The growth and development of dairy heifers fed a low, high and *ad libitum* allocation of milk replacer

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Abstract

Feeding calves more milk has been shown to increase their pre-weaning growth rate and is associated with improved lifetime performance, but few studies have determined the effect of providing greater milk allowance on the feed intake and growth of heifer calves in New Zealand dairy farming systems. The objective of this study was to determine the effect of 3 different milk replacer (MR) allowances when allocated via automated feeding machines on the feed intake, growth, mammary gland development and grazing behaviour of dairy heifers (Holstein-Friesian x Jersey) in a pastoral system. Calves were allocated MR at either a low allowance, fed at 10% of initial body weight (BW) (LA; n = 67), a high allowance, fed at 20% of initial BW (HA; n = 65) or an *ad libitum* allowance (ADLIB; n = 66). Weaning began after 69 days on the study by gradually reducing MR allowance over 14 days, so that weaning was concluded by 83 days. All calves had free access to pelleted calf starter via automatic feeders until 121 days, and to ryegrass hay from 21 to 91 days. Calves were put outdoors and given access to pasture at 91 days. Calves that were fed more MR had greater total dry matter intake and greater growth rate before weaning (ADLIB > HA > LA; $P < 0.01$), but ADLIB calves had lower intake of calf-starter and lower growth rate in the first 5-weeks after weaning than HA and LA calves ($P < 0.01$). At 6 months of age, ADLIB and HA calves were heavier than LA ($P < 0.05$), but there was no difference in BW at 10 months of age. Pre-weaning growth rate was positively associated with BW at 6 months of age ($R^2 = 0.37$; $P < 0.01$) but was not related to post-weaning growth rate. Pre-weaning growth of the mammary parenchyma, as measured by ultrasonography, was greater in LA than ADLIB calves ($P < 0.05$) but there was no difference in the mammary fat pad or total gland growth. A subset of calves (n = 28) had their behaviour monitored on 4 occasions over a 5-week period, beginning a day after being given access to pasture. One day after being given access to pasture, ADLIB calves spent more time grazing than LA calves, and LA calves spent more time ruminating than HA and ADLIB calves ($P < 0.05$). There was no difference among treatments in grazing behaviour at subsequent observations. This study demonstrates that group-housed crossbred heifer calves have greater pre-weaning growth rates when fed more milk (10% of initial BW vs 20% of initial BW vs *ad libitum* feeding), and maintain this weight advantage to 6 months, but not to 10 months of age when grazing pasture. The impact of increased pre-weaning growth rate and the effect of differences in pre-weaning mammary gland development on future lactation performance of heifers in a pastoral system require further investigation.

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Abbreviations used

LA = low allowance
HA = high allowance
ADLIB = ad libitum
MR = milk replacer
BW = body weight
ADG = average daily gain
DM = dry matter
DMI = dry matter intake
PAR = parenchyma
MG = mammary gland
FP = fat pad

Chapter 1. Introduction

The dairy industry is a significant contributor to New Zealand's (NZ) economy, with total export revenue of NZ$16.66 billion in the 2017/18 season, 39% of total primary industry exports (Ministry for Primary Industries, 2019). There were nearly 5 million dairy cows in NZ, producing a total of 1,840 million kg of milk solids in 2017/18 (DairyNZ Dairy Statistics, 2018). Cows are removed and replaced from the herd annually to improve herd genetic merit and due to failed reproduction, poor health and production or management issues (Kerslake et al., 2018). A herd replacement rate of around 22% per year results in approximately 1.14 million replacement dairy heifers being reared annually (Archer et al., 2014; DairyNZ Economic Survey, 2018). Calves are separated from their dams within 24 hours of birth and typically reared in group-housing by feeding whole milk or milk replacer (MR) (Margerison et al., 2003; Roth et al., 2009a).

Globally, research on calf rearing practices has traditionally focused on feeding strategies that involve the provision of restricted milk allocations (~10% of initial birth weight; Khan et al., 2011b), with the goal of reducing the overall cost of calf-rearing and avoiding a growth check after weaning (Muir et al., 2002; Khan et al., 2016). Calf rearing represents a significant cost to the dairy farming operation, and the provision of milk or MR, and the associated labour cost of milk feeding are the most expensive components of calf rearing. Therefore, providing restricted milk allowances encourages a greater intake of solid-feed, allowing earlier weaning and a reduction in the total amount of milk fed (Khan et al., 2011b).

In seasonal dairy farming systems such as NZ, replacement heifers are required to become pregnant at 15 months of age to calve by 24 months and maintain a 365-day calving interval. Conception rates are greatest from the third oestrous cycle following puberty (Byerley et al., 1987), therefore, reaching puberty at 12 months of age maximises the chance of successful conception by 15 months of age. Puberty occurs at 43-57% of mature body weight (BW) (McNaughton et al., 2002), and so the attainment of the appropriate BW targets leads to improved conception rates; heifers that reach their live weight target at 9 months of age are 10 times more likely to be pubertal at 12 months (Martín et al., 2018). However, many dairy heifers in NZ fail to reach the appropriate BW targets at mating (44% of all heifers between 2012 and 2015) and pre-calving at 22 months of age (65% of all heifers reared between 2012 and 2015 (Handcock et al., 2016). Improving pre-weaning growth rates may improve BW after weaning, thus improving heifer reproductive performance.

As well a potential benefit on reproduction, there is a positive effect of increased growth rate prior to weaning (before ~3 months of age) on future lactation performance; calves that are fed more MR are 2 times more likely to produce more milk in their first lactation, at an estimated increase of 1,550 kg of milk for an additional kg of ADG before weaning (Soberon and Van Amburgh, 2013) thought to be due to improved mammary gland development (Brown et al., 2005a). In NZ dairy herds, BW between 3 and 21 months of age has a curvilinear relationship to the combined 3-parity milk yield (Handcock et al., 2019).

Higher allowances of milk (≥ 20% initial birth weight as liquid milk or MR) improve growth rates before weaning (Khan et al., 2011b), as well as improving feed efficiency (Dennis et al., 2018a) and reducing hunger distress (de Passillé et al., 2011). The development and increased adoption of automatic milk feeders allow the implementation of a high milk-feeding regime without the increased labour requirement, making such a rearing system a more feasible option in larger dairy herds. However, little research has evaluated the effect of milk allowances on the performance of crossbred heifer calves in the pastoral dairy systems typical to NZ. Furthermore, the impact of milk allowance on the weaning transition of calves has typically been assessed in housed conditions, and the effect that milk allowance may have on the ability of calves to transition to grazing pasture is not well-researched. The aim of this research was to evaluate the effect of feeding different MR allowances via automated feeding machines on the growth and development of group-housed crossbred dairy calves up to 10 months of age in a pastoral dairy system.

Chapter 2 is a review of the literature on the current knowledge of the effect that pre-weaning milk allowance has on calf performance pre- and post-weaning, and on long-term performance, while Chapter 3 states the hypothesis and research questions of the study. In Chapter 4, the effect that milk allowance has on the performance of pastoral-heifers up to 10 months of age is investigated and discussed, which is supplemented with an observational study of calf grazing behaviour post-weaning in Chapter 5. Chapter 6 discusses the results, implication, limitations and future research required following Chapters 4 and 5.

Chapter 2. Review of Literature

2.1 Overview of calf digestive physiology

The calf is born as a monogastric with an undeveloped reticulorumen and relies completely on a liquid diet (milk or MR) to provide the energy and nutrients needed for maintenance and growth for the first few weeks of life (Drackley, 2008). Closure of the oesophageal groove occurs in response to suckling, diverting milk directly to the abomasum to avoid fermentation in the reticulorumen (Ørskov, 1972). Milk is a whole food for young calves, and provides a balanced source of highly digestible energy, protein and micronutrients (Drackley, 2008). Digestive enzymes that are present from birth are secreted from the salivary glands, abomasal tissue, pancreas and the small intestine to act upon the milk components to release amino acids, glucose and fatty acids for absorption (Sissons, 1981). Polysaccharides and cellulose are less digestible by the young calf as the foregut is not yet developed and has limited capacity for fermentation and digestion.

2.1.1 Milk and milk replacer as a calf feed

The main components of milk are water, lipids, carbohydrates, proteins, vitamins and minerals (Jenness, 1988). In NZ Friesian cows, protein concentration average approximately 3.2%, fat concentration 4.6% and lactose concentration 4.8% (Auldist et al., 1998), though this can vary significantly according to breed (Auldist et al., 2004) and season (Auldist et al., 1998). The major protein is casein, comprising an average concentration of 2.6%, with whey proteins making up the remaining 0.5% (Auldist et al., 1998). Within the fat portion, 98% are triglycerides (Jenness, 1988).

Milk replacer can vary widely in ingredients and composition. A protein source is typically either skim milk powder (clot-forming), or whey powder and whey protein concentrate (non-clot forming) (Lammers et al., 1998). Alternative sources of protein include vegetable proteins such as soy or wheat gluten (Kertz et al., 2017).

Given that lactose is the predominant carbohydrate in milk, the enzyme lactase has relatively high activity in the gut of the new-born calf and is secreted by the intestinal mucosa to act on the lactose in the small intestine, releasing mono-saccharides (Toullec and Guilloteau, 1989). Digestion of any carbohydrate other than lactose is limited before approximately 1 month of age (Toullec and Guilloteau, 1989).

Rennin and pepsin, the main proteolytic enzymes, are secreted by the abomasal mucosa in an inactive form and are then activated by low pH in the abomasum, caused by secretion of hydrochloric acid. Rennin causes coagulation of casein proteins, resulting in a clot that slows the rate of passage of casein to the small intestine. Whey proteins are either hydrolyzed in the abomasum (α-lactoglobulin) or pass through to the small intestine (β-lactoglobulin) where they are digested by proteases from the pancreas and intestinal mucosa. Upon exiting the small intestine, over 95% of milk proteins have been digested (Davis and Drackley, 1998). Despite no clotting ability, whey protein concentrates used in calf MR result in equal or greater performance when compared to skim milk powder (Lammers et al., 1998), though Thomson et al. (2018) suggest that such products in NZ are not suitable for rearing calves. Calf growth and feed efficiency when fed vegetable proteins (e.g., soy and wheat gluten) is less in comparison to milk proteins (Drackley et al., 2006).

Milk fat in the pre-ruminant is highly digestible. Salivary lipase begins lipid hydrolysis in the mouth and is continued once in the small intestine by pancreatic lipase. Other fats (from vegetable sources) are less digestible, and digestion and absorption largely depend on the ability of the fats to be emulsified or homogenized to a particle size of less than 10 μm (Davis and Drackley, 1998).

2.2 Development of the rumen and factors affecting rumen development

2.2.1 Development of the rumen

While the growth rate of calves is maximised when they are fed an *ad libitum* allowance of whole milk (Jasper and Weary, 2002), to maintain growth rates after milk or MR is removed from the diet, calves must have developed the ability to consume and utilise solid-feed. For this to occur, a dramatic change in the morphology and physiology of the calf gut must take place, namely the development of the rumen and acquisition of the capacity for ruminal fermentation of a plant-based diet and absorption of the fermentation end products (e.g., volatile fatty acids) (Khan et al., 2016). Rumen development involves the establishment of the necessary microbial populations, muscularization, epithelial differentiation, papillary development and vascularisation of the rumen wall, all of which require the ingestion of solid-feed (Baldwin et al., 2004). Ingestion of solid-feed is required for epithelial differentiation because volatile fatty acids, primarily butyrate triggers the proliferation and differentiation of rumen epithelium cells (Govil et al., 2017).

The transition from a pre-ruminant to a ruminant involves a shift of the feed source from lactose and milk proteins to structural carbohydrates (e.g., cellulose) and complex proteins in plant-based feeds; thus, a change in the mechanism of digestion occurs. The end products of digestion, and the primary energy source used by the calf change from glucose and long-chain fatty acids to volatile fatty acids as the calf consumes more solid-feed and ruminal fermentation increases (Baldwin et al., 2004). There is a change in the hepatic (liver) metabolism from glycolytic to glucogenic as the calf begins to form more propionate as a substrate for glucogenesis (Baldwin et al., 2004).

2.2.2 The role of concentrate feeds in rumen development

Butyrate and propionate have the greatest effect on the development of ruminal papillae and on rumen epithelial differentiation (Baldwin et al., 2004). As concentrate feeds (e.g., calf starter) with a high proportion of non-structural carbohydrates result in a high proportion of butyrate and propionate production after fermentation, feeding concentrates promotes rumen development (Stobo et al., 1966). However, the immature rumen has limited ability to absorb or clarify fermentation end-products, and diets that are very high in readily fermentable carbohydrates or that have a very small particle size can cause a decrease in rumen pH that has detrimental effects on rumen health and papillae development (Hinders and Owen, 1965; Beharka et al., 1998). The addition of a source of forage to the diet is therefore beneficial for good ruminal health and development (Khan et al., 2016).

2.2.3 The role of fibre sources in rumen development

Provision of bulky fibrous feeds to milk-fed calves has often been dissuaded, as there was evidence that the bulkiness decreases concentrate intake (Hill et al., 2008). However, addition of a fibrous source such as hay to the diet aids in muscular development of the rumen and encourages rumination, as well as increasing rumen buffering capacity by stimulating saliva secretion, resulting in greater rumen-reticulo weight and increased volatile fatty acid absorption (Baldwin et al., 2004; Khan et al., 2016). Provision of even small amounts of hay during weaning reduces the incidence and severity of sub-acute ruminal acidosis in calves (Laarman and Oba., 2011). Indeed, McCoard et al. (2019) demontrated that calves are able to be reared and weaned succesfully with only conserved alfafa as a source of solid-feed until 100 days of age.

