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BRIEF COMMUNICATION

Modelling the impact of nutrition and genotype on lactation

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Dairy cows grazed on pasture experience variation in their nutritional status during lactation, as both pasture quality and availability vary seasonally. This has both immediate and long-term consequences on cow performance. Acute effects of nutrition are related to availability of nutrients for milk secretion, and are manifested in day-to-day variation in milk yields. Of further importance are the chronic effects of nutrition, which act on the development of the mammary gland, impacting on the persistency of lactation. Typically, cows in a New Zealand, pasture-grazing environment exhibit a decline in milk yield of around 10% per month, after peak lactation, whereas cows fed a concentrate diet in Northern Hemisphere systems show declines of less than 4%. Post-peak declines in milk yield are associated with a proportional and permanent decline in the number of secretory cells in the udder, and this decline is modulated by nutrition (Davis *et al.*, 2000).

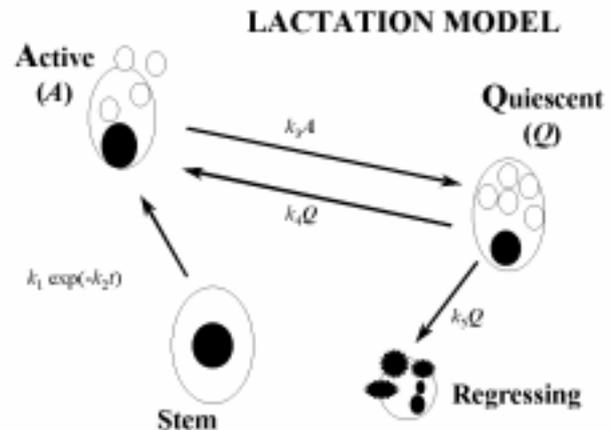
Quantifying the milk-yield response of a cow to different nutritional regimes is useful from a breeding and selection point of view, but on its own does not give insight into which pathways are likely to be affected by nutrition, nor does it explain the origin of differences in responses between cows. To this end, mechanistic mathematical models that reflect the underlying biology of the udder are particularly useful.

A mathematical model of mammary gland development and milk secretion has been developed and used to investigate how mammary dynamics are affected by nutrition, and to compare differences between genotypes in their responses to different diets (Vetharanim, Davis, Upsdell, Kolver & Pleasants, Unpublished).

Following the discovery by Molenaar *et al.* (1992) that a significant portion of a lactating udder is not secretory, the model considers the mammary gland as consisting of two pools of alveoli - those which are actively secreting and those which are quiescent (See Fig. 1). Each alveolus contains 150 to 300 cells (Weber *et al.*, 1955). The model adopts the assumptions made by Dijkstra *et al.* (1997), that endocrine changes associated with pregnancy cause cell division post-parturition, and that this is responsible for the production of new alveoli at an exponentially declining rate, $k_1 \exp(-k_2 t)$, where k_1 and k_2 have units of days⁻¹, and t is days since parturition. There is a flow from the active pool (A) to the quiescent pool (Q) of rate, $k_3 A$, as active alveoli change their gene expression and lose their secretory ability, and a reverse flow, $k_4 Q$, as quiescent alveoli become active again. Senescence of quiescent alveoli, at a rate $k_5 Q$, acts as a sink, and leads to permanent loss of secretory capacity. The parameters k_3 , k_4 , and k_5 are all considered to be constant, and each has units of days⁻¹.

Milk yield responds rapidly to nutritional stress (Knight *et al.*, 1994), although energy-deficient cows will partially buffer milk production at the expense of body reserves (Somerville *et al.*, 1983). The model addresses the acute

FIGURE 1: Schema of mammary gland used in the mathematical model, showing the flows into and out of the active and quiescent pools of alveoli.



effects of nutrition by relating the secretion rate, s , of active alveoli to the level of nutrition available to a cow with the expression, $s.E^L$, where $s = 3 \times 10^9$ MJ per day is the (assumed) maximum secretion rate of an alveolus. E is the relative energy status of the cow, taking a value from 0 (starvation) to 1 (maximal feeding), and L is a "genetically related parameter" that expresses the degree to which a cow buffers milk production when under nutritional stress.

It was assumed that, at parturition, all alveoli are active (with the size of the active pool at this time being A_0). The equations that underlie the model were solved analytically and used to investigate both the acute and chronic effects of nutrition on different genotypes. The model predicts active and quiescent alveolar populations as functions of time since parturition, and milk secretion in terms of nutritional status and alveolar populations. It was fitted to milk-production data from a 2x2 factorial trial (Kolver *et al.*, 2000) in which cows of two different genotypes (New Zealand and overseas Holstein-Friesians) were fed one of two diets (either pasture or a total mixed ration (TMR)), using least-squares minimisation.

Genotype had no influence on the parameter, L , which governs the buffering of milk secretion against any shortfall in nutrition. There was no nutritional effect on L , indicating that the model predicted milk production buffering well. L had the value 0.659 for all groups – indicating that a cow at 75% energy status ($E = 0.75$) would be secreting at 83% of its capacity.

The total number of alveoli produced per cow during pregnancy and lactation is given by the expression $A_0 + k_1/k_2$ and was $(3.2 \pm 0.2) \times 10^{10}$ for all groups, unaffected by both diet and genotype. There was a degree of variation in the

population of alveoli at parturition and the rate of production of new alveoli post-parturition, with initial alveolar population at parturition being negatively correlated with production of alveoli.

The rate constant, k_3 , for the loss of secretory capacity through the quiescence of actively secreting cells was higher for grass ($0.40 \pm 0.03 \text{ days}^{-1}$) than for TMR ($0.33 \pm 0.02 \text{ days}^{-1}$), although this difference was marginal ($P=0.076$). If this were a real effect, it would indicate that alveoli in cows fed grass could be more susceptible to quiescence than those fed TMR.

The rate constant, k_4 , for the reactivation of quiescent cells showed a genotype-diet interaction ($P=0.036$) with the overseas genotype having respective values of $4.7 \pm 0.8 \text{ days}^{-1}$ and $7.3 \pm 0.7 \text{ days}^{-1}$ for grass and TMR, and New Zealand cows having a value of $6.3 \pm 0.4 \text{ days}^{-1}$ for both diets. This indicates that, for the overseas genotype, a TMR diet enhanced the probability of a quiescent alveolus becoming reactivated, while in the New Zealand genotype, k_4 was unresponsive to TMR.

The rate constant, k_5 , for the loss of mammary gland tissue through senescence of quiescent alveoli was significantly ($P < 0.01$) greater for grass ($0.042 \pm 0.003 \text{ days}^{-1}$) than for TMR ($0.006 \pm 0.003 \text{ days}^{-1}$) but was unaffected by genotype. This outcome suggests that differences in persistency due to diet are a consequence of increased cell death under poorer nutritional conditions, rather than through a larger rate of quiescence or smaller rate of reactivation.

The study indicated that the difference in performance between overseas and New Zealand Holstein-Friesians is likely to arise in the pathway that controls the reactivation of quiescent alveoli to an actively secreting state, but that this difference is diet-dependent. The overseas genotype, having been selected for production under concentrate feeding conditions, showed greater responsiveness to the different diets. The New Zealand cows have been selected to produce consistently subject to the greater variation of a pasture-based system and this has resulted in less responsiveness of the reactivation of quiescent alveoli to diet. The difference between the two genotypes is manifest in differences in the k_4 parameter. Therefore, it is possible that performance of the overseas genotype may be most efficiently improved by selecting directly for an increase in k_4 when those cows are fed a grass diet.

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