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INTRODUCTION

Biological efficiency in a meat producing enterprise can be defined as the ratio of output (i.e. body weight, or the weight of lean produced), to input (i.e. the total weight of food consumed). There are numerous reports of genetic variation in food intake, food efficiency, growth rate and body weight in animals. However these parameters are often highly correlated, so that genetic change in the output can often result in a corresponding change in the input, and there may be little net change in the efficiency ratio.

This paper examines the relationship between food intake, food efficiency and growth characteristics for animals in a meat producing enterprise. The scope for independent genetic variation, and the effect of genetic change in such characters on both the shape of the growth curve, and the biological efficiency of the enterprise, will also be examined.

THE SIGMOIDAL GROWTH CURVE

If an animal is given access to unlimited food, the change in body weight with respect to age tends to follow the sigmoidal growth curve. That is, initially growth rate accelerates until the point of inflexion, whereupon growth rate decelerates as the animal approaches its asymptotic weight, i.e. the mature weight of the animal in that particular environment. The mature weight of an animal may be affected by the quality and quantity of the food on offer, and other aspects of the environment. Parks (1982) showed that in laboratory animals, mature weight declined as the energy concentration of the diet was reduced, although variation in protein concentration had little effect on mature weight. Parks (1982) also showed that an increase in ambient temperature resulted in a large decline in the mature weight of

laboratory animals. Therefore the mature weight that an animal expresses is specific to a particular environment, and as will be discussed later, may interact with the environment.

SCALING RULES

When raised in the same environment, animals from a large mature weight genotype will achieve a greater final weight than animals from a small mature weight genotype. As discussed by Taylor (1982), when examined over a range of genotypes, many parameters such as food intake, food efficiency, growth rate and body composition tend to be well related to stage of maturity of body weight. Therefore the final body weight that an animal achieves can be viewed as a physiological end-point of growth, which is similar for both large and small mature weight animals. If animals from large and small mature weight genotypes are compared at the same body weight, animals from the large genotype will be physiologically less mature than animals from the small genotype, and therefore differences in physiological parameters will be confounded by differences in stage of maturity.

Similarly, animals from a large mature weight genotype take longer to reach their mature weight, than animals from a small mature weight genotype. Taylor (1965, 1968, 1980) quantified the relationship between time taken to mature and mature weight for a wide range of species, showing that larger animals took longer to mature in proportion to their mature weight raised to the power 0.27. Therefore the comparison of physiological parameters in large and small genotypes at the same age will also be confounded by stage of maturity of the animal, although the magnitude of the bias will be less than for comparisons at the same weight.

As a means of overcoming the confounding with stage of maturity, Taylor (1980a) proposed two scaling rules. The first rule states that all age or time variables be scaled by mature weight raised to the power 0.27, and the second rule that all cumulative input and output variables be scaled by mature weight. The application of these rules and their corollaries should account for systematic changes in the input-output characteristics that are associated with genetic differences in mature weight. If physiological parameters of the animal, such as weight and growth rate at immature ages, food intake, milk production and body composition were perfectly associated with mature weight, then the application of the scaling rules would remove all variation in these parameters. Although a large proportion of the variation in physiological parameters is removed by scaling, Taylor (1980a) noted that there is usually some variation which is independent of mature weight. Taylor (1980a) stressed that although the amount of genetic variation which is independent of mature weight may often appear to be small, it should not be dismissed as being unimportant, but rather the reverse, as exceptions to the scaling rules will play an important role in future animal breeding.

THE STANDARDIZED GROWTH CURVE

As an application of these scaling rules, Taylor (1980c) examined growth patterns from the early embryonic stage to maturity in a number of domesticated species. He showed that a single standardized growth

curve could be used to describe the lifetime pattern of growth, in species which varied widely in mature weight. However for particular species, there were significant deviations from the mean growth curve. These included rabbits, which were estimated to mature faster than expected for their mature weight, and guinea pigs which matured at a slower rate than expected for their mature weight.

