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BRIEF COMMUNICATION

Modelling the impact of milking frequency on lactation

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Increasing milking frequency from the usual practice of twice-daily can enhance milk production and, thus, may be profitable in high-intensity dairy production systems. A decrease of milking frequency to once-daily decreases yield but may be used to alleviate nutritional stress, to conserve cow condition, or simply as a lifestyle choice. Published values in the literature indicate that reducing milking frequency from twice daily to once daily decreases yield by 7–34%, and increasing milking frequency from twice daily to thrice daily increases yield by 7–20% (Davis *et al.*, 1999; Stelwagen, 2001). Additionally, milking frequency can influence the rate of decline in post-peak production in cows (Stelwagen, 2001).

In order to further understand and quantify the manner in which milking frequency affects lactation, a mechanistic mathematical model of mammary function has been developed (Vetharanim, Davis, Soboleva, Shorten & Wake, Unpublished), based on mechanisms presented by Davis *et al.* (1999). As well as allowing analysis of the effect of milking frequency, this model also facilitated the exploration of some of the pathways through which nutrition influences mammary gland development (Davis *et al.* 2001).

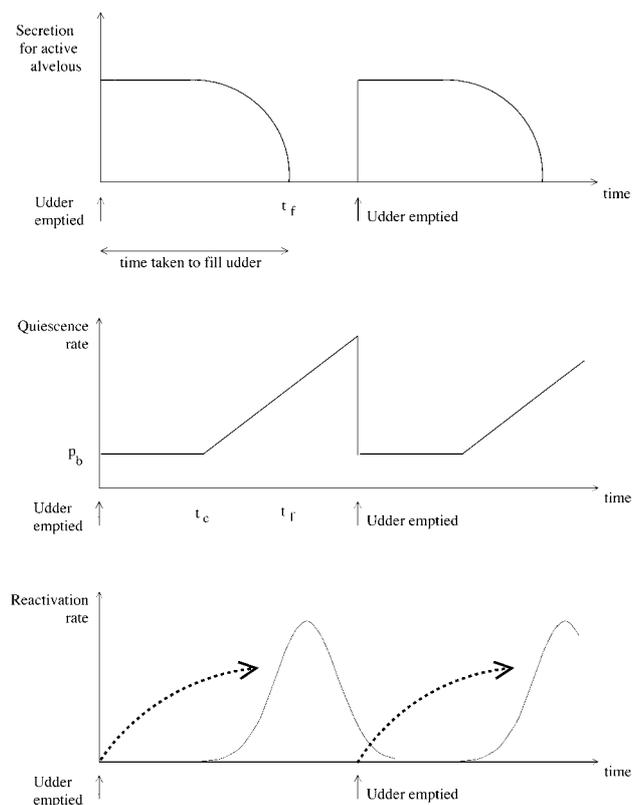
The secretory cells in the mammary gland can exist in either active (secreting) or quiescent (engorged) states (Molenaar *et al.*, 1992). Thus the mammary gland is represented as two pools of alveoli – active and quiescent (see Fig. 1 in Davis *et al.*, 2001).

An alveolus consists of 150-300 secretory cells (Weber *et al.*, 1955) and empties via a narrow duct that is the major source of resistance to milk flow. The alveolus will thus accumulate secretion and become engorged, changing the shape of the secretory cells. The response to alveolar milk accumulation consists of several phases that occur after an alveolus was last emptied (Davis *et al.*, 1999). In the bovine udder, all alveoli are full at about 16 hours post milking (Davis *et al.*, 1998). After around 18 hours there is a breakdown of the tight junctions located between epithelial cells and a mixing of milk with extracellular fluid (Stelwagen *et al.*, 1995). Eventually changes in gene expression occur that lead to quiescence.