2.3 Calf rearing systems

2.3.1 Natural rearing systems or calves reared by a dam or nurse cows

Removal of the calf almost immediately after birth is typically the most preferred option in dairy farm systems to maximise the harvest of saleable milk, and because of increased difficulty to separate the cow and calf after prolonged contact with the dam (Flower and Weary, 2003). Where calves are reared by the dam without disturbance, they will suckle their dam approximately 8-12 times/day for 10 minutes each time (Reinhardt and Reinhardt, 1981). Holstein calves nursing on their dam have been found to consume around 6 kg of milk/day in the first week of age, rising to a maximum of 12 kg/day at 9 weeks of age (Wagenaar and Langhout, 2007; de Passillé et al., 2008). Calves are naturally weaned from the cow by a gradual reduction in suckling frequency which results in a simultaneous decrease in the quantity of milk consumed, as the calves become more reliant on other food sources. Full milk removal can occur when calves are as old as 10 months, or at least before the birth of the dam's next offspring (Reinhardt and Reinhardt, 1981). Several options exist for cow-calf rearing systems in a modern dairy system, such as restricted access to the dam by the calf while machine milk removal continues or putting several calves onto a nurse cow (Johnsen et al., 2016). The growth rate of calves that are allowed some form of suckling is typically greater than in artificially reared systems with restricted milk allowances (Meagher et al., 2019), with average daily gain up to 1.2 – 1.4 kg/day in the first 3 months of age (Flower and Weary, 2001; Roth et al., 2009a). The difference in feeding frequency and duration, milk intake and growth between calves that are naturally, or semi-naturally reared compared to restricted rearing systems suggest that the artificial rearing systems are not optimising animal nutrition.

2.3.2 Artificial calf rearing in New Zealand

Artificial calf-rearing involves removal of the calf from the dam around birth, in most cases within 24 hours. Calves are typically reared in group-housing and fed colostrum and whole milk, waste milk or MR, with calf starter often provided *ad libitum* within several weeks of age (Thompson et al., 2018). Calves are often given free access to pasture prior to weaning while also having access to indoor housing or are put on to pasture immediately after weaning. There are three general approaches for milk feeding to artificially reared calves; either offering restricted amounts of milk or MR (~10% of initial BW; On-Farm Research, n.d; Khan et al., 2011b) to encourage starter intake and facilitate and early weaning, an 'enhanced nutrition' approach where high allowances are offered (~20% of initial BW; On-Farm Research, n.d; Khan et al., 2011b), or *ad libitum* quantities of milk are offered to accelerate early-life growth rate (Jasper and Weary, 2002). Calf rearing systems in NZ typically involve feeding restricted quantities of milk to reduce costs and allow early weaning, with specialised calf-rearing units typically feeding less milk and weaning at a younger age than dairy farmers rearing replacement calves (Thompson et al., 2018). Replacement calves reared on NZ dairy farms are fed, on average, 316 litres of milk prior to weaning and are weaned at an average of 68 days of age, meaning that the average amount fed is 4.6 litres/calf per day (Thompson et al., 2018), or approximately 12.7% to 17.7% of their initial BW (Hickson et al., 2015). However, there is large variation amongst NZ dairy farmers in their replacement calf-rearing practices. A survey reported that weaning ages range from 3 to 24 weeks old, and milk quantities range from less than 99 litres/calf over the course of rearing (9% of respondents), to feeding milk *ad libitum* (6% of respondents; Thompson et al., 2018). Another NZ survey reported a range in the weaning age of calves from 9.2 to 15.9 weeks of age, at an average of 13 weeks (Cuttance et al., 2017).

2.3.3 Automatic milk feeders

Automatic milk feeders present an opportunity to implement a more natural feeding regime in artificial rearing systems, as they allow the allocation of smaller, more regular meals, while avoiding an increase in labour requirement. With automatic feeders, calves can consume greater volumes of milk without increasing the risk of scours that arises when calves are fed high milk allowances with less frequent meals (Albright and Arave, 1997). Automated milk feeding machines also provide the ability to tailor milk allowance for individual calves, which leads to an improved transition to solid-feed due to the ability to precisely control the time and rate with which individual calves are weaned (de Passillé and Rushen, 2016; Welboren et al., 2019; Benetton et al., 2019). Control of individual intake also has the benefit of equal milk allocation to calves, as group-feeders can lead to the stronger, or faster drinking calves consuming more than their allocation to the detriment of others in the group (Hepola, 2003). Another advantage of an automated milk feeder is the ability to earlier detect illness that is exhibited by changes in feeding behaviour (Svensson and Jensen, 2007; Borderas et al., 2009b).

2.4 Effect of milk allowance on pre-weaning performance

2.4.1 Effect of milk allowance on pre-weaning solid-feed intake

There is an inverse relationship between milk intake and solid-feed intake in the period before weaning, as calves show a strong preference for milk or MR over solid-feeds. When milk intakes are restricted, calves will begin to consume solid-feed in greater amounts at a younger age than when fed unrestricted milk (Table 1).

Even when calves are fed milk *ad libitum* and can be satiated from milk intake alone, they still consume low amounts of concentrate (Jasper and Weary, 2002; Rosenberger et al., 2017), and when denied access to solid-feed, they may begin to consume bedding material even when large allowances of milk being provided (Diaz et al., 2001). Calves will begin to show abnormal oral behaviour (e.g., cross-sucking, tongue playing) after approximately 3 months of age when given limited access to roughage and no opportunities for rumination (Webb et al., 2014). These authors also reported that the proportion of dry matter (DM) in the diet comprising of MR reduced from 52% at 3 months of age to 30% at 6 months of age when given *ad libitum* access to MR and different sources of solid-feed, demonstrating an innate desire to consume solid-feed, and a natural shift in diet selection as calves change from monogastric to ruminant digestion.

Although milk allowance has a direct effect on concentrate consumption, other factors influence how much solid-feed is consumed prior to weaning. Despite being fed the same milk allowance (12 litres/day) and in the same housing conditions, de Passillé et al. (2012) reported that the age at which calves first begin to consume 200 grams of concentrate per day ranged from 23 to 82 days. Calves that are more active and exploratory will consume more concentrate, showing that behaviour influences the extent of food neophobia (Neave et al., 2018), and peer-housing increases concentrate consumption (Costa et al., 2016). Age is also a significant driver of concentrate intake, with older calves consuming more concentrate (Silva et al., 2018).

Table 1. Whole milk or milk replacer intake, concentrate intake per day (d) and average daily gain (ADG) before and after weaning in a range of studies evaluating different milk or milk replacer intakes.

Before weaning						After weaning			
Milk feeding age, weeks	Milk intake, kgDM/d	Concentrate intake, kgDM/d	Total intake, kgDM/d	ADG, kg/d	Weaning length, d	Age during period, weeks	Concentrate intake, kgDM/d	ADG, kg/d	Reference
1-6	0.53	0.17	0.70	0.49	7	7-9	1.85	0.85	Jasper and Weary., 2002
1-6	0.94	0.09	1.03	0.72	7	7-9	1.89	0.68	
1-3	0.45	0.27	0.72	0.15	7	4-8	1.01	0.73	Kehoe et al., 2007
1-4	0.46	0.32	0.78	0.31	7	5-8	1.14	0.75	
1-5	0.44	0.41	0.85	0.37	7	6-8	1.37	0.87	
1-6	0.48	0.49	0.97	0.46	7	7-8	1.72	0.88	
1-6	0.49	0.42	0.91	0.53	7	6-7	2.14	0.91	Raeth-Knight et al., 2009
1-6	0.60	0.45	1.05	0.66	7	6-7	2.30	1.03	
1-6	0.57	0.42	0.99	0.63	7	6-7	2.17	0.77	
1-6	0.90	0.24	1.14	0.79	7	6-7	2.13	0.78	
1-6	0.44	0.72	1.16	0.48	3	8-12	2.58	1.00	Hill et al., 2010
1-6	0.66	0.73	1.39	0.60	3	8-12	2.72	1.06	
1-7	1.09	0.67	1.76	0.65	7	8-12	2.83	0.95	
1-7	1.77	0.10	1.89	1.2	7	8-14	3.38	1.20	Miller-Cushon et al., 2013
1-7	0.67	0.45	1.12	0.60	7	8-14	3.17	1.20	
1-5	0.43	0.68	1.11	0.79	7	6-7	2.52	1.38	Terré et al., 2007
1-5	0.90	0.36	1.26	0.88	7	6-7	1.90	1.37	
2-6	0.57	0.30	0.87	0.58	12	8-10	2.70	1.27	Rosenberger et al., 2017
2-6	0.72	0.10	0.82	0.57	12	8-10	2.80	1.23	
2-6	0.83	0.10	0.93	0.65	12	8-10	2.90	1.32	
2-6	0.94	0	0.94	0.88	12	8-10	2.90	1.26	
1-7	1.35	0.09	1.44	1.04	0	8-9	0.99	0.22	Steele et al., 2017
1-5	1.35	0.09	1.44	1.13	12	8-9	1.32	0.83	
1-5	0.64	0.51	1.15	0.64	7	6-8	2.60	1.14	Kmicikewycz et al., 2013
1-5	0.70	0.44	1.14	0.63	7	6-8	2.25	0.76	
1-5	0.87	0.25	1.12	0.74	7	6-8	2.21	1.09	
1-5	0.88	0.34	1.22	0.70	7	6-8	2.41	0.91	
1-6	0.55	0.39	0.93	0.48	7	7-9	1.93	0.67	Cowles et al., 2006
1-6	1.08	0.21	1.29	0.77	7	7-9	1.67	0.69	
1-8	0.73	0.19	0.92	0.66	5	9-13	2.06	1.04	Azevedo et al., 2016
1-8	0.88	0.18	1.06	0.69	5	9-13	2.03	0.96	
1-8	0.96	0.16	1.12	0.75	5	9-13	2.06	0.98	
1-8	1.07	0.13	1.2	0.78	5	9-13	2.2	1.02	

2.4.2 Effect of milk allowance on total nutrient intake before weaning

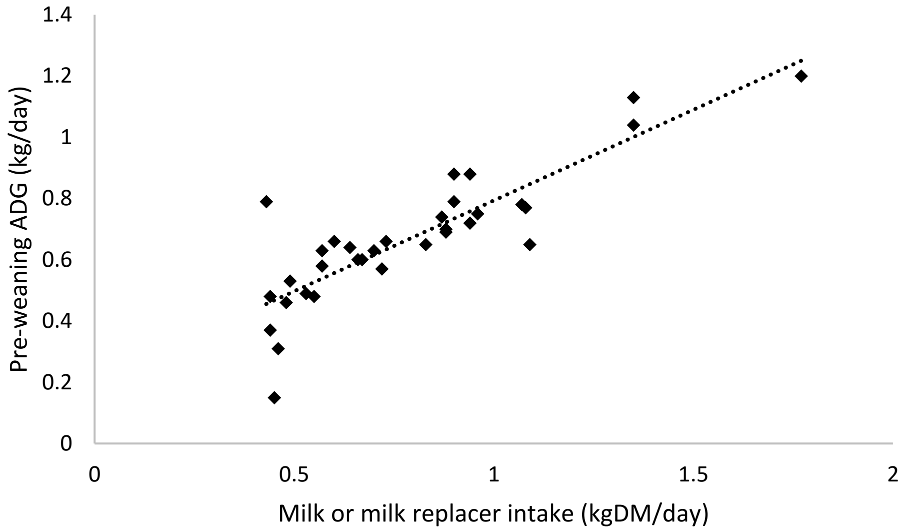
Despite calves increasing their pre-weaning solid-feed intake when fed restricted quantities of milk, the extent to which they do this does not fully compensate for the lower intake of energy and protein from milk (Table 1). An array of studies demonstrates that total dry matter intake (DMI) before weaning increases with increasing milk allowance (Table 1). Regardless of milk intake, solid-feed intake is negligible until they are around 2 weeks of age, so during this period, total nutrient intake is closely related to milk allowance (Jasper and Weary, 2002). As calves age and begin to consume more concentrate, the relationship between milk intake and total nutrient intake weakens, so that calves weaned from milk at an older age have greater daily nutrient intakes before weaning (Kehoe et al., 2007). While total milk allowance is positively related to the total nutrient intake before weaning, total nutrient intake in calves fed lower milk allowance can be the same as those fed more milk on a given day due to the increase in concentrate intake as calves age (Terré et al., 2009).

2.4.3 Effect of milk allowance on growth before weaning

As total DMI increases with additional milk or MR intake, growth rate also increases (Figure 1). Other factors can also affect pre-weaning growth, such as breed, dam parity, birth weight, feeding and housing, management, the incidence of disease, climatic conditions, and the quality of the milk or MR offered (Cardoso et al., 2015; Shivley et al., 2018).

When fed *ad libitum* milk or MR, growth rates between 0.8 kg/day and 1.2 kg/day have been observed in Holstein Friesian calves reared for indoor systems (Borderas et al., 2009a; Miller-Cushon et al., 2013; Welboren et al., 2019). Conversely, Holstein Friesian calves that are fed restricted milk allowances and weaned early can have growth rates as low as 0.15 kg/day (Table 1; Kehoe et al., 2007).

