Effects of an acute feed restriction at the onset of the seasonal breeding period on reproductive performance and milk production in pasture-grazed dairy cows

C. R. Burke,¹ Y. J. Williams,² L. Hofmann,³ J. K. Kay, C. V. C. Phyn, and S. Meier

DairyNZ Limited, Private Bag 3221, Hamilton 3240, New Zealand

ABSTRACT

Reproduction and milk production responses were compared between dairy cows offered a high (HPA; $n = 453$ in 4 replicates) or low (LPA; $n = 317$ in 3 replicates) pasture allowance for the first 14 d after the planned start of mating (d 0 of experiment) in 2 seasonal, pasture-based dairy herds. Estimated pasture dry matter intake (DMI) between d -1 and 13 were 14.3 ± 2.8 and 8.0 ± 1.7 kg of DM/cow per day for HPA and LPA cows, respectively. The LPA cows produced 22% less energy-corrected milk during the 14-d feeding treatment period, and milk yield remained less in LPA cows at d 53 despite all cows receiving pasture allowances to support DMI of 16 kg of dry matter/cow per day from d 14 onwards. The 3-wk submission rate (percentage of cows inseminated at least once from d 0 to 20) and the 3- and 6-wk pregnancy rates of LPA cows (88, 45, and 71%, respectively) were lower than those of HPA cows (94, 53, and 78%, respectively), but conception rates to first (50%) or second (47%) service and final pregnancy rates (93%) did not differ between treatments. These results quantify the immediate and subsequent responses in reproductive performance and milk production to a severe restriction in DMI at the onset of a seasonal breeding period in pasture-grazed dairy cows.

Key words: dairy cow, reproduction, milk production, feed restriction

INTRODUCTION

Feed deficits can be problematic in seasonal calving, pasture-based systems in which pasture availability and

quality are dependent on climatic conditions (Lambert et al., 2004; Waghorn and Clark, 2004) and on the competency of grazing management (Bryant, 1986; Verkerk, 2003). This contrasts with a TMR feeding system, in which DMI can be maximized using a consistently high-quality diet fed to appetite (Kolver and Muller, 1998).

The beneficial effect of maximizing DMI and minimizing negative energy balance during early lactation on subsequent fertility has been demonstrated in TMR (Beam and Butler, 1997; Westwood et al., 2002) and pasture-grazed systems (Grainger and Wilhelms, 1979; Patton et al., 2007). Associative analyses between fertility and BCS and BW in early lactation support the beneficial effect of improved nutritional state on reproductive performance in pasture-grazing systems (Fulkerson et al., 2001; Buckley et al., 2003; Roche et al., 2007). However, in pasture-grazing systems, the positive association between DMI in early lactation and fertility is not always apparent (McDougall et al., 1995c; Kennedy et al., 2003; Burke and Roche, 2007), perhaps because of preferential partitioning of energy intake toward milk synthesis (Roche, 2007; Leroy et al., 2008a).

The influence of altering DMI several weeks later, at the commencement of a seasonal breeding period, is not well documented, although it has been implied that reproductive performance will decrease if DMI is not maintained or improved throughout the breeding period of lactating dairy cows (McClure, 1961; Diskin, 2008; Diskin and Morris, 2008). In nonlactating beef heifers, an increasing plane of nutrition did not improve embryo survival, but reducing the plane of nutrition postinsemination was detrimental (71 vs. 38%; Dunne et al., 1999). Whether a similar type of response is apparent in lactating dairy cattle is uncertain.

Using a large-scale, controlled experimental approach, the aim of this experiment was to quantify the effect of an acute feed restriction at the onset of the seasonal breeding season on various reproductive performance indices and milk production responses in pasture-grazed dairy cows.

Received July 12, 2009.

Accepted November 16, 2009.

¹Corresponding author: chris.burke@dairynz.co.nz

²Present address: Department of Primary Industries, 255 Ferguson Rd., Tatura, Victoria 3616, Australia.

³Present address: FarmWise Consultancy LIC, 461 B South Rd., RD12, Hawera 4672, New Zealand.