If all feeding and growth parameters were assumed to be perfectly associated with mature weight, equations which describe the feeding and growth processes could be scaled, so that the parameters of such equations were independent of the mature weight of the animal (Taylor 1980c). As these standardized equations can describe both the outputs and inputs of a production system they can be used to model biological efficiency of the production unit.

Taylor et al. (1985) used standardized feeding and growth equations to model the effect of various management options on the biological efficiency of the dam/offspring unit in a cattle enterprise. The costs of various events, such as the onset of puberty, pregnancy and the calving interval were defined in terms of standardized food units (ie kg of food/mature weight). They showed that if reproductive rate was assumed to be independent of mature weight, then biological efficiency of the dam/offspring unit in a self-replacing herd was independent of mature weight of the genotype. This is perhaps not surprising, as all inputs and outputs in the dam/offspring unit were assumed to be perfectly associated with mature weight. In pasture-based cattle and sheep enterprises, age at first mating, the calving or lambing interval, and culling age for mature females are not proportional to mature weight, but rather are generally timed to fit into an annual management system. Therefore when these events are constrained to an annual production system, biological efficiency of the dam/offspring unit is positively related to mature weight, as smaller genotypes are disadvantaged by being kept for a metabolically longer time (Thompson and Barlow 1986). However the magnitude of this increase in biological efficiency is small, with a 25% increase in mature weight resulting in only a 4% increase in biological efficiency.

If all food intake, food efficiency and growth parameters were perfectly associated with mature weight, the opportunity to change the shape of the growth curve and therefore improve biological efficiency of the dam/offspring unit in a self-replacing herd or flock would be limited. However as mentioned previously, the association is not perfect, thereby providing opportunities to bend the shape of the growth curve and consequently change the biological efficiency of the dam/offspring unit. The following sections will examine genetic variation in feeding and growth parameters which is independent of mature weight, and the effect of such variation on the shape of the growth curve and the subsequent biological efficiency of the dam/offspring unit.

GENETIC VARIATION IN THE SHAPE OF THE GROWTH CURVE

Body weight at immature ages tends to be moderately heritable and positively correlated with mature weight (Brinks et al. 1964). Therefore selection for body weight at a particular age will generally result in an increase in body weight at that age, along with a

correlated response in mature weight. Unfortunately most selection experiments which have examined the response to weight selection, have not reported the correlated response in mature weight, whilst correlated responses in other parameters such as food intake, food efficiency, growth rate and body composition have generally been reported at the same age, or at the same weight, and are therefore to some extent confounded by differences in stage of maturity.

The extent of genetic flexibility in the shape of the growth curve depends on the strength and nature of the genetic relationship between immature weights and mature weight. Fitzhugh (1976) discussed the possibility of improving the production characteristics of animals by changing the shape of the growth curve. He listed several advantages of moving the growth curve to the left (that is producing faster maturing animals) which included; the ability to have efficient early growth in slaughter progeny combined with a lower maintenance cost of parental stock, improved intrinsic efficiency through improved maturation rate, reduced dystocia and finally a lower age to first breeding. Results from studies which have attempted to quantify the genetic flexibility of the growth curve have been variable. Taylor and Fitzhugh (1971) found for Hereford cows that 78% of the genetic variation in time taken to mature was independent of mature body weight. Similarly, Smith et al. (1976) found that at immature ages, approximately 80% of the genetic variation in stage of maturity was independent of mature weight. In contrast, Brown et al. (1972) reported that in fitting Brody's function to growth data for Hereford cows only 10% of the genetic variation in the shape parameter (k) was independent of mature body weight, while for contemporary Angus cows 92% of the variation in the shape parameter (k) was independent of mature weight.

