed, Roberts and Coward (1984) indicated that lactating rats used significantly less energy for activity and maintenance than virgin animals and suggested that this is due in part to decreased rates of protein turnover. A shortage of amino acids because of protein restriction in the diet showed that lactating women adapt rapidly by down-regulating rates of body protein degradation and synthesis (Motil *et al.*, 1996). They suggest that a significant decrease in body protein turnover is an unfavourable metabolic condition that is inconsistent with an acceptable protein nutritional status over the long term, because in this condition it would be hard to support maternal well-being as well as milk production.

The most commonly used technique for the measurement of total body protein synthesis involves infusion or oral ingestion of a labelled amino acid (e.g.,  $^{13}\text{C}$ -,  $^{14}\text{C}$ -,  $^{15}\text{N}$ -, or  $^3\text{H}$ -labelled lysine, tyrosine, leucine or glycine) and the monitoring of the specific activity of the amino acid in the plasma (Butterly, 1981). The specific activity tends to plateau after several hours at which moment the flux of the particular amino acid (*i. e.*, synthesis and breakdown) can be

calculated. There can be no definite statement as to which is the best labelled amino acid to be used in protein metabolism studies with intact animals. The advantage of <sup>15</sup>N-labelled (*i. e.*, a stable isotope) amino acids is that the carcass may still be suitable for human consumption (Butterly, 1981). Several studies in pigs have used <sup>15</sup>N-glycine (*e. g.*, Roth *et al.*, 1999). With a slower protein turnover rate the scope for adaptability of the body to environmental stressors and challenges becomes narrower, putting the animal at a higher risk to behavioural, physiological and immunological problems. Further research should investigate how changes in resource allocation patterns relate to changes in protein turnover rates. Insight into this topic may provide solutions to the problem of production stress in highly producing animals.

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