Figure 1. Schematic of the experimental timing of the treatment pasture allowances (high pasture allowance, $n = 451$; low pasture allowance, $n = 314$), transitional period before feeding treatment, milk yield and composition sampling, milk progesterone sampling, and detailed measurement of pre- and postgrazing pasture masses.

MATERIALS AND METHODS

Animal Management

The study involved 770 mixed-age dairy cows on 2 separately managed dairy farms (farms F and W) in Hawera, New Zealand ($39^{\circ}36'S$ $174^{\circ}18'E$). Farm F comprised 494 multiparous Holstein-Friesian (**HF**) $\times$ Jersey (**J**) crossbred cows. Farm W comprised 276 HF, J, and HF $\times$ J crossbred cows, including 57 primiparous cows. Apart from the 3-wk experimental period described below, cows were managed in accordance with best-practice guidelines for pasture-based seasonal dairying (Macdonald and Penno, 1998). All procedures had prior approval from the Ruakura Animal Ethics Committee (Hamilton, New Zealand).

Experimental Design and Treatments

A single-factor treatment comparison within a randomized complete block design with subsampling (Tempelman, 2009) was used to test the effect of high pasture allowance (**HPA**; $n = 453$ in 4 replicates) or low pasture allowance (**LPA**; $n = 317$ in 3 replicates) during the first 14 d of the seasonal breeding period (Figure 1). The planned start of mating (**PSM**) date, designated as d 0 of the experiment, was the same for each herd (October 11, 2007). Only cows that had calved by d -28 were eligible for enrollment. On d -14 , cows were allocated to treatment groups for socialization by stratified randomization to balance for calving date, age and BCS before calving, and PSM (Table 1). Pasture allowances were controlled by establishing appropriately sized grazing areas for the replicate herds based on the pasture mass present and the number of animals in the replicate. Average ($\pm$ SD) pasture allowances (38.6 ± 11.0 kg of DM/cow per day), DMI (14.3 ± 5.5 kg of DM/cow per day), and estimated energy

intakes (167 ± 65 MJ of ME/cow per day) were the same for HPA and LPA cows between d -14 and -8 . A transition feeding period (Figure 1) was implemented from d -7 to -2 during which pasture allowances were incrementally reduced by 2.4 kg of DM/cow per day for LPA cows and incrementally increased by 0.8 kg of DM/cow per day for HPA cows. Between d -1 and 13 (Figure 1), daily pasture allowances were managed to achieve an average DMI of 14.3 kg of DM/cow per day for HPA cows and 8.0 kg of DM/cow per day for LPA cows (Table 1). From d 14, pasture allowances for all groups were readjusted to best-practice procedures (Macdonald and Penno, 1998), allowing cows to achieve DMI of at least 16 kg of DM/cow per day. Cows remained in their allocated treatment groups until the first pregnancy diagnosis on d 61, after which the farm managers were free to arrange herd groupings at their discretion.

Pasture Measurements

The rising plate meter (Farmworks, Palmerston North, New Zealand) technique described previously by Roche et al. (2005) was used to estimate the mass of pasture before and after grazing on 5 d each week from d -7 to 13 (Figure 1). At each sampling, 100-m readings were taken within the grazed area. Quadrants (0.3 m^2) were cut to ground level every 3 d during the experimental feeding period. These cut pasture samples were dried at 100°C for 24 h for conversion of meter readings to pasture mass. Data from 72 pregrazing and 40 postgrazing quadrants were used to construct calibration equations to convert meter readings to pasture mass. The coefficients of variation were 15.2 and 14.1%, respectively. Grazing area was manipulated to achieve average ($\pm$ SD) pasture allowances of 43.6 ± 4.8 kg of DM/cow per day for HPA and 24.5 ± 5.5 kg

Table 1. Average age, interval from calving to the planned start of mating (PSM), and pasture feeding variables for cows assigned to a high (HPA) or low (LPA) pasture allowance for the first 2 wk of the seasonal breeding period¹

Item	HPA	LPA
Cows (n)	451	314
Replicates (n)	4	3
Age (y)	5.3 ± 2.0	5.2 ± 2.1
Prepartum BCS (1–10 scale)	5.3 ± 0.5	5.2 ± 0.5
Calving to PSM (d)	63.0 ± 14.7	63.9 ± 15.4
Pregrazed pasture mass (kg of DM/ha)	2,833 ± 153	2,198 ± 124
Postgrazed pasture mass (kg of DM/ha)	1,823 ± 107	1,455 ± 61
Pasture allowance ² (kg of DM/cow per day)	43.6 ± 4.8	24.5 ± 5.5
DMI ³ (kg of DM/cow per day)	14.3 ± 2.8	8.0 ± 1.7
Energy intake ⁴ (MJ of ME/cow per day)	171 ± 32	94 ± 20

¹Values are actual averages ± SD.