Figure 1. Milk or milk replacer intake and pre-weaning average daily gain (ADG) from the studies listed in Table 1



2.4.4 Effect of milk allowance on health before weaning

Calves are most susceptible to illness and disease in the first month of life as they have not yet developed their own antibodies, and maternal antibodies from colostrum start reducing after 2 weeks of age (Hulbert and Monthsisá, 2016). Common illnesses in pre-weaning calves include respiratory diseases (e.g., pneumonia), umbilical infections, calf diarrhoea and bovine viral diarrhoea (Heuer et al., 2007; Windeyer 2014).

Calf diarrhoea, or scours, can be caused by pathogens (Cho and Yoon, 2014) or by overfeeding, termed ‘nutritional scours’ (Albright and Arave, 1997). A range of pathogens can lead to an infection that causes scours, and includes viruses such as bovine rotavirus, bovine coronavirus and bovine viral diarrhoea virus, bacteria such as salmonella and *E. coli*, and protozoa such as *C. parvum* (Cho and Yoon, 2014). Infection from these pathogens is normally due to contamination of the environment or feed. Nutrition is crucial in determining the calves’ immune response (Nonnecke et al., 2003), and so increasing milk allowance could benefit the calf immune system by supplying energy and other essential nutrients (Schäff et al., 2016).

Some studies have demonstrated that feeding more milk does not affect the incidence of scours (Jasper and Weary, 2002; de Paula Vieira et al., 2008; Borderas et al., 2009a), while others report increased scouring with greater milk intake (Quigley et al., 2006; Raeth-Knight et al., 2009; Davis Rincker et al., 2011). Nutritional scours are caused by feeding of milk beyond the capacity of the abomasum, causing backflow into the reticulorumen. Lactose and milk proteins are then fermented, leading to indigestion and diarrhoea (Sjaastad et al., 2010). The volume of the abomasum in young calves is calculated to be around 2 litres, but due to the ability of the abomasum for distension, 3-week old calves are able to consume up to 6.8 litres of milk in a single meal with no adverse effects (Ellingsen et al., 2016b). The discrepancies in results of calves fed high milk allowances might be due to differences in the fecal scoring system used, or management of the calf in terms of colostrum feeding, housing and sanitation (Khan et al., 2011b).

2.4.5 Effect of milk allowance on mammary gland development

Growth rate of the mammary gland in calves has traditionally been described as being isometric in the pre-weaning period (up to ~3 months of age), at which point positive allometric growth of the mammary gland begins to occur at a rate of up to 3-times the rest of the body, until the onset of puberty (Sinha and Tucker, 1969; Monthsallem et al., 2010). Recent studies have indicated that high levels of nutrition, and increased growth rate, can initiate positive allometric growth of the mammary gland in the first ~3 months of life, as well as increased epithelial cell proliferation and parenchyma DNA content (Table 2).

High growth rates prior to puberty can detrimentally affect mammary gland development and subsequent milk yield in first lactation due to greater fat deposition that inhibits parenchyma growth in heifers (Sejrsen and Purup, 1997), but this effect does not occur from high pre-weaning growth rates (Brown et al., 2005a; Daniels et al., 2009). When comparing high and low pre-weaning milk intakes, an increase in mammary cell proliferation and an increase in parenchymal DNA has been reported, with no increase in fat content (Table 2; Brown et al., 2005a; Meyer et al., 2006a), as energy partitioning in the pre-weaning period is heavily favoured towards skeletal and muscle growth in calves, rather than fat deposition (Diaz et al., 2001).

Table 2. Effect of milk or milk replacer (MR) allowance on pre-weaning mammary gland development in young calves
PAR=parenchyma; MG=mammary gland; FP=fat pad, BW=body weight

Control	**Treatment**	**Effect of treatment on mammary gland**	**Reference**
Fixed MR allowance (0.6 kgDM/day)	MR allowance increased with BW (average of 1.3 kgDM/day)	↑ whole MG and PAR mass as a proportion of BW	Soberon and Van Amburgh, 2017
Fed to reach a growth of 0.65 kg/day	Fed to reach a growth rate of 0.95 kg/day	↑ PAR DNA at 100kg BW but confounded by age.	Meyer et al., 2006b
Fed to reach a growth of 0.65 kg/day	Fed to reach a growth rate of 0.95 kg/day	No effect on PAR DNA accretion or mammary epithelial cell proliferation	Meyer et al., 2006a
MR at 1.1% BW as dry matter and restricted starter	MR at 2.0% BW as dry matter and *ad libitum* starter	↑ PAR mass and PAR DNA and RNA. ↓ ductal epithelial differentiation.	Brown et al., 2005a
MR at 0.45 kg/day	MR at 1.13 kg/day	↑ PAR and FP mass and DNA. ↑ epithelium and stromal tissue.	Geiger et al., 2016
MR at 0.44 kgDM/day and moderate protein and fat	MR at 0.95 kgDM/d and high protein and low/high fat; MR at 1.43 kgDM/d and high protein high fat	↑ total MG mass and FP mass. No effect of nutrient intake on PAR mass.	Daniels et al., 2009
6 litres/day at 13.5% DM	6 litres/day at 16%, 18% or 20% DM	No effect of diet on mammary parenchyma or adipose tissue growth	Furini et al., 2018
MR at 660gDM/day	MR at 660gDM/day supplemented with butyrate and fatty acids or supplemented with milk fat	No effect of diet on PAR area or mass	Esselburn et al., 2015

2.5 Effect of weaning methods on calf performance

The success of the weaning transition largely depends on the ability of the calf to ingest and digest a sufficient quantity of solid-feed to sustain body function and growth prior to the cessation of milk feeding. Weaning as gradually as possible to enable a smooth transition from milk to solid-feed will enhance post-weaning performance (Welboren et al., 2019). Methods can include gradually reducing milk allowance over a period of 14 days or more (Khan et al., 2016), and a 'step-down' method where a high milk allowance is provided for a month, and then fed at half the rate for a further 2 weeks before weaning (Khan et al., 2007).
Large differences can exist amongst individual calves in their diet selection and developmental capacity (Roth et al., 2009b; Neave et al., 2018). Group-wide feeding regimes are optimal for the 'average' calf, and weaning calves according to individual indicators of their 'readiness' to be weaned, such as concentrate intake or blood β-hydroxybutyrate levels, could improve the weaning transition (de Passillé and Rushen, 2012; Deelen et al., 2016).

2.5.1 Weaning according to solid-feed intake

Reducing milk allowance of individual calves in response to an increase in their solid-feed intake allows a smooth weaning transition in calves that are fed a high milk allowance; by decreasing milk allowance only as solid-feed intake increases, total nutrient intake remains consistent (de Passillé and Rushen, 2012). Weaning according to concentrate intake also allows weaning at a younger age with no effect on growth rates, resulting in less total milk consumption (de Passillé and Rushen, 2016). Benetton et al. (2019) also demonstrated that weaning according to concentrate intake resulted in calves that had greater growth rates during weaning, were heavier after weaning and consumed less milk in total than those weaned gradually at a set age.

2.5.2 Weaning according to indicators of rumen development

β-hydroxybutyrate, the ketone of butyrate, is an indicator of rumen papillae and epithelial development (Quigley et al., 1991). There is a strong curvilinear relationship between β-hydroxybutyrate and total rumen volatile fatty acids, and a strong linear relationship between circulating whole-blood β-hydroxybutyrate levels and starter intake of calves (Deelen et al., 2016). Due to the relationship between rumen development and solid-feed intake (Baldwin et al., 2004), β-hydroxybutyrate may be useful in determining when calves should be weaned, particularly with the development of calf-side β-hydroxybutyrate tests (Deelen et al., 2016). Deelen et al. (2016) found that 100 µmol of circulating β-hydroxybutyrate per litre of blood accurately predicted a calf-starter intake of 1 kg/day over a 3-day period. However, the relationship between β-hydroxybutyrate concentrations is far weaker when calves are subjected to stress (e.g., weaning) as β-hydroxybutyrate is also produced from fatty acid catabolism (Suarez-Mena et al., 2017).

2.6 Effect of milk allowance on post-weaning performance

2.6.1 Effect of milk allowance on post-weaning nutrient intake

When milk allowance is reduced or removed, solid-feed intake increases as it becomes the only nutrient source (Table 1). Intake of solid-feed is dependent on sufficient development of rumen digestive capacity, and it takes longer for calves fed greater milk allowances to develop this capacity. Therefore, in calves that are fed a high milk allowance, there is an increased delay in solid-feed intake after milk allowance is reduced that can lead to a deficient nutrient intake after weaning (Table 1; Steele et al., 2017). Weaning calves when they are older (3 weeks *vs* 6 weeks of age; Eckert et al., 2015) and by gradually reducing milk allowance over an extended period (Dennis et al., 2018b) results in a minimal reduction in total nutrient intake, except in cases where *ad libitum* milk allowances are fed (Welboren et al., 2019).

2.6.3 Effect of milk allowance on growth after weaning

A reduction in growth rate during and immediately after weaning tends to occur when milk intake exceeds ~0.7 kgDM per day, and when weaning occurs over a period of 7 days or less (Table 1; Cowles et al., 2006; Hill et al., 2013). Lower post-weaning growth rates in calves fed more milk are due to lower solid-feed intake (Hill et al., 2010) and reduced digestibility of solid-feed (Terré et al., 2007).

Providing adequate time for concentrate intake to increase and for the rumen to develop by weaning calves through gradual procedures over a week or more can minimize the loss in the growth rate after weaning (Sweeney et al., 2010; Dennis et al., 2018a). Meale et al. (2015) weaned calves fed 8 litres/day at 8, 10 or 12 weeks of age and reported heavier BW at 13 weeks of age in calves weaned at 12 weeks of age compared to 8 weeks of age. This suggests that weaning *ad libitum* milk fed calves at an older age increases the success of the weaning transition.

2.7 Effect of milk allowance on long-term performance

2.7.1 Effect of milk allowance on long-term growth

Aside from nutrition, the primary determinant of growth rate in cattle is the mature size (Owens et al., 1993). Mature size is genetically determined, but can be altered through environmental effects, particularly a nutrient deficiency in early life (Owens et al., 1993).) Severe underfeeding of cattle in the first 16 weeks of life can detrimentally impact growth rates up to maturity (Everitt and Jury 1977). However, several recent studies involving housed cattle have shown that the weight advantage of calves fed more milk is lost during the pre-pubertal period (Terré et al., 2009; Kiezebrink et al., 2015; Lage et al., 2017). In these studies, it is likely that the underfeeding of calves fed low milk allowances was not severe enough to cause lasting effects on growth (Everitt and Jury, 1977). Shamay et al. (2005) fed *ad libitum* whole milk and restricted MR before weaning, and reported greater BW up to calving, and earlier onset of puberty in calves fed *ad libitum* whole milk. The age at which heifers reached their first service (pre-determined at a minimum BW of 380 kg) tended to be earlier (62.6 *vs* 65.3 weeks of age; P = 0.072) in Holstein heifers fed *ad libitum* MR than those fed 5 litres/day of MR (Curtis et al., 2018), and heifers that were fed 6 litres/day or 8 litres/day of MR before weaning were heavier at 300 days of age than those fed 4 litres/day (Yunta et al., 2015). In NZ pastoral systems, heifer calves fed more milk before weaning maintained their BW advantage up to 135 days of age (MacDonald and Penno, 1997). It appears that the ability of heifers to maintain an advantage in BW at weaning for an extended period after weaning (3-9 months) is dependent on the magnitude of the weight difference, and on avoiding a growth-check immediately after weaning.

2.7.2 Effect of milk allowance on lactation performance

An increasing amount of literature demonstrates a positive relationship between pre-weaning growth rate and lactation performance (Soberon and Van Amburgh, 2013; Gelsinger et al., 2016). While many studies lack the statistical power to demonstrate differences in milk yield, a meta-analysis of studies done in North America showed an increase in first-lactation milk yield by 1,550 kg of milk per kg of ADG before weaning (Soberon et al., 2012), and an analysis of commercial and study herds showed an increase of 1,113 kg of milk per kg of pre-weaning ADG (Soberon et al., 2012). In the latter study, it was found that 22% of the variation in first-lactation milk yield could be explained by pre-weaning ADG.

As well as a direct relationship between pre-weaning growth rate and lactation performance, calves that are heavier at weaning may have improved milk production by retaining their weight advantage after weaning. Body weight between 3 months and 21 months of age has a linear relationship to first lactation milk yield, and a curvilinear relationship to the combined milk yield in the first 3 parity's in NZ dairy herds (Handcock et al., 2019).

Chapter 3. Hypothesis and Research Questions

The effects that milk allowance has on the nutrient intake and growth of calves before and after weaning has predominantly been investigated in North America and Europe using Holstein Friesian calves that are housed indoors and fed a total-mixed ration. Few studies have described the effect that milk allowance has on the pre and post-weaning growth performance of crossbred heifers in a NZ pastoral dairy system.

Research shows that increased growth rates before weaning allows for increased future milk production which is thought to be due to improved mammary gland development. However, in the published literature, the effect that milk allowance has on mammary gland development is not clear and has not been extensively studied in NZ dairy calves.

Calves are typically provided a concentrate feed (e.g., calf starter) in addition to milk or MR prior to weaning, and concentrate feeds are also used to transition calves to a solid or pasture diet after weaning. Compared to overseas indoor systems where calves are transitioned onto a total-mixed ration at weaning, calves in pastoral systems are managed in large mobs and start to graze pasture before or immediately after weaning. The effect that milk allowance has on the ability of calves to transition from a diet of milk and concentrate feeds to grazing pasture is not well understood.

Therefore, the aim of this study was to determine the effect of allocating a low (control), a high or an *ad libitum* milk allowance via automated feeders on:

1. Pre-weaning calf-starter intake, nutrient intake and growth.
2. Pre-weaning development of the mammary gland as measured by ultrasound.
3. Calf-starter intake and growth immediately after weaning
4. The behaviour (grazing and rumination) of calves after weaning on pasture.
5. Body weight and growth rate up to 10 months of age.