Several poultry studies have examined the effect of various selection procedures on the shape of the growth curve with varying degrees of success. Both Merritt (1974) and Ricard (1975) selected for various combinations of early and late body weights. In both studies, the combination of a high early weight and a low later weight resulted in an earlier maturing bird, with little change in mature weight. Pym and Nicholls (1979) reported both direct and correlated responses to selection for increased 5 to 9 week weight gain, food consumption and food conversion ratio (ie the weight of food consumed/body weight gain) in chickens. The direction of the correlated responses over the 5 to 9 week period suggest some bending of the growth curve, although this is difficult to quantify as only data over the 5 to 9 week period was reported.

A change in the shape of the growth curve is a change in the output of the animal, which must result from a change in either the inputs (that is food intake), or the efficiency with which these inputs are utilized by the animal (that is food efficiency). Without a knowledge of the change in input factors associated with a change in the shape of the growth curve there can be no assessment of the effects of such changes on the biological efficiency of the dam/offspring unit. Unfortunately most experiments which have examined the effect of various selection procedures on the shape of the growth curve have not reported the changes in inputs. In lieu of experimental data, Thompson and Barlow (1986) used the standardized feeding and growth equations

proposed by Parks (1982) to model the effect of changing food efficiency and food intake parameters independently of mature weight, on the shape of the growth curve, and the subsequent effect of such changes on the biological efficiency of the dam/offspring unit.

a) Scaled food efficiency factor

Thompson and Barlow (1986) calculated that an increase of 25% in the scaled food efficiency factor (i.e. the exponential rate of change of food consumed into liveweight) would result in a decrease of 14% in the age required to reach 50% of mature body weight (i.e. an earlier maturing animal), and an increase of 9% in biological efficiency of the dam/offspring unit.

Parratt (1983) reported that in mice, the scaled food efficiency factor had a high heritability and was positively correlated with both mature food intake and the reciprocal of appetite. Although there are no estimates of genetic parameters for the scaled food efficiency factor in domestic species, the stability of the scaled food efficiency factor across a wide range of species and breeds (Taylor 1982, Parks 1982) suggest little genetic variation in domestic species. The stability of the food efficiency factor was also demonstrated by Thompson et al. (1985), who showed its lack of any correlated response to selection for high and low weaning weight. Furthermore Gunsett et al. (1981) reported that in mice, selection for gross food efficiency (as either weight gain on a fixed food intake, or decreased food intake for a fixed change in weight) showed little change in the scaled food efficiency factor, although a response in gross food efficiency was achieved via changes in both mature weight and food intake parameters.

b) Appetite

Thompson and Barlow (1986) calculated that a 25% increase in appetite (i.e. the rate at which an animal increased food intake to reach its mature food intake), resulted in a 7% reduction in the age required to reach 50% maturity, although this change had little effect on biological efficiency of the dam/offspring unit.

Thompson et al. (1985) examined the correlated response in the shape of the standardized growth curve to selection for high and low weaning weight. They showed that selection for high and low weaning weight did result in slightly faster and slower maturing animals respectively, and this change in the shape of the growth curve was due to a change in appetite. Since there was no change in the efficiency of food utilization, the correlated change in appetite had little effect on the biological efficiency of the dam/offspring unit (Thompson and Kinghorn 1985). Similarly, Parks (1982) predicted that the change in the shape of the growth curve obtained in chickens by Ricard (1975), was largely due to a correlated response in appetite.

The results of the above studies suggest that selection for increased weight at immature ages will result in an earlier maturing animal. However this change in the shape of the growth curve is likely to be due largely to an increased appetite, and as such have little impact on biological efficiency of the dam/offspring unit.

c) Maintenance cost of the mature animal

Thompson and Barlow (1986) calculated that a 25% decrease in mature food intake resulted in a slower maturing animal, with a 17% increase in the age required to reach 50% of mature weight. Since the food consumed by the dam comprises such a large proportion of the total food consumed by the dam/offspring unit, this 25% decrease in mature food intake resulted in a 14% increase in biological efficiency of the dam/offspring unit.