²Pasture allowance was estimated using pregrazed pasture mass and grazed area per cow.

³The DMI was estimated by subtracting postgrazed from pregrazed pasture mass and then dividing by the number of cows in the grazed area.

⁴Energy intake was estimated by multiplying DMI measured 3 times weekly by ME content measured in weekly bulked samples.

of DM/cow per day for LPA replicates. The average DMI of cows within replicate was estimated 3 d/wk by subtracting the postgrazed from the pregrazed pasture mass and then dividing by the number of cows in the replicate (Table 1).

Pasture samples representative of the material eaten were collected 5 d/wk and bulked weekly. Samples were collected by hand-clipping 8 quadrants (50 cm²) to estimate grazing height across a diagonal transect of the grazing area. Samples were oven-dried at 60°C for 72 h and ground through a 1-mm screen before near-infrared reflectance spectroscopy (feedTECH, AgResearch, Hamilton, New Zealand). Pasture was of high quality throughout (ME = 11.9 ± 0.05 MJ/kg of DM; CP = 25.3 ± 0.1% DM; OM digestibility = 84.0 ± 0.2% DM; NDF = 45.6 ± 0.2% DM; ADF = 24.9 ± 0.2% DM; lipids = 4.5 ± 0.04% DM; NSC = 14.7 ± 0.3% DM; ash = 11.5 ± 0.05% DM). Pasture quality was similar for both treatments except for CP, which was greater ($P = 0.04$) in pasture eaten by LPA cows (25.6%) than in that eaten by HPA cows (25.0%). Average daily ME intakes were estimated by multiplying DMI by the average ME content of the pasture (Table 1).

Milk Production

Individual milk yield and composition were measured on d 5 and 13 for all experimental cows (Figure 1) in order to assess the immediate effect of feeding treatment on milk production. Fat and protein concentrations were determined from a composite of samples collected during consecutive a.m. and p.m. milkings by the infrared technique (FT120, Foss Electric, Hillerød, Denmark). Milk yield data are presented as ECM

[calculated as milk weight (kilograms/cow per day) × (383 × fat % + 242 × protein % + 783.2)/3,140]. In addition, milk yield and composition from cows in herd W were measured (GEA, Oelde, Germany) on d −17, −9, 5, 13, 25, 39, 53, and 102 (Figure 1) in order to investigate the effects of the 14-d feed restriction on immediate and subsequent milk production.

Milk Progesterone

Progesterone content was measured in milk samples collected from every cow on d −16, −9, −2, 5, and 13 (Figure 1). A standard herd-test sample of milk was collected at the morning or afternoon milking. A subsample (8–10 mL) was collected into a vial containing 100 µL of 10% bronopol (Spec Chem Industry Inc., Nanjing, China), refrigerated, and transported to DairyNZ Ltd. (Hamilton, New Zealand). An RIA kit (Progesterone Coat-a-Count, DPC, Los Angeles, CA) was used to determine progesterone concentrations within 2 d of sample collection following the procedure recommended by the manufacturer. Inter- and intraassay coefficients of variation were 7.7 and 5.3%, respectively. Sensitivity of the assay was 0.06 ng/mL.

Progesterone data were used to define ovulatory status, with any concentration ≥3 ng/mL indicating presence of a functional corpus luteum (ovulatory). Cows with at least 1 sample ≥3 ng/mL among those collected on d −16, −9, and −2 were defined as ovulatory before the feeding treatments started. Cows with at least 1 sample ≥3 ng/mL of those collected on d 5 and 13 were defined as ovulatory at the end of the feeding treatment period. Cows that did not meet these conditions were defined as anovulatory.