It is hypothesised that calves that are fed a greater allowance of MR will have lower pre-weaning calf-starter intake, but greater total nutrient intake and growth rate. We also anticipate that the depth of the mammary pad at weaning will be greater in calves fed more MR.

With the gradual weaning implemented, no difference in the post-weaning growth rate, calf-starter intake or time spent grazing and ruminating is expected. Thus, we anticipate that the greater BW at weaning of calves fed more MR will be maintained until 10 months of age.

Chapter 4. Effect of milk allowance on feed intake, scour incidence, pre-weaning mammary gland development and growth performance of heifer calves up to 10 months of age

4.1 Introduction

In seasonal dairy farming systems used in NZ, to achieve their first calving at 24 months-of-age, replacement dairy heifers are required to become pregnant at 15 months-of-age. Heifers that calve earlier in the calving season are also more likely to become early-calving cows (Pryce et al., 2007), which enhances their performance and longevity in pastoral herds (Troccon, 1993; Martín et al., 2018). However, recent data from NZ shows that many heifers are failing to attain their target BW at mating (44% of heifers) or pre-calving (65% of heifers; Handcock et al., 2016) which is contributing to a high annual heifer culling and herd replacement rate (22% replacement rate; DairyNZ Economic Survey, 2018). Improving both the pre-weaning and post-weaning growth of replacement heifers in pastoral systems is therefore required for longevity and to achieve performance targets.

Provision of milk and the associated labour cost of feeding calves milk is one of the major operational expenses on dairy farms for both indoor and outdoor systems. Therefore, a restricted milk allowance is often fed to encourage calf starter intake and trigger rumen development to allow early weaning (Muir et al., 2002; Khan et al., 2011). Regardless, there are benefits of providing greater milk allowance on pre-weaning growth, health and welfare of dairy calves reared indoors (de Passillé et al., 2011; Khan et al., 2011; Dennis et al., 2018a). Studies conducted for indoor dairy systems indicate that greater pre-weaning ADG in calves can promote greater milk production later in life (Soberon and Van Amburgh, 2013; Gelsinger et al., 2016; Chuck et al., 2018) due to enhanced mammary gland growth, which is sensitive to early-life nutrition (Meyer et al., 2006a; Geiger et al., 2016).

Genetics, feeding, and management of dairy animals in a pastoral system as used in NZ are different (e.g., crossbred heifers reared on pasture in extensive systems) to indoor systems (e.g., US and European; Kolver and Muller, 1998; Horan et al., 2004) and, therefore, the effect of milk allowance on feed intake, growth performance and mammary gland development could also differ. It is unknown whether achieving greater pre-weaning growth by increasing milk allowance would affect the post-weaning growth of NZ dairy heifers on pasture. Automated milk feeders are now being adopted on farms in NZ as they can provide farmers an opportunity to save on labour and the cost of milk feeding. Automatic milk feeders also allow the implementation of a more natural milk feeding frequency (e.g. frequent and small meals) and gradual weaning methods (de Passillé and Rushen, 2016).

The primary objective of the research in this chapter was to assess the influence of feeding different MR allowances via automatic milk feeders on pre-weaning feed and nutrient intake, selected blood metabolites and growth performance of heifer calves (Kiwi-cross: Holstein Friesian x Jersey). Secondly, the influence of pre-weaning milk allowance and ADG on pre-weaning mammary gland growth is assessed using ultrasonography, and post-weaning growth of heifers until 10 months of age in a NZ pastoral system evaluated.

4.2 Material and Methods

An animal ethics application was approved by the Grasslands AgResearch Animal Ethics Committee (GAEC # 14249), including all procedures, sampling and measurements as described below.

4.2.1 Experimental Design, Treatments and Management of Calves

The study was conducted using Kiwi-cross calves (Holstein-Friesian x Jersey) born on 2 commercial farms in the Manawatu, New Zealand during the 2017 spring calving-season (July - September). Calves on each farm were collected twice daily from the calving paddocks. Birth date was recorded upon collection, and their navels were dipped in iodine solution. All calves received 2 litres of the first-milking colostrum at the time of calf collection (within 12 hours of birth) and then 2 litres twice daily until 2 days of age. The calves were kept on their source farms until a minimum of 4 days of age and then transported to a dedicated calf-rearing facility. Experienced farm staff were responsible for the transportation of calves according to the Dairy Cattle Code of Welfare (2016). All calves were manually fed whole milk using an artificial teat attached to a bottle (2 litres in the morning and 2 litres in the afternoon) from 3 to 7 days of age. The calves were trained to use automatic milk feeders twice daily from 8 to 10 days of age and were fed 4 litres/day of MR during this time.

The calf-rearing facility had 3 indoor calf pens (20.5m x 10m; minimum 2.53 m^2 per calf), each fitted with 1 water supply system, 2 automatic milk feeding stalls (Zeddy, Palmerston North, New Zealand), and 4 automatic pellet-feeding stalls (Zeddy, Palmerston North, New Zealand) which allowed individualised feeding of MR and calf starter to calves. The automatic milk-and starter-feeding systems were fitted with radio-frequency identification readers to recognise each calf's individual electronic identification, and stored intake data in a central computer. Milk-feeding stalls were fitted with sides to avoid disruption from other calves whilst feeding. Calves on all 3 treatments were allocated to each pen and calves with an approximate age difference of 2 weeks or less were kept together. All pens were bedded with wood chips and sprayed with a disinfectant (Virkon; DuPont, Auckland, New Zealand) fortnightly. Fresh wood chips were completely replaced on 2 occasions over the course of the experiment.

Calves (n = 199) with no apparent sign of illness (e.g., diarrhoea, respiratory disease, umbilical swelling) were weighed at 11 ± 4 days of age (defined as day 0 of the study) and allocated to 3 treatments, balanced for source farm, date of birth and initial BW. Low allowance (LA; n = 67) calves were given MR at the rate of 10% of their initial BW, high allowance (HA; n = 65) calves were given MR at the rate of 20% of their initial BW, and *ad libitum* (ADLIB; n = 66) calves were given *ad libitum* access to MR.

A commercially available MR (Table 3; Ancalf, NZAgbiz Ltd., Hamilton, New Zealand) was diluted in lukewarm water (150 gram/litre) and fed to all calves using automatic milk feeders. The automatic milk feeders were programmed to allow calves a maximum consumption of 4 litres MR at a single visit with a 2-hour wait time between consecutive feedings to avoid over-feeding. All calves had *ad libitum* access to clean drinking water and to a pelleted calf-starter (Table 3, 20% crude protein pellets, SealesWinslow Limited, Tauranga, New Zealand) along with *ad libitum* access to ryegrass hay (Table 3) from the third week of the experiment. Weaning from MR began at day 69 ± 2 on the study, and MR was gradually reduced over 14 days by linearly reducing the volume of MR based on each calves' mean consumption in the 3 days prior to the start of weaning. Weaning from MR was completed by day 83 ± 2 on the study, and calves were moved outdoors and given access to pasture at day 91 ± 2 on the study. Calves were managed together on ryegrass pasture as 1 mob in an area of approximately 5 ha until day 121 ± 9 on the study. Calf starter remained available *ad libitum* from automatic feeders for the first 14 ± 3 days on pasture and was then gradually reduced to zero over the following 17 ± 3 days, so that calf starter was completely removed by day 121 ± 9 on the study. The pasture had an average ME content of 9.8 ± 0.4 megajoules/kg DM, crude protein of 11.2 ± 2.5% and neutral detergent fibre of 54.7 ± 3% (on a DM basis). Thereafter, heifers were sent for grazing at two locations where they were managed on pasture according to standard farm routine until 10 months of age. The pre-weaning period refers to the period before calves were completely weaned from MR (day 0 – 83 on the study) and post-weaning refers to the period from when calves were completely weaned from MR until calf-starter was completely removed (day 83 – 121 on the study).

Table 3. Nutritional composition of milk replacer, pelleted calf starter and ryegrass hay

Analysis, DM basis[1]	Calf starter[2]	Milk replacer[3]	Hay
DM, %	87.1	96.1	92.6
ME, MJ/kgDM[4]	13.7	20.6	11.0
Crude protein, %	20.4	24.9	12.7
Lactose, %	-	39.5	
ADF, %	4.1	-	36.6
NDF, %	9.6	-	47.7
Ash, %	7.5	6.4	10.0
OM, %	92.5	-	-
Soluble sugars, %	5.55	-	-
Starch, %	40.5	-	-
Crude Fat, %	2.05	21.0	-
NSC, %	60.4	-	-
OM digestibility in-vitro, %	93.1	-	68.9
pH	-	-	4.1

ME = metabolizable energy; ADF = acid detergent fibre; NDF = neutral detergent fibre; OM = organic matter; NSC = non-soluble carbohydrates

[1]except where otherwise stated.

[2]20% pellets, SealesWinslow Ltd., Tauranga, New Zealand.

[3]Ancalf, NZAgbiz Ltd., Hamilton, New Zealand.

[4]ME in calf starter was calculated according to equations from AFRC (1993) and in MR according to NRC (2001) equations.

All calves were vaccinated for prevention of leptospirosis and major clostridial diseases (Ultravac 7in1, Zoetis, Auckland, New Zealand) between 4 and 8 weeks of age, and all calves received antibiotics (Alamycin LA300, Norbrook, Auckland, New Zealand) on the same date as prevention for pneumonia. All calves were disbudded between 4 and 8 weeks of age using a hot iron under local anaesthesia by a certified contractor. All calves received a dual-combination oral drench for parasite control when they went to their grazing locations after weaning, and monthly thereafter.

4.2.2 Measurements and Sampling

Calf health. The daily incidence and severity of diarrhoea was recorded by farm staff while walking through the pens and observing calves. The presence of scours was ascertained using the Wisconsin University Calf Health Scoring Chart where 0 = normal, 1 = semi-formed, pasty, 2 = loose, but stays on top of bedding, 3 = water, sifts through bedding. Calves with a faecal score of 2 or 3 were considered as scouring. Scouring days is the total number of calves with scours multiplied by the number of days they were scouring. Scouring days were only calculated for the first 3 weeks of calves being on the experiment because scouring was negligible after the first 3 weeks for all treatments. Calves with a depressed appetite or scours or both were given electrolyte therapy and where needed treated with antibiotics as recommended by the herd veterinarian. Animals that became sick (e.g. animals with diarrhoea or fever) were isolated and fed manually from a bottle (2 litres in the morning and 2 litres in the afternoon).

Feed intake. Individual intake of MR (litres/calf per day) and calf starter intakes (kg/calf per day) were recorded by the automatic feeders. Access to calf starter was available for 24 hours/day during both the indoor and outdoor periods, and access to MR was always available, excluding a period of approximately 1 hour/day to allow for cleaning of the machines. Feeders (MR and calf starter) were calibrated before the start of the experiment and their functions were monitored for accuracy by Zeddy staff throughout the study. Daily feed DM intake (MR, calf starter and total) and nutrient intakes (metabolizable energy and crude protein) were calculated for the pre-weaning period (day 0 to 83 on the study) for each calf. For the post-weaning period (day 84 to 121 on the study), daily DMI of calf starter was calculated. Water and hay intake was not measured.

Body weights and dimensions. Body weight of all calves were recorded using a digital weigh-scale monitor (Gallagher TW1 Data Monitor, Hamilton New Zealand) attached to a double load-bar scale (Technipharm, Rotorua, New Zealand). All heifers were weighed at the start of the study (11 ± 4 days of age; day 0 on the study), at the end of weaning from MR (day 83 ± 2 on the study), after the complete removal of calf starter (day 121 ± 8 on the study), at 6 months (day 188 ± 7 on the study) and at 10 months (day 287 ± 9 on the study). Average daily gain was calculated for each of the different periods based on the number of days for each calf in that period. Calves were also weighed fortnightly on the same day of the week until 120 days on the study. Some heifers were unavailable for weighing at 10 months, therefore, BW at 10 months, ADG from 6 to 10 months and ADG from 0 to 10 months was calculated with ADLIB; n = 64, HA; n = 54, LA; n = 56.

Measurements of body dimensions were taken of all calves (n = 199) at the start of the study (day 0) at weaning (day 83 ± 2 on the study), and at 6 months of age (day 188 ± 7 on the study; ADLIB, n = 48, HA, n = 41, LA, n = 44). Hip and wither height was determined using a measurement stick and heart girth (smallest circumference behind the forelegs) was measured using a measuring tape while the animal was standing on a flat surface and with their head in an upright position.

Feed analysis. Samples of MR and calf starter were taken at regular intervals over the course of the study period (n = 5 each of MR and calf starter) and pooled (n = 2 of each) for analysis. Pasture samples (n = 5) were collected by weekly pluck sampling over 5 consecutive weeks and analysed individually. Composition of MR and calf starter was determined following the procedures of AOAC (1990; Nutrition Laboratory, Massey University, Palmerston North, New Zealand). Composition of hay and pasture was determined using near infra-red spectrometry and conventional wet-chemistry methods (RJ Hill Laboratories, Hamilton, New Zealand). Metabolizable energy in calf starter, hay and pasture was calculated using equations from AFRC (1993) and in MR according to the equations given by NRC (2001).