After each milking, a fraction of engorged active alveoli will not be emptied (Molenaar *et al.* 1992), and, thus, the rate of quiescence will have a non-zero base value, p_b . It is assumed in the model to be constant for a “critical” time t_c , after which the rate of quiescence increases (with slope k) as alveoli that were emptied, or partly emptied, start to become engorged and embark on the pathway towards quiescence. This increase will be interrupted only by milk removal from the udder (Fig. 1).

Secretion of milk by an active alveolus is not limited by the resistance of the alveolar duct to emptying, but is ultimately limited by hydrostatic pressure as columns of milk build up in the cistern of the udder (Fig. 1). Emptying a quiescent alveolus can reverse the changes in gene

FIGURE 1: Secretion rate, quiescence rate of active alveoli, and reactivation of quiescent alveoli with time since last milking.



expression caused by alveolar engorgement, and reactivate milk synthesis and secretion. Because the stimulus causing engorged alveoli to empty occurs at milking times, recruitment of quiescent alveoli to the active population is pulsed, coinciding with each milking time. However, there is a time delay before a quiescent alveolus becomes active again and a degree of variation in this time depending upon the time the alveolus spent in a quiescent state (Farr *et al.*, 1998). Thus, while the reactivation process results in a loss of quiescent alveoli in well-defined pulses, coinciding with milking times, the arrival of these alveoli into the active pool is temporally distributed and lags milking times (Fig. 1).

The changes in gene expression caused by the engorgement of an alveolus initiate a pathway that eventually leads to apoptosis unless this pathway is interrupted by the reactivation of the alveolus through milking. An alveolus will stay in a quiescent state for a finite time – its *duration of quiescence*, t_d – before apoptosis of its constituent cells is initiated (after which it cannot be rescued and will regress). Alveoli can be expected to show variation in their duration of quiescence.

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Each milking is associated with the probability p_e that any given alveolus will be emptied. Increasing milking frequency increases the probability that a quiescent alveolus will be rescued from apoptosis before its duration of quiescence expires. Thus, increasing milking frequency will increase the rate of reactivation of quiescent alveoli, and decrease their rate of senescence.

The model's qualitative behaviour in predicting populations of alveoli in response to different milking frequencies are consistent with what one would expect from a mammary gland. For a demonstration parameter set, the model can predict the variation in milk yield with milking frequency reported in the literature. Comparing thrice-daily and once-daily milking with twice-daily milking, peak udder size was respectively 5% larger and 7% smaller, udder size at the end of lactation was respectively 38% larger and 64% smaller, and utilisation of the secretory capacity of the udder was respectively 1.6% higher and 4.9% smaller. Increasing milking frequency reduces rates of quiescence and senescence of alveoli, increases rates of reactivation of alveoli, and thereby increases secretory capability.

Revisiting the results of Davis *et al.* (2001), in the context of our milking frequency model, indicates that some differences in cows' response to nutritional stress may originate at milking time. Davis *et al.* found that in Holstein-Friesian (HF) cows of overseas origin, the reactivation rate of quiescent alveoli decreased with decreased diet quality, whereas there was no such effect in HF cows of New Zealand origin. In our model, the reactivation rate is governed by p_e , the probability of emptying a quiescent alveolus at milking. Thus the possibility exists of an interaction between nutrition and milk ejection such that the overseas genotype may exhibit decreased ability to empty engorged, quiescent alveoli. This may arise through some as yet unidentified element of the oxytocin endocrine axis or possibly downstream of the alveolus in the regulation of ductal tone in the milk ducts.

In conclusion, the model provides a mechanistic description of how the dynamics of the mammary gland are driven by milking frequency. The nature of the model also facilitated a theoretical analysis of some of the pathways through which nutrition influences mammary gland development. However, the model can be used to make quantitative predictions of the lactational performance of a cow under different nutritional and milking regimes. Thus, it would prove invaluable in the analysis of multi-factorial trials that included different diets, milking frequencies and genotypes, allowing quantification of the differences in mechanisms which give rise to the observable differences in performance.

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