Breeding Management and Cow Health

Identification of behavioral estrus using the tail-painting technique (Macmillan et al., 1988) was performed twice daily from d -28 (farm F) or d -22 (farm W) throughout the AI (farm F, d 0–35; farm W, d 0–45) and bull mating (farm F, d 36–85; farm W, d 46–116) periods. The proportion of cows inseminated within the first 3 wk of the breeding period (d 0–20) was defined as the 3-wk submission rate. Return-to-service (**RtS**) intervals between first and second insemination (AI or bull) were defined as short (<18 d), normal (18–24 d), and long (≥ 24 d; Castle, 1963). Conception rates were calculated for all first AI and any second AI that occurred between 2 to 24 d after the first AI. Pregnancy rates were considered to be the product of submission and conceptions rates, with an emphasis on the 3-, 6- and 12-wk pregnancy rates (i.e., the seasonal breeding period).

Diagnosis and treatment of cows with endometritis using the MetriCheck technique (McDougall et al., 2007) was performed on all (farm W) or selected (farm F) cows before initiation of the feeding treatment period. Cows requiring treatment for endometritis were randomly allocated across the treatment groups. The decision to treat anestrous cows was at the discretion of the farm managers, but treatment could be performed only after d 65 as an experimental constraint.

Pregnancy diagnoses were performed by ultrasonography at d 65 and again by manual palpation 6 to 8 wk following the end of mating. These diagnoses confirmed whether the cow was pregnant (i.e., fetal age was not estimated). A total of 50 (6.5%) cows were confirmed nonpregnant. A further 53 (6.9%) cows, confirmed pregnant, were culled before subsequent calving. Data from the subsequent calving (2008) were used to confirm current conception dates for the 661 (85.8%) nonculled cows. Gestation lengths between 272 and 293 d were considered normal for HF- or J-sired calves (Macmillan and Curnow, 1976). Farm F used Hereford bulls for natural mating, for which gestation lengths of 276 to 297 d were considered normal (Macmillan and Curnow, 1976). Gestation lengths shorter than 272 d, or 276 for Hereford sires, indicated either a premature calving or conception to an earlier mating date where applicable. An abnormally low calf birth weight and farm staff notes of premature calvings were used to differentiate between these possible outcomes. Gestation lengths greater than 293 d, or 297 d for Hereford sires, indicated that the cow conceived to a later bull mating date than that recorded. Five cows (2 HPA and 3 LPA) were removed from the study for health reasons and were excluded from analyses.

Statistical Analyses

Data were analyzed using generalized linear mixed models in GenStat (version 11.1, VSN International, Hemel Hempstead; Payne et al., 2008). Treatment and farm were included as fixed effects, and replicate (herd) as a random effect. The statistical model considered treatment herd replicate as the experimental unit, but the variance component of replicate was generally zero and was eliminated automatically from the model. The same model was used to compare pasture measurements with REML variance components analysis, with replicate remaining in the model as a random effect. Results are presented as mean $\pm$ standard error of the difference unless otherwise stated.

RESULTS

Milk Production

Average daily yield of ECM for all cows (farms F and W) between d 5 and 13 was 22% greater ($P < 0.05$) in HPA than LPA cows (23.5 vs. 18.3 ± 1.7 kg of ECM/cow per day). Fat content ($5.15 \pm 0.15\%$) was similar between treatments, but the milk of HPA cows had greater ($P < 0.01$) protein concentrations (3.94 vs. $3.63 \pm 0.06\%$) than the milk of LPA cows during the period of d 5 to 13.

Milk composition data from herd W (HPA, $n = 137$; LPA, $n = 137$) are presented in Table 2. The LPA cows from herd W produced 30% less ECM (16.4 vs. 23.5 kg/d), 30% less fat (0.71 vs. 1.01 kg/d), and 34% less protein (0.52 vs. 0.79 kg/d) during the 14-d feeding treatment period compared with HPA cows in herd W. A subsequent effect of treatment (Figure 2) was apparent at d 25, where LPA cows from herd W produced 14% less ECM, 17% less fat, and 11% less protein (Table 2). At d 39, LPA cows from herd W produced 8, 10, and 7% less ECM, fat, and protein, respectively. These treatment differences were still evident at d 53, but not at d 102 (Table 2).