Mammary gland ultrasound scanning. Mammary glands of a randomly selected group of calves (n = 119) were measured using ultrasonography (M-Turbo with C60x/5.2-MHz transducer; Sonosite USA, Bothell, WA) at the start of study (day 1) and at MR weaning (day 83 ± 3 on the study). Scanning of heifer calves at the start of the study was done by laying calves in a recumbent position on their hind quarters and subsequently capturing an image of each of the 4 quarters. Heifer calves scanned at weaning were restrained in a crush and ultrasound images captured from beneath. Any dirt was removed from the surface of the skin prior to scanning, and food-grade oil was used to provide a good signal transduction. The probe head was placed on the skin adjacent to or on the base of each teat parallel to the body of the calf. The probe head was angled consistently perpendicular to the gland so that the underlying fat pad and parenchymal tissue of the gland could be observed, with both sides of the peak preferably captured in the image. Images were transferred to a computer and depth of the parenchyma and fat pad within each quarter was manually measured (parenchyma is hypoechoic and appears black, while the fat pad is hyperechoic and appears white in the ultrasound image; Esselburn et al., 2015) by an independent operator, and the depth from the 4 quarters was then averaged for each calf. Operators were blinded to treatment groups during image recording and image measurement. In some cases, the image quality did not enable measurement with sufficient accuracy, and so these images were removed. Calves which had scores from 2 or less quarters at either time point were removed from the analysis. In some cases, the measurement at weaning (day 83 on the study) was smaller than the initial measurement (day 1 on the study); these were deemed as measurement errors and removed from the analysis. The number of calves included in the final analysis was ADLIB; n = 28, HA; n = 34, LA; n = 38.

Blood metabolites. Blood samples were collected from the jugular vein of all heifer calves at the start of the study (day 0), immediately after MR weaning (day 86 ± 2 on the study) and at 6 months of age (day 188 ± 7 on the study; ADLIB; n = 48, HA; n = 41, LA; n = 44). Blood samples were taken at the start of the study to see if there were differences in passive immunity or energy balance amongst treatment groups before treatments were applied. A 10-ml blood sample was collected in evacuated tubes (Vacutainer containing EDTA; Becton-Dickinson, Wellington, New Zealand) from each calf to harvest plasma. The blood samples were centrifuged (20 minutes at 1300 *g*) and 3 sub-samples of plasma were archived at about -80°C until analysis. Total protein, glucose, blood urea nitrogen, non-esterified fatty acids (NEFA) and β-hydroxybutyric were analysed from plasma at AgResearch Grasslands, Palmerston North, New Zealand using a spectrophotometer (Spectra Max 250; Molecular Devices LLC, Sunnyvale, CA, USA). For measurement of metabolites, kits were sourced from Randox Laboratories Ltd. (Crumlin, County Antrim, UK).

4.2.3 Statistical Analysis

Treatments were applied at calf level, and so each individual calf was considered as the experimental unit for analysis among treatments. As calves were kept in pens of approximately the same age groups, the date of inclusion in the study was included in all analysis of treatment differences to account for any variation in pen. Least squared means are presented for each treatment.

Daily feed intake data (MR, calf starter, total DMI and percentage of calf starter DM in total DMI) were analysed as a repeat measure using PROC MIXED in SAS 9.4 (SAS institute Inc, Cary, NC, USA), with milk allowance, time (day on the study) and their interaction as fixed effects. Daily calf-starter intakes were only analysed from day 7 onwards as calf-starter intake was negligible before this time. Farm source, grazing location and age of the calf at the measurement were considered as random effects but were not included in the final model as they were not significant effects. Treatments were balanced for initial BW, but it was not included in the analysis as milk allowance on the LA and HA treatments were applied according to initial BW.

Blood metabolites, BW, body dimensions at specific time points and ADG for each period were analysed using PROC MIXED in SAS 9.4 with treatment as a fixed effect and with age of the calf at the time of the measurement included as a random effect for all variables. For blood, BW, body dimension and ADG data from after calves were sent to their grazing locations, grazing location was included as a class effect. Regression analysis using all calves of pre-weaning feed intakes with ADG, and of pre-weaning ADG, feed intakes, β-hydroxybutyrate with post-weaning ADG and BW at 6 months were analysed using PROC REG in SAS 9.4. The lowest bayesian information criterion (BIC: fit statistic) level was used to select covariance structure of the model for each parameter.

A stepwise regression analysis was also done in R 3.4.1 (R Core Team, 2016) with BW at 6 months and ADG from weaning to 6 months as the response variables. Predictor variables were in the order of heifer age at the 6 months BW, pre-weaning ADG, calf-starter intake, DMI and β-hydroxybutyric at weaning. Heifer age at the 6-month measurement was included as the first predictor to remove any variation in BW caused by age, but it was not significant in the model and therefore it was not included in other regression analysis. Pre-weaning ADG, rather than BW at weaning, was used for these regressions as it accounted for differences in initial BW.

A linear mixed model (REML) was used to model the effect of treatment on the weight of calves from enrolment in the study to calf starter removal (day 120 on the study) using fortnightly body weights in R 3.4.1. The weight of calves at enrolment was used as a covariate and was centred by deducting each value by the mean. A third-degree polynomial was used to model the effect of age on the weight of the calf. Age, treatment, initial calf weight and the interaction between age and treatment were significant predictors of calf weight.

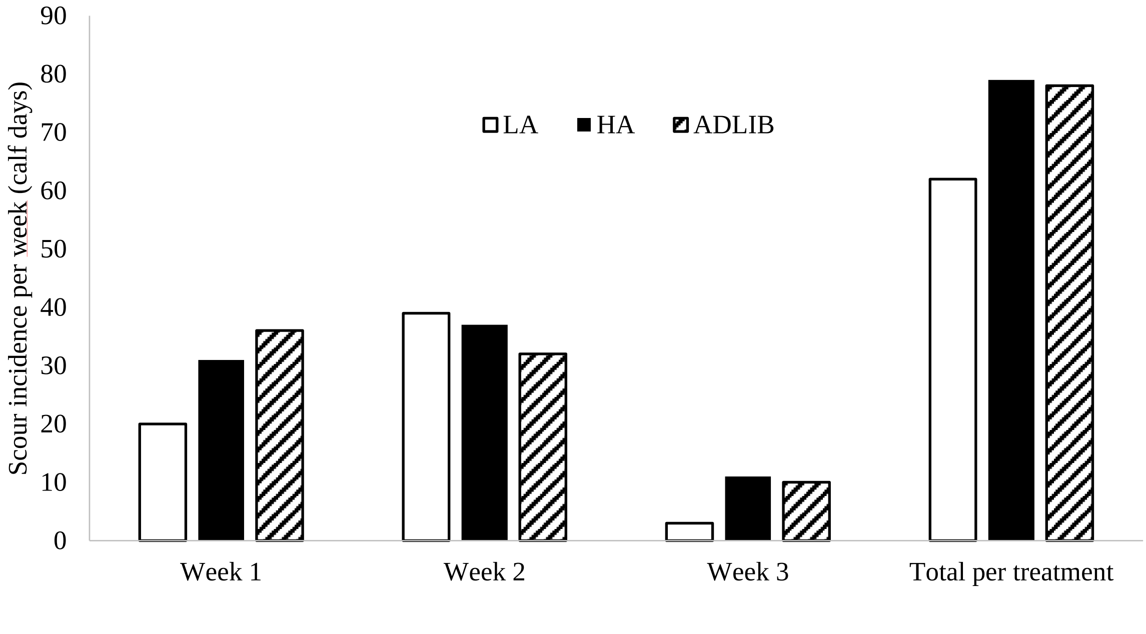
Treatment differences for mammary gland data was analysed in R.3.4.1 using the package “predictmeans”, with P-values adjusted by the “Benjamini-Hochberg” method. A regression analysis with independent values of total mammary gland, parenchyma or fat pad growth with predictor variables in the order of age of calf at weaning, BW at weaning, initial plasma total protein and treatment was used. Scour incidence was analysed using pairwise comparison of proportions, and P-values adjusted by the “Holm-Bonferroni” method in R 3.4.1.

4.3 Results

4.3.1 Health of the Calves

There were no differences amongst treatments in the number of days of calf scours per week (Figure 2). Total incidence of scours in the first 3 weeks was 62 calf-days for LA, 79 calf-days for HA and 78 calf-days for ADLIB calves. For all calves, there were 87 calf-days of scouring in week 1, 108 days in week 2 and 24 days in week 3. No scouring was observed in calves after week 3 of the study. A total of 14 calves (2, 5 and 7 on LA, HA and ADLIB treatments, respectively) out of 217 initially enrolled in the study died or were euthanized on veterinary advice, and 4 calves were excluded from the study before weaning for not meeting the weaning criteria. After being sent to their grazing locations, a further 2 calves were removed. Therefore, 199 calves completed the study to post-weaning, and 197 completed the study to 6 months of age.

Figure 2. Number of scour calf-days per week (first 3 weeks of the study) and total scours days during the study in calves fed different milk allowance. Calf-days are calculated from the number of calves with scours by the number days calves had scours.



4.3.2 Feed and Nutrient Intake

Milk replacer intake did not differ between ADLIB and HA calves until after day 18 on the study ($P < 0.05$) when HA calves began consuming their full allowance. Milk replacer and total

DMI was lower in LA calves than ADLIB and HA calves by day 4 ($P < 0.01$; Figure 3. a, c). The MR intake of ADLIB calves on a single day was greatest on day 61 (1.95 ± 0.04 kg DM; 13.6 ± 0.25 L; 36.7 ± 0.7% of their initial BW). Average daily MR intakes within ADLIB calves during the entire pre-weaning period ranged from 6.0 to 11.2 litres/day (17% to 33% of their initial BW).

Average daily starter intake over the entire pre-weaning period was greatest for LA calves, followed by HA, with ADLIB calves having the lowest calf-starter intakes ($P < 0.01$; Table 4). Total DM, metabolizable energy and crude protein intakes (MR + calf starter) were greatest for ADLIB, followed by HA calves, and LA calves were the lowest ($P < 0.01$; Table 4). Calves on the HA treatment consumed 41% more total metabolizable energy and 33% more total crude protein pre-weaning than LA calves, and ADLIB calves consumed 79% more total metabolizable energy and 67% more total CP pre-weaning than LA calves. Calves on all treatments consumed more DM, metabolizable energy and crude protein from MR than calf starter pre-weaning. During the 5-week post-weaning period (day 83 – 121 on the study), calf starter DMI was lower in ADLIB than HA and LA ($P < 0.05$) but was the same in HA and LA calves (Table 4).

Calf starter intake between HA and ADLIB calves consistently differed after day 44 ($P < 0.05$), at which point HA calves steadily increased their daily intake of starter, whereas there were less marked changes in calf starter intake for ADLIB calves until MR weaning began (Figure 3. b). Average starter DMI in the 3 days prior to the start of MR weaning (day 66 to 69 on the study) were 0.17, 0.46 and 0.62 kg for ADLIB, HA and LA calves respectively. During weaning (day 69 – 83 on the study), ADLIB calves increased their starter intake from 0.16 ± 0.04 to 0.72 ± 0.04 kg DM, whereas LA calves had a less marked increase from 0.59 ± 0.03 to 0.90 ± 0.05 kg DM. At the end of weaning (day 83 on the study), starter intake was similar in LA and HA calves but was lower in ADLIB calves ($P < 0.01$; Figure 3. b). The percentage contribution of calf starter to total DMI gradual increased with the advancing age of calves and exceeded 50% on day 54 in LA calves but did not exceed 50% in HA or ADLIB calves until after MR weaning had begun (Figure 3. d). Calf starter intakes in the final 3 days of weaning (day 80 – 83) was 0.72 kg DM/day for ADLIB, 0.93 kg DM/day for HA and 0.90 kg DM/day for LA calves.