There are no estimates of genetic parameters for efficiency of maintenance of mature animals, although Ferrell and Jenkins (1985) concluded that between breed variation was large. They also reviewed the factors affecting the maintenance requirements in the mature animal, and concluded that a large proportion of such variation is likely to be associated with the metabolism of the visceral organs. Ferrell and Jenkins (1985) also suggested that animals with a lower maintenance cost may have an advantage in unfavourable environments, or in drought. Results from Frisch and Vercoe (1977) show a large difference in the maintenance cost between Bos taurus and Bos indicus cattle. They reported that in a favourable environment, Brahman cross steers had a lower maintenance cost and a lower growth rate, than Hereford Shorthorn cross steers. Also Butler et al. (1956) reported a lower weight of visceral organs in Brahman cross steers. Frisch (1976) proposed a model based on variation in mature food intake, to explain the genotype x environment interaction in growth rate, observed between Bos indicus and Bos taurus cattle. In subsequent papers, Frisch (1981) and Frisch and Vercoe (1984) reported showed that the correlated responses to selection for growth rate may interact with the environment. In a low stress environment selection for increased growth rate resulted in an increase in both food intake and mature weight. Conversely in a high stress environment, selection for increased growth resulted in a decreased food intake with little change in mature weight. Although in a low stress environment a reduction in mature food intake will result in slower growing animals, the results of Thompson and Barlow (1986) suggest that such a change will give the greatest increase in biological efficiency. With the development of techniques for the measurement of food intake in the field (Barlow 1984), or perhaps indirect selection for weight of visceral organs, it may be possible to select for efficiency of maintenance in low stress environments.

CONCLUSION

Animals tend to grow in a predictable manner, whereby growth rate increases until the point of inflexion, and then decreases until zero at maturity. Input and output parameters of the animal tend to be highly associated with mature weight. Therefore if such parameters are scaled for differences in mature weight, this removes a large proportion of the variation previously apparent in comparisons at the same weight, or at the same age. If all variation is removed by scaling, then all animals will have similarly shaped growth curves and the opportunities to increase biological efficiency of the dam/offspring unit by genetic changes in food intake, food efficiency and growth characters will be limited.

The extent of genetic flexibility in the shape of the growth curve will depend upon the degree to which food intake, food efficiency and growth characters are independent of mature weight. However not all the changes in feeding and growth parameters, will result in increases in biological efficiency of the dam/offspring unit. Evidence to date suggests limited genetic variation in the scaled food efficiency factor in domestic animals. However if such genetic variation does exist, it is predicted that an increase of 25% in the scaled food efficiency factor will result in an increase of 9% in biological efficiency. Previous experiments have shown that selection for body weight at immature ages will generally result in faster maturing animals, although if this change in the shape of the growth curve is due solely to an increase in appetite it will have little effect on biological efficiency. A decrease of 25% in mature food intake will produce slower growing animals, although this change will result in a 14% increase in biological efficiency of the dam/offspring unit. The increase in biological efficiency associated with a decrease in mature food intake reflects the high proportion of the total food costs in sheep and cattle enterprises that are consumed by the dam.

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The amount of food which is consumed by an animal will depend upon the degree to which the animal is able to utilize the food which is available to it. The changes in feeding and growth parameters, which result in biological efficiency, will result in a decrease in biological efficiency. However, if such genetic variation does exist in domestic animals, it is predicted that an increase of 25% in the scaled food efficiency factor will result in an increase of 25% in biological efficiency. Previous experiments have shown that selection for body weight in animals will generally result in a decrease in biological efficiency, although it has been shown that selection for a higher rate of gain to an increase in specific live weight will result in a decrease in biological efficiency. A decrease of 25% in mature food intake will result in a 25% increase in biological efficiency, although this change will result in a 25% increase in biological efficiency of the dam/farrow unit. The increase in biological efficiency associated with a decrease in mature food intake reflects the high proportion of the total food costs in sheep and cattle enterprises that are consumed by the lambs.

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