Ovulatory Status

On the basis of milk progesterone analysis, the majority (85%) of cows were having ovulatory cycles by d -2, and all but 14 of these 653 cows (2%) were deemed to be ovulatory by d 13. Eighty of the 115 cows (70%) that were anovulatory at d -2 had spontaneously ovulated before d 13. There was no effect of treatment on these variables (Table 3).

Submission Rate and Return-to-Service Intervals

The overall 3-wk submission rate was 90%, with a tendency ($P = 0.06$) for a greater percentage (4.2%) of HPA cows to be presented for AI in the first 3 wk (Table 3). The mean RtS interval between first and second insemination (21.2 ± 0.6 d) did not differ between

treatments (Table 3), but LPA cows had fewer ($P < 0.001$) normal (18–24 d; 65 vs. 82%) and more ($P < 0.01$) long (≥ 25 d; 17 vs. 7%) RtS intervals, compared with HPA cows (Figure 3). The proportion of short RtS intervals (2–17 d) also tended ($P = 0.08$) to be greater among LPA cows (18%) compared with HPA cows (11%).

Table 2. Milk production in a subset of cows (farm W¹) assigned to a high (HPA; $n = 137$) or low (LPA; $n = 137$) pasture allowance for the first 2 wk of the seasonal breeding period²

Variable	Day ³	Treatment		SED	P-value
		HPA	LPA		
Milk yield (kg/d)	–17	22.50	22.10	0.81	0.63
	–9	22.24	21.36	0.88	0.32
	5	20.80	15.12	0.68	<0.01
	13	20.29	15.09	0.66	<0.01
	25	18.42	16.92	0.57	<0.01
	39	17.74	16.85	0.58	0.13
	53	17.33	16.75	0.63	0.36
ECM (kg/d)	102	13.90	13.54	0.61	0.56
	–17	24.56	23.94	0.76	0.42
	–9	25.82	24.32	0.83	0.09
	5	23.93	16.82	0.73	<0.01
	13	23.09	15.94	0.66	<0.01
	25	22.07	19.04	0.60	<0.01
	39	20.59	18.92	0.56	<0.01
Fat (%)	53	20.82	19.17	0.56	<0.01
	102	15.78	14.92	0.61	0.17
	–17	4.66	4.61	0.13	0.67
	–9	5.12	5.03	0.15	0.55
	5	5.06	5.10	0.14	0.79
	13	4.89	4.57	0.14	0.02
	25	5.53	4.93	0.17	<0.01
Protein (%)	39	5.11	4.88	0.15	0.14
	53	5.12	4.73	0.18	0.03
	102	5.05	4.80	0.17	0.14
	–17	3.67	3.60	0.04	0.10
	–9	3.77	3.8	0.05	0.53
	5	3.83	3.48	0.05	<0.01
	13	3.91	3.49	0.05	<0.01
Fat (kg/d)	25	3.84	3.71	0.05	<0.01
	39	3.90	3.82	0.05	0.16
	53	3.92	3.83	0.06	0.17
	102	3.86	3.73	0.07	0.07
	–17	1.03	1.01	0.03	0.41
	–9	1.13	1.05	0.04	0.06
	5	1.04	0.75	0.04	<0.01
Protein (kg/d)	13	0.98	0.67	0.03	<0.01
	25	0.99	0.82	0.03	<0.01
	39	0.89	0.80	0.03	<0.01
	53	0.89	0.80	0.02	<0.01
	102	0.68	0.63	0.03	0.10
	–17	0.82	0.79	0.02	0.32
	–9	0.84	0.80	0.03	0.16
	5	0.79	0.52	0.02	<0.01
	13	0.78	0.52	0.02	<0.01
	25	0.70	0.62	0.02	<0.01
	39	0.69	0.64	0.02	<0.01
	53	0.70	0.66	0.02	0.05
	102	0.52	0.50	0.02	0.16

¹Farm W comprised 276 Holstein-Friesian (HF), Jersey (J), and HF $\times$ J crossbreds, including 57 primiparous cows.