Figure 3. Mean (± standard error) daily intake of heifer calves fed milk replacer (MR) at 10% initial BW (LA; n = 67), 20% initial BW (HA; n = 65) or *ad libitum* (ADLIB; n = 66). (a) Milk replacer DMI, (b) pelleted calf starter DMI, (c) total DMI (MR + calf starter), (d) percentage of calf starter DMI in total DMI. Vertical dotted line represents the beginning of MR weaning at day 69. Calves on all treatments were weaned by day 83. For all parameters, $P < 0.01$ for milk allowance, days on study and milk allowance x days on study

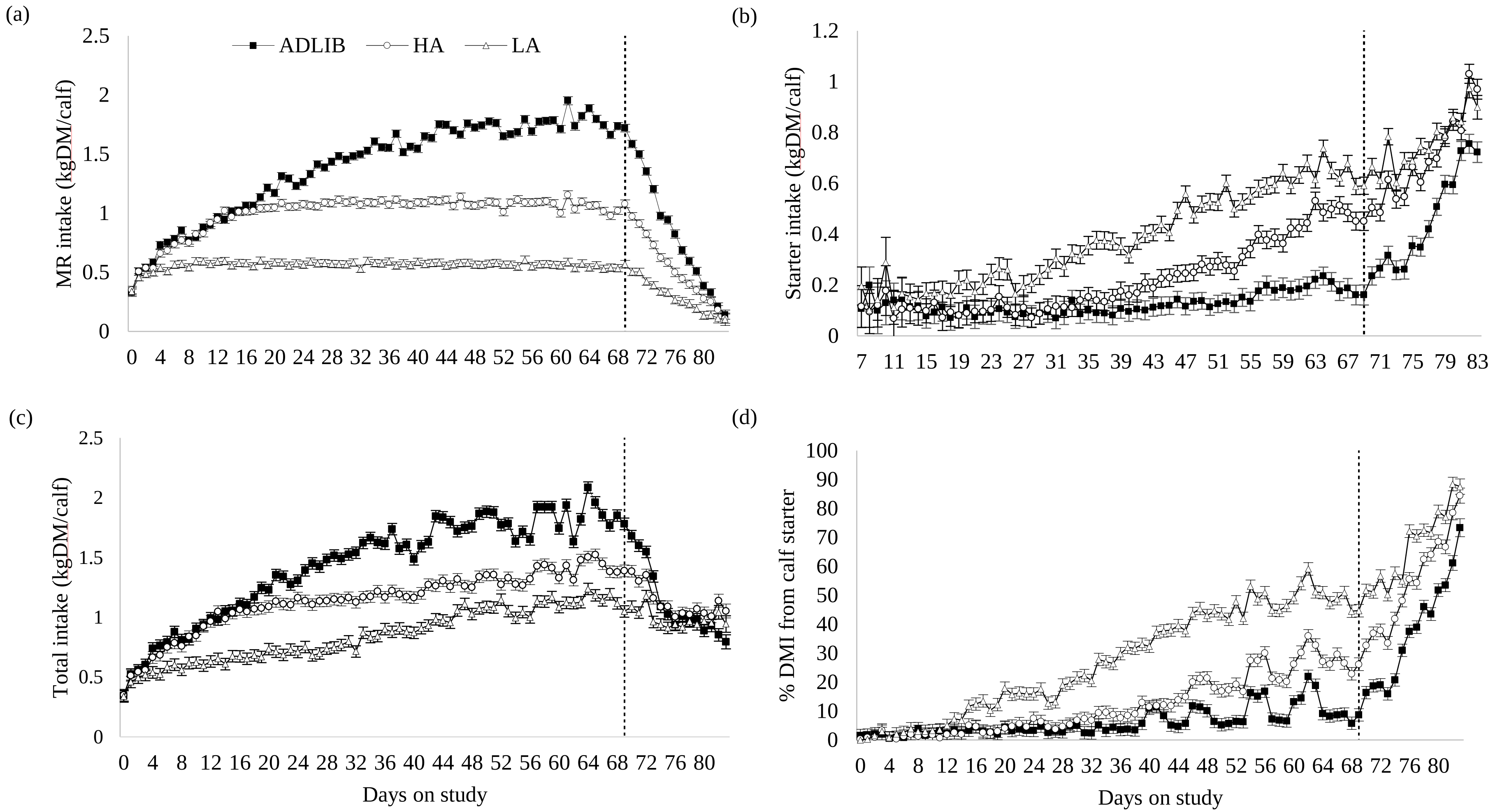


Table 4. Mean (± standard error) average daily milk replacer (MR) and calf starter intake of heifer calves during the pre-weaning and post-weaning periods. Calves were fed MR at 10% initial BW (LA; n = 67), 20% initial BW (HA; n = 65) or *ad libitum* (ADLIB; n = 66) MR

	Milk Allowance[1]			
Item	LA	HA	ADLIB	P-value
Pre-weaning[1] MR intake				
Liquid, litres/calf	3.5 ± 0.1[c]	6.25 ± 0.11[b]	8.7 ± 0.1[a]	< 0.01
Liquid, % of initial BW/calf	9.3 ± 0.3[c]	16.8 ± 0.3[b]	23.7 ± 0.3[a]	< 0.01
DM, kgDM/calf	0.51 ± 0.02[c]	0.90 ± 0.02[b]	1.26 ± 0.02[a]	< 0.01
ME, MJ/calf [2]	10.37 ± 0.29[c]	18.49 ± 0.29[b]	25.9 ± 0.29[a]	< 0.01
CP, kg/calf	0.13 ± 0.004[a]	0.23 ± 0.004[b]	0.33 ± 0.004[c]	< 0.01
Pre-weaning starter intake				
DM, kg/calf	0.36 ± 0.01[a]	0.23 ± 0.01[b]	0.12 ± 0.01[c]	< 0.01
ME, MJ/calf[2]	4.94 ± 0.17[a]	3.18 ± 0.17[b]	1.67 ± 0.17[c]	< 0.01
CP, kg/calf	0.074 ± 0.003[a]	0.048 ± 0.003[b]	0.024 ± 0.003[c]	< 0.01
Total pre-weaning intake				
DM, kg/calf	0.86 ± 0.02[c]	1.13 ± 0.02[b]	1.38 ± 0.02[a]	< 0.01
ME, MJ/calf	15.4 ± 0.4[c]	21.7 ± 0.4[b]	27.6 ± 0.4[a]	< 0.01
CP, kg/calf	0.21 ± 0.005[c]	0.28 ± 0.005[b]	0.35 ± 0.005[a]	< 0.01
Percentage of total pre-weaning intake from starter				
DM %	39.9 ± 0.9[a]	19.6 ± 0.9[b]	8.8 ± 0.9[c]	< 0.01
ME, %	31.1 ± 0.7[a]	14.2 ± 0.8[b]	6.1 ± 0.7[c]	< 0.01
CP, %	34.5 ± 0.8[a]	16.2 ± 0.8[b]	7.1 ± 0.8[c]	< 0.01
Post-weaning[2] starter intake				
DM, kg/calf	0.86 ± 0.05[a]	0.92 ± 0.05[a]	0.72 ± 0.05[b]	0.01
ME, MJ/calf	11.80 ± 0.67[a]	12.68 ± 0.67[a]	9.92 ± 0.67[b]	0.01
CP, kg/calf	0.18 ± 0.01[a]	0.19 ± 0.01[a]	0.15 ± 0.01[b]	0.01

[a-c] Means with different superscripts within a row differ ($P < 0.05$). DM = dry matter; ME = metabolizable energy; CP = crude protein.

Calves were given access to pasture at day 91, and calf-starter was available until day 121.

[1]Pre-weaning period = day 0 - 83; Post-weaning period = day 84 – 121.

[2]ME in calf starter was calculated according to AFRC (1993) and in milk replacer according to NRC (2001) equation.

4.3.3 Effect of Milk Allowance on the Growth Performance of Heifer Calves

Average daily gain. Pre-weaning ADG was greatest for ADLIB calves, followed by HA, then LA calves (P < 0.01; Table 5). During the 5-week post-weaning period (day 84 to 121 on the study, ADG was the lowest for ADLIB calves (P < 0.05) but was the same for HA and LA calves (Table 5). Milk allowance did not influence ADG from the end of the post-weaning period to 6 months (day 122 to 188), but from the start of the study to 6 months (day 0 to 188), ADG was higher in ADLIB and HA than LA calves (P < 0.05; Table 5). There was a tendency (P < 0.10) for ADG from 0 – 10 months to be higher in ADLIB and HA calves than LA calves (Table 5).

Table 5. Mean (± standard error) average daily gain (ADG) of heifer calves fed different milk replacer (MR) allowances. Calves were fed MR at 10% initial BW (LA; n = 67), 20% initial BW (HA; n = 65) or *ad libitum* (ADLIB; n = 66)

	Milk Allowance			
ADG, kg/d[1]	LA	HA	ADLIB	P-value
Pre-weaning	0.53 ± 0.02^{c}	0.60 ± 0.02^{b}	0.70 ± 0.02^{a}	<0.01
Post-weaning	0.66 ± 0.03^{a}	0.66 ± 0.03^{a}	0.57 ± 0.03^{b}	0.03
Post-weaning to 6 months	0.55 ± 0.02	0.55 ± 0.02	0.55 ± 0.02	0.98
6 months to 10 months	0.96 ± 0.02	0.99 ± 0.02	0.97 ± 0.02	0.43
0 – 6 months	0.53 ± 0.01^{b}	0.56 ± 0.01^{a}	0.57 ± 0.01^{a}	0.02
0 – 10 months	0.63 ± 0.008	0.65 ± 0.008	0.65 ± 0.008	0.13

[a-c] Means with different superscripts within a row differ (P < 0.05).

[1]Milk feeding = day 0 – 83; Post-weaning = day 84 – 121; Post-weaning to 6 months = day 122 – 188; 6 months to 10 months = day 188 to 286; 0 to 6 months = day 0 – 188; 0 to 10 months = day 0 – 286.

Calves were weaned from MR at day 83, given access to pasture at day 91, and calf-starter was available until day 121.

Body weights and measurements. Body weight, wither height, hip height and heart girth of calves were the same at the start of the study (Table 6). Body weight and body measurements at MR weaning (day 83) were greatest in ADLIB followed by HA, with LA calves the lowest (P < 0.01; Table 6). At the end of the post-weaning period (day 121), ADLIB calves were heavier than LA calves (P < 0.05), but HA were similar to LA and ADLIB (Table 6). At 6 months, ADLIB and HA were heavier than LA heifers (P < 0.05; Table 6). There was no effect of MR allowance on any of the body measurement at 6 months (Table 6).

Table 6. Mean (± standard error) body weights (BW) and body measurements of heifer calves fed milk replacer (MR) at 10% initial BW (LA; n = 67), 20% initial BW (HA; n = 65) or *ad libitum* (ADLIB; n = 66) from day 0 to 83

	Milk Allowance			
Item[1]	LA	HA	ADLIB	P-value
BW, kg				
Initial	37.8 ± 0.6	37.3 ± 0.6	37.2 ± 0.6	0.73
MR weaning	82.7 ± 1.6[c]	88.3 ± 1.6[b]	95.4 ± 1.6[a]	< 0.01
Post-weaning	112.5 ± 1.8[b]	116.0 ± 1.9[ab]	118.5 ± 1.8[a]	0.02
6 months	146.5 ± 2.2[b]	153.2 ± 2.2[a]	153.4 ± 2.2[a]	0.03
10 months	218.8 ± 2.8	224.1 ± 2.8	223.5 ± 2.7	0.3
Wither height, cm				
Initial	70.2 ± 0.4	69.9 ± 0.5	69.4 ± 0.5	0.46
MR weaning	81.3 ± 0.4[c]	82.8 ± 0.4[b]	84.2 ± 0.4[a]	< 0.01
6 months	97.1 ± 0.6	98.5 ± 0.6	98.6 ± 0.6	0.15
Hip height, cm				
Initial	73.3 ± 0.4	72.8 ± 0.4	73.2 ± 0.4	0.64
MR weaning	85.8 ± 0.4[c]	87.5 ± 0.4[b]	89.1 ± 0.4[a]	< 0.01
6 months	102.1 ± 0.6	102.1 ± 0.6	103.2 ± 0.6	0.23
Heart girth, cm				
Initial	81.2 ± 0.6	80.8 ± 0.7	81..3 ± 0.6	0.89
MR weaning	103.4 ± 0.6[c]	105.3 ± 0.6[b]	107.6 ± 0.6[a]	< 0.01
6 months	121.1 ± 0.7	120.8 ± 0.8	121 ± 0.7	0.96

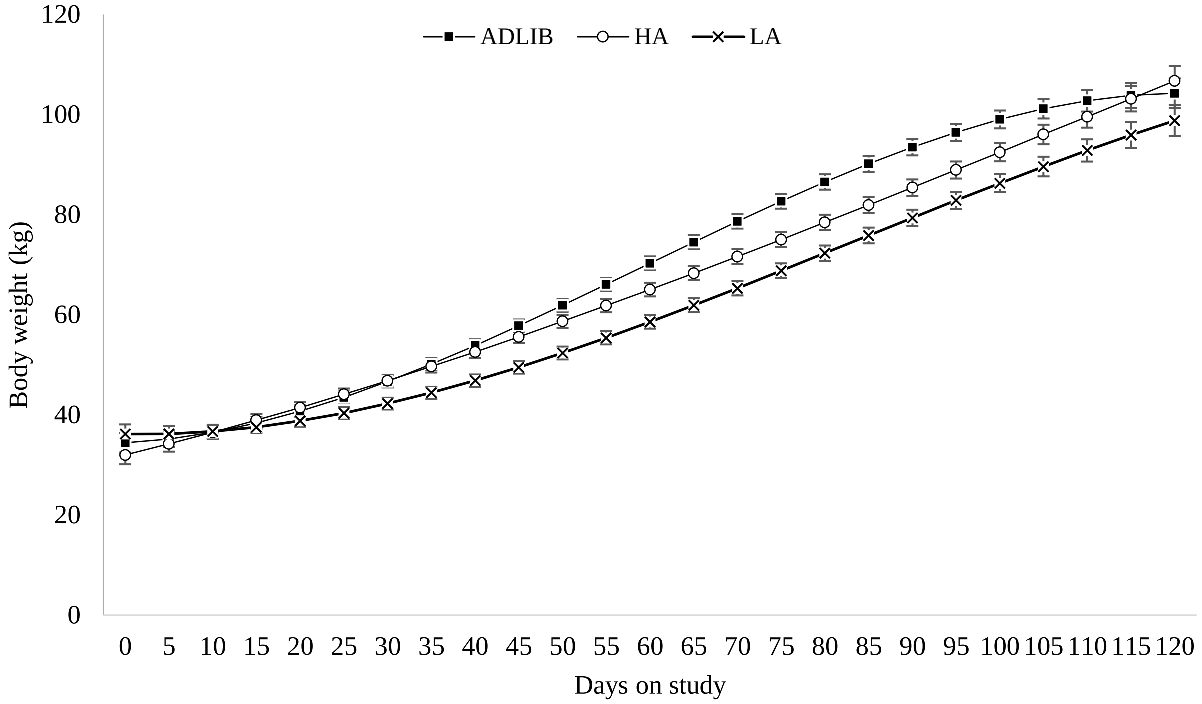
[a-c] Means with different superscripts within a row differ (P < 0.05).

[1]Initial = 11 days of age, day 0; MR weaning = day 83; starter weaning = day 121; 6 months = day 188; 10 months = day 286.