²Mean percentages or values and standard error of the difference (SED) are presented.

³Planned start of mating (d 0) of the seasonal breeding period.

Figure 2. Yield of ECM in a subset of cows (farm W) assigned to a high (W-HPA) or low (W-LPA) pasture allowance for the first 2 wk of the seasonal breeding period. Day 0 is the planned start of mating date of the seasonal breeding period. Mean values $\pm$ standard error of the difference are presented.

Figure 3. Proportional distribution of return-to-service intervals between first and second insemination (AI or bull) for cows assigned to a high (HPA; $n = 451$) or low (LPA; $n = 314$) pasture allowance for the first 2 wk of the seasonal breeding period.

Conception and Pregnancy Rates

Conception rates to first or second AI and the interval from PSM to conception were not affected ($P > 0.1$) by treatment (Table 3). Proportionately more HPA cows were pregnant by 3 wk ($P = 0.05$) and 6 wk ($P = 0.04$) of mating, but the 12-wk and final pregnancy rates were not different between treatments ($P > 0.1$; Table 3). The proportions of cows not pregnant with progression of the breeding period are depicted as survival curves in Figure 4. The HPA (herd means; dotted line) curve

depicts the mean values of herd F and W calculated independently to adjust for a greater number of HPA cows in herd F. The unadjusted values for HPA cows (solid circles) were only marginally more divergent from LPA (open circles) as compared with the adjusted mean for HPA cows (dotted line). Although descriptive, these curves show that the advantage in HPA cows was confined to wk 3 and 6 of the breeding period and was not consistent through time.

Table 3. Reproduction response variables in cows assigned to a high (HPA) or low (LPA) pasture allowance for the first 2 wk of the seasonal breeding period¹

Item	Treatment		SED	P-value
	HPA	LPA		
Ovulatory ² by d -2 (%)	85.6	84.2	2.7	>0.5
Ovulatory ² by d 13 (%)	94.0	93.1	2.7	>0.5
3-wk submission rate ³ (%)	91.8	87.6	2.3	0.06
Conception rate to first AI (%)	52.2	46.6	3.7	0.13
Conception rate to second AI ⁴ (%)	45.1	49.9	6.4	0.46
Return-to-service interval ⁵ (d)	20.7	21.9	1.2	0.28
PSM to conception interval ⁶ (d)	24.6	25.8	1.5	0.41
3-wk pregnancy rate (%)	52.5	45.4	3.7	0.05
6-wk pregnancy rate (%)	77.5	70.9	3.2	0.04
12-wk pregnancy rate (%)	93.3	91.5	2.0	0.37
Final pregnancy rate ⁷ (%)	94.0	92.6	1.9	0.44

¹Mean percentages or values and the standard error of the difference (SED) are presented.

²Ovulatory status as determined by milk progesterone concentration(s) ≥ 3 ng/mL.

³Proportion of cows AI in first 3 wk.

⁴Proportion of cows conceiving to a second AI occurring 2 to 24 d after first AI.

⁵Interval (d) between the first and second insemination (AI or bull), excluding 1-d intervals ($n = 4$).

⁶PSM = planned start of mating (d 0) of the seasonal breeding period.

⁷Proportion of cows pregnant after mating durations of 85 d (farm F) or 116 d (farm W). Farms F and W are separately managed dairy farms in Hawera, New Zealand (39°36'S 174°18'E).

Figure 4. Proportion of cows not pregnant during the first 12 wk of the seasonal breeding period among those assigned to a high (HPA; $n = 451$) or low (LPA; $n = 314$) pasture allowance for the first 2 wk of the seasonal breeding period. HPA (herd means) are the means of the separately calculated proportions for HPA cows in herds F and W, which accounts for a greater number of HPA cows in herd F.

DISCUSSION

This study was conducted in 2 dairy herds that emphasize best-practice management to optimize milk production and general herd performance. Although accustomed to scientific investigation, the measurements undertaken were constrained, for reasons discussed by Tempelman (2009). These included the wishes of farm F management to exclude primiparous cows from the study and not expose too many of the cows in the herd to the restricted feeding treatment. There was also a reliance on preexisting recording systems, which may fail. Despite these constraints, the experimental design and execution was sufficiently robust to test a simple question: Does a severe but short feed restriction at the onset of a seasonal breeding period in pasture-grazed dairy cows reduce reproductive performance? These results are novel and describe short- and long-term responses in milk production and fertility following a 14-d period of restricted pasture DMI at the onset of the seasonal breeding season.

Although not directly measured in the present study, the reduced DMI, milk yield, and milk protein concentration imply that the LPA cows were in poorer energy balance compared with HPA cows; this is a possible underlying cause for the reduced 3- and 6-wk pregnancy rates (Beam and Butler, 1997; Roche et al., 2007). Patton et al. (2007) reported a detrimental effect of negative energy balance on fertility of pasture-grazed dairy cows and also reported that DMI was a principle component of energy balance. Results presented here are consistent with this previous study, where a short

but severe restriction in DMI during peak lactation likely resulted in a poorer energy balance, with reductions in milk protein content and fertility.

Reproduction

The 14-d feed restriction reduced the 3- and 6-wk pregnancy rates by 7.1 and 6.6%, respectively. Because pregnancy rates are the product of both submission and conception rate, it follows that a depression in one or both of these reproduction variables was responsible for the reduced pregnancy rates. Although both the 3-wk submission rate and first-service conception rate were numerically reduced in LPA groups, only the 3-wk submission rate qualified as approaching statistical difference ($P = 0.06$). The effect was isolated to the third week of the breeding period and was more pronounced in herd W (data not shown), but, despite the size of the study, insufficient statistical power was available to test this significance.

Milk progesterone data indicated that most cows were ovulating at the start of the experiment and continued to do so through d 13 irrespective of feeding treatment. Further, the rate of nonovulatory cows that spontaneously resumed ovulating during the feeding treatment period was identical between the treatment groups. Some (Grainger and Wilhelms, 1979; McDougall et al., 1995b), but not all (McDougall et al., 1995c; Burke and Roche, 2007), studies have reported that reduced pasture DMI in early lactation extends the postpartum anovulatory interval and reduces conception rates. Regardless, the majority of cows in the present study had already commenced ovulating before the feeding treatments were imposed. This may have protected the LPA cows somewhat from a more deleterious effect of the severe restriction in DMI.

The 4.2% lower 3-wk submission rate among LPA cows could have been caused by some LPA cows reverting to an anestrus state after d 13. This would be consistent with the greater proportion of long RtS intervals observed in LPA cows, provided the delayed second service reflected a resumption of ovulatory function after the reversion. Burke et al. (1996a) reported that a DMI restriction in lactating primiparous cows resulted in some animals reverting to an anestrus state, although the majority continued to have estrous cycles (Burke et al., 1996a). Numerous reports on nonlactating cattle suggest that estrous cycles continue during prolonged periods of DMI restriction until at least 20% of the animal's BW is lost (Richards et al., 1989; Burns et al., 1997; Bossis et al., 1999).

An alternative possibility for the lower 3-wk submission rate among LPA cows is weaker displays of estrus, making estrous detection more difficult. The tendency

for LPA cows to have a greater proportion of short cycles after the first AI is consistent with an increase in incorrect heat detection, but may also indicate a greater proportion of genuine short cycles that typically occur after the first ovulation postpartum (McDougall et al., 1995a). The preceding explanations are speculative because the precise reason for the reduced 3-wk submission rate and greater prevalence of abnormal RtS intervals in LPA cows cannot be determined from this present study.

Although the results showed that the 3- and 6-wk pregnancy rates were significantly reduced in LPA cows, data depicted by the survival curves (Figure 4) indicate temporal inconsistencies in this effect. They suggest that reduced pregnancy rates among LPA cows occurred during the third and sixth weeks but not at other times, with the implication being that there were periods of compensatory improvement among LPA cows. For example, a convergence in the proportion of cows not pregnant by d 28 implies that LPA cows were establishing pregnancies faster than HPA cows during the fourth week of the breeding period. An experimental constraint on the herd managers included the rule that estrous synchronization or anestrous treatments were not to be employed before d 65. This requirement precluded the possibility of estrous synchrony influencing the pregnancy survival curves. Whether or not the transition from 8 to at least 16 kg of DMI/cow per day in the third week had a positive carryover effect on pregnancy rates during the fourth week for LPA cows cannot be properly tested in the present study, but remains a possibility given that metabolic extremes or changes affect gonadotropic hormone concentrations (Randel, 1990; Schillo, 1992; Grimard et al., 1995), function of ovarian follicles (Diskin et al., 2003; Jorritsma et al., 2004; Vanholder et al., 2005), oocyte competence and embryo quality (Adamiak et al., 2005; Leroy et al., 2005, 2008b), and early fetal development (Diskin and Morris, 2008).