Calves were given access to pasture at day 91; calf-starter was available until day 121 and then calves were switched to a pasture only diet.

The BW of HA and ADLIB calves was greater than that of LA calves after 20 days in the study, and the BW of ADLIB calves was greater than that of HA calves from day 50 in the study (Figure 4). While the BW trajectory of HA and LA calves shows accelerating growth, the rate of increase in BW of ADLIB calves indicates a deceleration at 90 to 120 days in the study.

Figure 4. Body weights (± standard error) from day 0 on the study to day 120 of heifer calves fed milk replacer at 10% initial body weight (LA; n = 67), 20% initial body weight (HA; n = 65) or ad libitum (ADLIB; n = 66) modelled using a third-degree polynomial



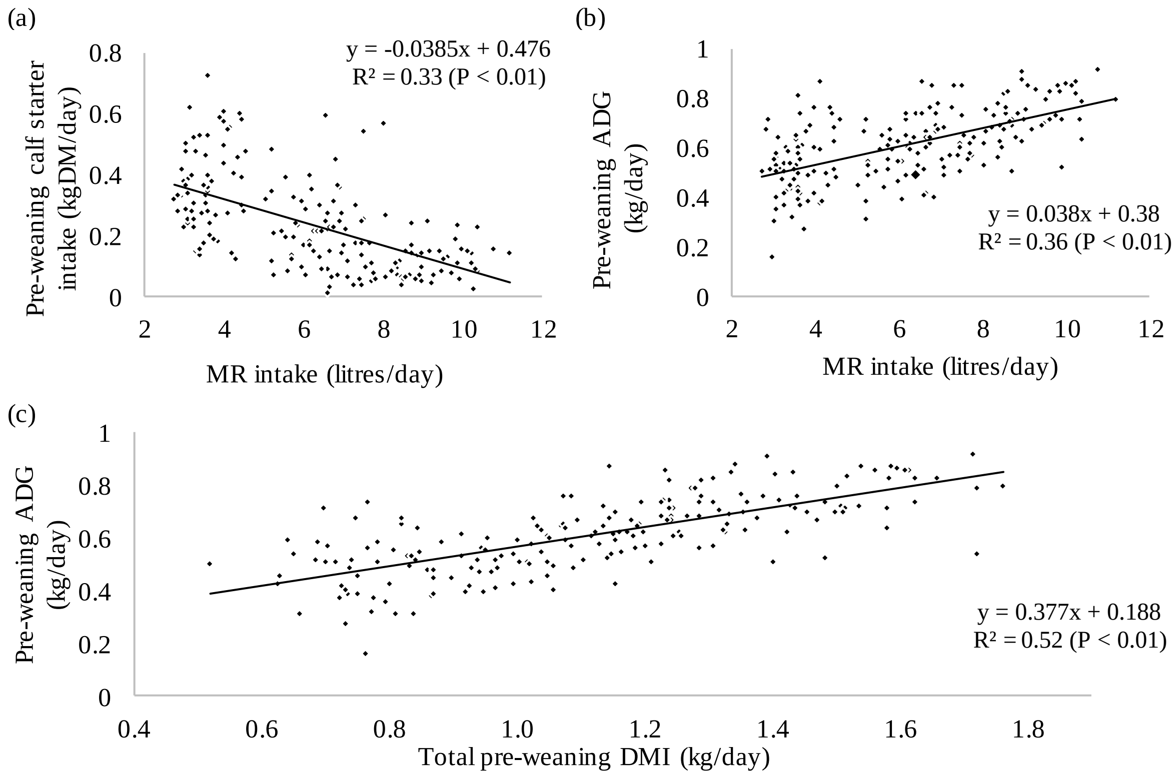
Pre-weaning mammary gland growth. Milk allowance had no effect on pre-weaning growth of the fat pad or the total depth of the mammary gland (Table 7). Parenchyma tissue growth was greater in LA calves than ADLIB calves ($P < 0.05$), but HA had similar growth to LA and ADLIB calves (Table 7). Using a step-wise regression and accounting for age at weaning, BW at weaning was not a predictor of parenchyma, fat pad or total gland growth measured using ultrasound scans (data not presented).

Table 7. Effect of milk allowance on the difference in depth of the ultrasound measured mammary parenchyma, fat pad and total depth (parenchyma plus fat pad) of the mammary gland of heifer calves during the milk-feeding period (day 0 to 83 in study). Calves were fed milk replacer at 10% initial body weight (LA; n = 32), 20% initial body weight (HA; n = 32) or *ad libitum* (ADLIB; n = 32) from day 0 to day 83

	Milk Allowance			
Item	LA	HA	ADLIB	P-value
Mammary parenchyma (cm)	1.10 ± 0.11[a]	0.97 ± 0.11[ab]	0.80 ± 0.12[b]	0.04
Fat pad (cm)	1.25 ± 0.15	1.50 ± 0.15	1.28 ± 0.16	0.19
Total depth of tissue (cm)	2.31 ± 0.21	2.47 ± 0.20	2.07 ± 0.21	0.18

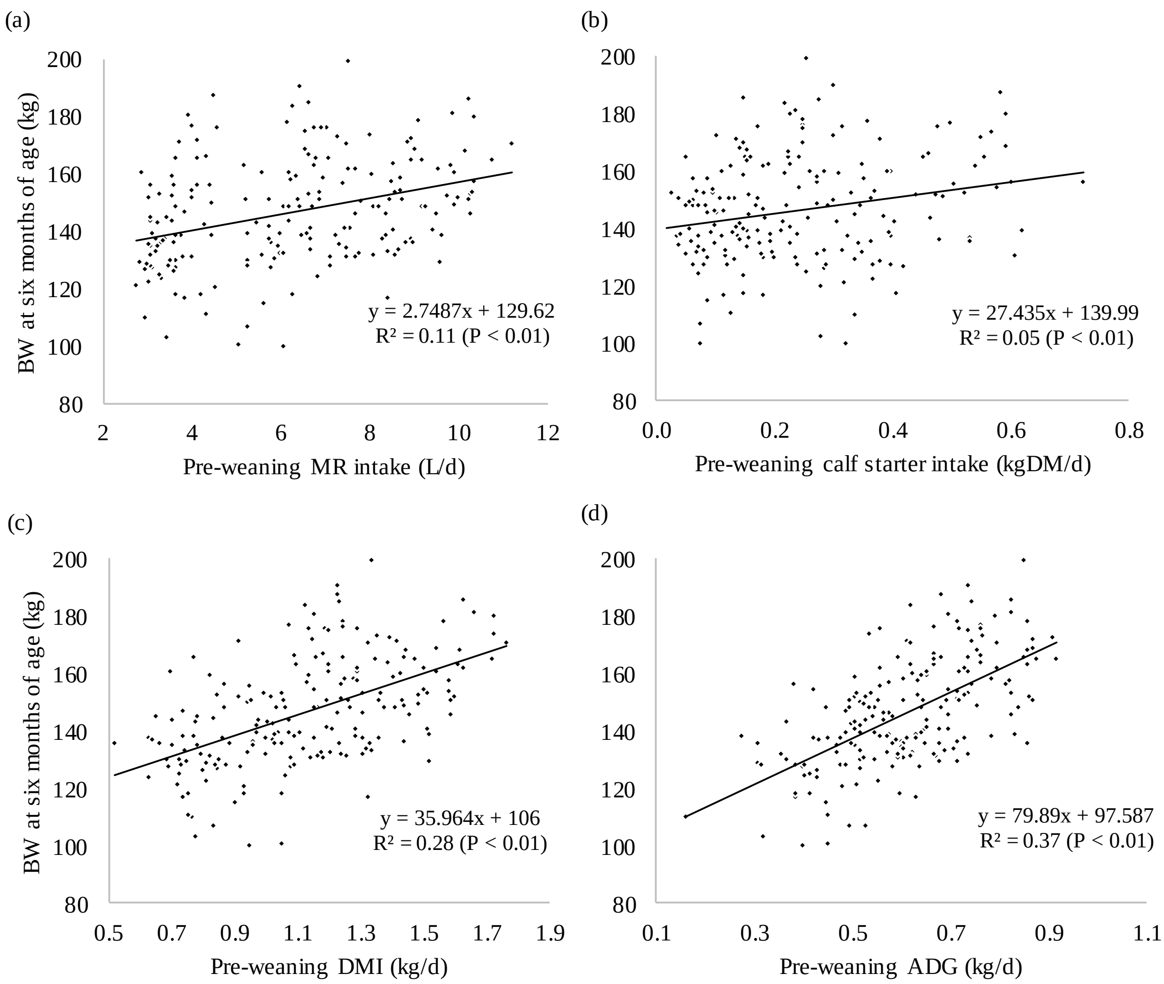
Relationship between pre-weaning intake and growth. When pre-weaning MR intake increased, calf-starter intake decreased (R^2 = 0.33, P < 0.01; Figure 5.a). There was no relationship between pre-weaning calf-starter intake and ADG (R^2 = 0.00, P = 0.86; data not presented). An increase in total DMI (R^2 = 0.52, P < 0.01; Figure 5. c) and daily MR intake (R^2 = 0.36, P <0.01) was associated with an increase in pre-weaning ADG (Figure 5. b).

Figure 5. The relationship between pre-weaning intake and average daily gain (ADG) of calves fed milk replacer (MR) at 10% initial body weight (n = 67), 20% initial body weight (n = 65) or *ad libitum* (n = 66) with free access to calf starter. (a) MR intake and calf starter intake, (b) MR intake and ADG, (c) total DMI and ADG



Relationship of pre-weaning intake and pre-weaning ADG with post-weaning ADG and BW at 6 months. When pre-weaning MR intake, calf-starter intake or total DMI increased, the ADG to 6 months-of-age and the BW of heifers at 6 months-of-age increased (Figure 6). The relationship with ADG was strongest ($R^2 = 0.37$), followed by total DMI ($R^2 = 0.28$; Figure 6). There was a weak relationship between plasma β-hydroxybutyrate at weaning and BW of heifers at 6 months ($R^2 = 0.03$, $P = 0.015$; data not presented). The stepwise regression analysis for BW at six months revealed that pre-weaning ADG, MR, calf starter and total DMI were all significant predictors of six months BW of heifers ($P < 0.01$), but β-hydroxybutyrate at weaning was not.

Figure 6. The relationship between pre-weaning intakes and ADG to BW at six months of age. (a) Milk replacer (MR) intake, (b) pre-weaning calf starter intake, (c) total pre-weaning DMI, (d) pre-weaning ADG.



There was a weak relationship between pre-weaning calf-starter intake and ADG of heifer calves from MR weaning to 6 months ($R^2 = 0.086$, $P < 0.01$; $y = 0.2526x + 0.491$), and there was a tendency for an increased MR intake to be weakly associated with a lower ADG from weaning to 6 months ($R^2 = 0.012$, $P = 0.07$; $y = -0.0073x + 0.597$). There was no relationship of pre-weaning total DMI ($P = 0.9$) and pre-weaning ADG ($P = 0.23$) with ADG from MR weaning to 6 months. Weaning β- hydroxybutyrate was associated with decreased BW at 6 months ($R^2 = 0.03$, $P = 0.015$, $y = -19.775x + 151.31$), but there was no relationship between β- hydroxybutyrate at weaning and ADG from weaning to 6 months ($P = 0.42$).

4.3.4 Blood metabolites

Total protein was tested at the start of the study to evaluate the status of passive transfer of immunity to calves, and there was no difference between the treatments (Table 8). At the end of weaning from MR, the plasma NEFA was greater in ADLIB than LA calves ($P < 0.05$), though HA calves had similar concentration to ADLIB and LA calves (Table 8). Plasma glucose at weaning was lower in ADLIB than LA calves ($P < 0.05$), and there was a tendency ($P < 0.10$) for plasma β- hydroxybutyrate at weaning to be lower in HA than LA calves (Table 8). There was no difference between treatments in total protein and blood urea nitrogen at the time of MR weaning, and no difference between any plasma metabolites at 6 months (Table 8).

Table 8. Mean (± standard error) concentration of selected plasma metabolites in heifer calves fed different milk allowance. Calves were fed milk replacer (MR) at 10% initial BW (LA; n = 67), 20% initial BW (HA; n = 65) or *ad libitum* (ADLIB; n = 66) from day 0 to d 83

	Milk Allowance[1]			
Item[1]	LA	HA	ADLIB	P-value
Total protein, gram/litre				
Initial	55.45 ± 1.03	55.15 ± 1.07	55.95 ± 1.05	0.86
MR weaning	58.68 ± 0.58	58.91 ± 0.61	58.23 ± 0.59	0.71
6 months	59.62 ± 0.54	58.52 ± 0.56	58.70 ± 0.55	0.30
β- hydroxybutyrate, mmol/ litre				
MR weaning	0.27 ± 0.02	0.22 ± 0.02	0.23 ± 0.02	0.16
6 months	0.33 ± 0.01	0.31 ± 0.01	0.30 ± 0.01	0.18
NEFA, mmol/ litre				
MR weaning	0.11 ± 0.02[b]	0.12 ± 0.02[ab]	0.16 ± 0.02[a]	0.05
6 months	0.13 ± 0.01	0.13 ± 0.01	0.12 ± 0.01	0.80
Blood Urea Nitrogen, mmol/litre				
MR weaning	2.86 ± 0.14	3.04 ± 0.15	3.11 ± 0.14	0.49
6 months	6.33 ± 0.13	6.07 ± 0.14	6.19 ± 0.13	0.39
Glucose, mmol/litre				
MR weaning	4.73 ± 0.10[a]	4.50 ± 0.10[ab]	4.45 ± 0.10[b]	0.09
6 months	4.54 ± 0.06	4.44 ± 0.07	4.42 ± 0.06	0.30

[a-c] Means with different superscripts within a row differ ($P < 0.05$).