Milk Production

Pasture DMI and milk production were necessary measures to describe the nutritional conditions experienced by the HPA and LPA cows, but were not primary points of interest in this study. Although sampling frequency was less than desired, the data remain effective descriptive estimates of the effect of a short but severe underfeeding episode on production. The LPA cows responded by reducing ECM yield to about 78% of that being achieved by HPA cows, with lower protein concentrations. The immediate decrease in milk yield evident in LPA cows during the feeding treatment period is consistent with previous studies in which pasture

DMI restrictions have been imposed during peak lactation (Bryant and Trigg, 1979; Auldist et al., 2000).

A combination of physiological factors is likely to have contributed to the milk yield depression. First, restricted DMI reduces cardiac output and decreases blood flow and nutrient supply to the mammary gland (Guinard-Flament et al., 2006). Second, there is a concomitant reduction in mammary glucose uptake per unit blood flow following a feed restriction-induced downregulation of the glucose transporter-1 and sodium glucose cotransporter-1 genes (Boutinaud et al., 2008). Because glucose is the primary precursor for lactose synthesis and lactose is the major osmotic agent in milk, reduced mammary glucose uptake has a major rate-limiting effect on milk synthesis.

In addition to an immediate decrease, subsequent effects of restricted DMI on components of milk yield were evident through d 53 in LPA cows in herd W, possibly because of decreased mammary epithelial cell activity and proliferation (Nørgaard et al., 2005; Guinard-Flament et al., 2006) as a consequence of 14-d feed restriction. Although there is no documented effect of a feed restriction on mammary tissue regression via apoptosis, reduced dietary energy intake prompts active secretory cells to enter a quiescent, nonsecretory state (Vetharanim et al., 2003). The net result is a reduction in the capacity of the mammary gland to synthesize milk (Guinard-Flament et al., 2006). Cells that enter the quiescent state can be reactivated (Vetharanim et al., 2003). The eventual recovery in milk yield among LPA cows in herd W, once feed energy intakes were normalized, may reflect this reactivation process.

In the current study, the feed restriction on LPA cows was experimentally imposed to mimic a potential worst case scenario commercially; notwithstanding catastrophic events such as severe flooding, such a feed restriction is unlikely to eventuate in common practice. Astute dairy herd managers would foresee an impending feed shortage and plan accordingly. Responsive management options might include a preemptive adjustment to feeding allowances to ensure a more gradual and less severe period of restricted feeding, an introduction of supplementary feeds, or a reduction in feed demand (e.g., once-daily milking or destocking). From a systems perspective, it could be interpreted that feed shortages during the seasonal mating period will reduce milk production substantially but have only a small effect on reproductive performance.

CONCLUSIONS

A short but severe pasture DMI restriction at the start of a seasonal breeding period reduced some key indicators of reproductive performance and milk pro-

duction. At least 6 wk of restorative DMI were required before fertility and production indices were equivalent to those in cows that did not experience the DMI restriction.

ACKNOWLEDGMENTS

The authors are grateful to B. Atrill, B. Walsh, and the farm staff at the Fonterra and Westpac Taranaki Agricultural Research Station dairy farms (Hawera, New Zealand). The statistical support of B. Dow (Dairy NZ Ltd.) is also highly appreciated, as are the contributions of K. Macdonald and J. Roche (Dairy NZ Ltd.) to the experimental design and implementation and manuscript preparation. This study was funded by New Zealand dairy farmers through DairyNZ Inc. (Hamilton, New Zealand; project AN708) and Fonterra (Auckland, New Zealand).

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