[1]Initial = 11 days of age, day 0 on the study; MR weaning = day 83 on the study; 6 months = day 188 on the study.

4.4 Discussion

Of the 14 mortalities in the study, most died during the first 3 weeks in the experiment. Post-mortem findings on 7 calves indicated multiple causes of death including twisted gut, pneumonia, enteritis, jejunal intersusception and bloat. One calf with a broken leg was euthanized on the recommendation of the herd veterinarian. The postnatal mortality rate of calves in this study (6.6%) was similar to the average mortality for replacement dairy calves in NZ (4.1%; Cuttance et al., 2017).

We have demonstrated that NZ dairy heifer calves are able to safely consume far greater MR intakes than is generally being recommended for indoor (10 – 20% initial BW; Khan et al. 011) and pastoral systems (4 – 8 litres/day; Muir et al., 2002; Cardoso et al., 2015), with ADLIB calves consuming a maximum of 13.6 litres/day by day 61 of the study. Other studies where *ad libitum* milk was offered to calves report a range of maximum milk intakes from 10 – 16 litres/day (Borderas et al., 2009a; Frieten et al., 2017; Welboren et al., 2019). Pre-weaning ADG of ADLIB fed calves in our study was 0.70 kg/day, lower than that reported (0.8 to 1.2 kg/day in *ad libitum* fed calves) by others for indoor dairy systems (Borderas et al., 2009a; Miller-Cushon et al., 2013; Curtis et al., 2018; Welboren et al., 2019). Breed differences likely contributed to the difference in milk consumption and growth rate of calves, as the Kiwi-cross calves used in our study have a lower mature weight and, therefore, lower potential growth rates than the Holstein-Friesians used in studies from North America or Europe. Also, the pre-weaning period in our study included the weaning phase, and low nutrient intakes of ADLIB calves during this time may have impeded the pre-weaning ADG.

While ADLIB calves were restricted to 4 litres per meal with a minimum wait time of 2 hours between meals, this is unlikely to have affected their maximum intakes. Previously, Appleby et al. (2001) provided calves *ad libitum* milk for 4 hours per day or 24 hours per day and found no difference in intake. Large variation in MR intake was observed in ADLIB calves (6.0 to 11.2 litres/day during pre-weaning) reflecting the difference between individual calves in their desire or ability to drink MR. Differences in the birth weights and genetics of dairy calves that is typical to the dairy herd in NZ (Lopez-Villalobos et al., 2000) could be considered one of the major factors dictating individual calf nutrient requirements and milk consumption. Variation in MR consumption could also be a reflection of the ability of the calves to learn and use the automated feeders. Large differences can exist between calves in their vigour and behaviour, and those that learn slower or are less dominant have lower milk intakes in group feeding situations (Fujiwara et al., 2014; Neave et al., 2018; Gillingham et al., 2018). Calves that are introduced to automatic milk feeders when they are older (from 2 to 8 days of age) tend to drink more milk (Medrano-Galarza et al., 2018a), likely because they are larger in size, but also due to adapting faster to automatic feeders (Fujiwara et al., 2014). In our study, calves were enrolled in the study from 4 to 19 days of age, which may have accentuated variation in MR intake when on automatic milk feeders. Competition of calves at the automatic milk feeders could also affect intakes (Rosenberger et al., 2017), though calves had access to the feeders for 23 hours/day, so group competition may not have been a factor in our study. Therefore, the wide range in MR intakes by ADLIB calves in our study is likely due to variation in genetics of the crossbred dairy calves that influenced their desire and ability to suckle, as well as differences in the age of introduction to automatic milk feeders.

Greater MR allowances led to increased pre-weaning growth rate which is consistent across studies with calves reared indoors (Khan et al., 2011), as restricted MR fed calves were unable to increase their starter intake to match the nutrient intake associated with greater MR allowance. In our study, calf-starter was lower in metabolizable energy than the MR, and so the proportion of metabolizable energy and crude protein consumed increased with greater MR intakes. The relationship between pre-weaning MR intake and growth in our study ($R^2 = 0.37$) was similar to Holstein calves that were fed 4 different MR allowances ($R^2 = 0.42$) in the study of Dennis et al. (2018b). Calves that consumed more MR therefore had greater BW and body measurements at weaning. While BW at weaning may not be a true reflection of pre-weaning growth due to differences in gut-fill from different concentrate intake (Khan et al., 2016), the smaller difference in body dimensions compared to BW at weaning between the treatments suggests that gut-fill was not likely to have had an effect on BW.

Due to a lack of digestive tract development, the digestion of carbohydrate (apart from lactose) is very low in calves before 1 month of age (Drackley, 2008) and calves do not consume substantial quantities of solid-feed before this age. The LA calves in the present study did not begin to continuously increase their starter intake until around day 26 on the study, at which point they were on average 37 days of age. The percentage contribution of calf-starter to total DMI for LA calves did not exceed 50% until day 54 and did not exceed 50% in HA or ADLIB calves until after weaning had begun on day 69 of the study. The greatest difference in total DMI between LA and HA calves was at day 16 to 27 when HA calves began consuming their maximum allowance of MR. Curtis et al. (2018) reported that the disparity in ADG between calves fed *ad libitum* and restricted milk is greatest in the first 3 week of age. Thus, feeding calves high allowances of milk during the first 3-4 weeks of age is needed to increase the growth rate and meet the requirements of calves as they do not consume significant quantities of solid-feed before this age (de Paula Vieira et al., 2008; Jasper and Weary, 2002).

Pre-weaning starter-intake was lower with ADLIB compared to LA and HA calves, averaging 120 gram/day for the total pre-weaning period. Calf-starter intake by ADLIB calves did, however, increase during pre-weaning as they got older, reaching 200 gram/day prior to the beginning of weaning on day 69. This may reflect the innate desire of calves to consume solid-feed (Khan et al., 2011).

As anticipated, calf-starter intake increased in all treatments when weaning began (day 69). The rate at which starter intake increased during weaning (day 69 – 83) was similar for HA and ADLIB calves, but as intake of starter was lower in ADLIB calves at the beginning of weaning, they did not reach the same starter intake by the end of weaning. Therefore, there was a greater reduction in total DMI over weaning for ADLIB compared to HA and LA calves which maintained a constant total DMI throughout the 14-day weaning period. A successful weaning transition relies on sufficient intake of solid-feed to support post-weaning growth (Khan et al., 2016). Previous studies have demonstrated that the implementation of gradual weaning strategies in calves fed high milk allowances fosters sufficient solid-feed consumption to avoid any reduction in growth rate after weaning (de Passillé and Rushen, 2016; Benetton et al., 2019; Welboren et al., 2019). A gradual MR weaning was implemented in our study (linearly reducing MR allowance over 14 days according to individual calf intakes) that enabled HA calves to transition to a diet of calf-starter and pasture with a similar calf-starter intake and growth rate in the post-weaning period as LA calves, but ADLIB calves experienced lower starter intakes and ADG in the post-weaning period. The findings of ADLIB calves are consistent with Dennis et al. (2018b), who reported that calves fed MR *ad libitum* had lower ADG in an 8-week post-weaning period in comparison to those fed at 4.4 litres/day, despite being weaned gradually over 10 days. However, contrasting our study, calves fed at 7.3 litres/day also had lower post-weaning ADG compared to those fed at 4.4 litres/day (Dennis et al. 2018b).

At weaning, circulating NEFA was higher and plasma glucose was lower in ADLIB than LA calves. Because calves were receiving the same fat source at weaning, circulating NEFA levels would reflect the extent of adipose tissue metabolism and indicates a negative energy balance in ADLIB calves (Daniels et al., 2008). The main source of glucose in the pre-ruminant calf is milk or MR, and as the rumen develops, the hepatic metabolism shifts from glycolytic to gluceogenic (Baldwin et al., 2004). With the dietary shift from milk to solid feeds, the ability of calves to metabolise volatile fatty acids arising from rumen fermentation influences the circulating glucose concentrations (Balwin et al., 2004). In our study, calves were no longer receiving MR at the time of blood sampling (day 86), therefore, the blood glucose was likely present in the blood from hepatic gluconeogenesis (Suarez-Mena et al., 2017). Greater circulating glucose levels in LA compared to ADLIB calves may be due greater solid-feed intake, ruminal fermentation and volatile fatty acid absorption in LA calves, leading to more propionate production, thus increased gluconeogenesis. Suarez-Mena et al. (2017) reported that greater starter intakes were associated with decreased blood glucose levels before weaning, but then increased with starter intake after weaning. However, circulating β- hydroxybutyrate, which can indicate the extent to which the rumen epithelium is developed (Quigley et al., 1991), was not different among calves offered different MR allowances. The indication from blood metabolites is that ADLIB calves were in a negative energy balance at weaning, so, a portion of the plasma β- hydroxybutyrate may have been due to hepatic ketogenesis in ADLIB calves, rather than from oxidation of ruminal butyrate (Van Soest, 1994).

There was no difference among treatments in calf BW or plasma total protein levels at the start of the study, and the mean concentration of plasma total protein in all calves was > 52 gram/litre, indicating adequate passive transfer of immunity (Cuttance et al., 2017). Overall during the study, we observed a lower incidence of scouring in week 3 (24 days) compared to week 1 and 2 (87 and 108 days, respectively), and negligible scours after week 3. Calves are most susceptible to illness in the first 5 weeks of life as they have not yet developed their own immunity against disease, and maternal antibodies from colostrum are going down after the first 2 weeks of age (Hulbert and Monthsisá, 2016). Calves were on average 11 days of age at the start of the study, and so the period of high scours coincided with low immunity. There was no effect of MR feeding on the incidence of scours, in agreement with some previous studies (Jasper and Weary, 2002; de Paula Vieira et al., 2008; Borderas et al., 2009a), but contrasting others (Brown et al., 2005b; Quigley et al., 2006; Raeth-Knight et al., 2009; Davis Rincker et al., 2011). Differences in scoring systems used, hygiene, feeding methods, housing facilities and management of calves may explain the differences in results (Khan et al., 2011; Medrano-Galarza et al., 2018b). The risk of scours increases with excessive MR intakes or inconsistent feeding (Ellingsen et al., 2016), but with the use of automatic feeders, the calves in our study were restricted to a maximum of 4 litres MR per meal with a minimum wait time of 2 hour between meals, avoiding the risk of the risk of over-feeding (Ellingsen et al., 2016). This highlights the benefit of automatic feeders to feeding high or *ad libitum* milk allowances without the risk of nutritional scours.

Lower ADG and starter intake during the first 5 weeks post-weaning, and lower glucose and higher NEFA in circulation at weaning indicate that the weaning transition did not foster sufficient rumen development in ADLIB calves. When weaning calves that are fed *ad libitum* milk allowances, weaning according to individual starter intakes (Benetton et al., 2019), or reducing milk as gradually as possible (Welboren et al., 2019) should be done to avoid a growth-check at weaning. Automatic milk and starter feeders could aid in managing a successful weaning transition of calves that are fed high or *ad libitum* milk allowances.

It was anticipated that starter intakes of all calves would further increase after MR weaning, (Rosenberger et al., 2017). However, we observed that the average-daily starter intake in the post-weaning period (day 84 – 121; ADLIB = 0.72 kg DM, HA = 0.92 kg DM, LA = 0.86 kg DM) was similar to intakes in the final 3 days of weaning (day 80 – 83; ADLIB = 0.72 kg DM, HA = 0.93 kg DM, LA = 0.90 kg DM). The measured intakes of solid-feed after weaning were lower compared to other studies (2-3 kg DM/day; Raeth-Knight et al., 2009; Rosenberger et al., 2017; Dennis et al., 2018a). Calves were given access to pasture 1-week after the end of MR weaning and, therefore, may have been less motivated to consume calf starter during this period. Additionally, the post-weaning period in our study included the 17-day weaning period from calf-starter, and so starter intakes were restricted during this period.

In the 5-week post-weaning period while on pasture, ADG was lower in ADLIB calves than HA or LA likely due to consuming less calf-starter, as well as potenitally reduced digestion of solid-feed (Terré et al., 2007; Chapman et al., 2016; Dennis et al., 2018b). While intakes of hay and pasture were not measured in our study, Jasper and Weary (2002) previously demonstrated that calves fed MR *ad libitum* consumed less hay before weaning compared to restricted levels, but similar amounts after weaning, and that hay intake in all calves increased during weaning but remained constant in a 20-day period after weaning. In our study, calves that were consuming less MR may have had greater intakes of hay pre-weaning, but any potential differences in hay intake after weaning were unlikely to have affected post-weaning growth rate, as a relatively large difference in hay intake would be necessary to have a significant impact on growth due to its high bulk and low metabolizable energy content relative to MR and calf-starter.

To determine the effect of pre-weaning feeding management on the growth of calves after weaning on pasture, we evaluated the relationship between pre-weaning ADG and feed intake with BW at 6 months, as well as to ADG from weaning to 6 months (day 83 to 188 on study) using data from all calves. Six-months of age represents the first BW target for growing heifers in NZ of 30% of mature BW (Burke et al., 2007). Average daily MR intake did not influence the growth rate of heifers during the period from weaning to 6 months, but it did influence the BW of calves at 6 months ($R^2 = 0.11$, $P < 0.01$), and pre-weaning ADG was associated with BW at 6 months of age ($R^2 = 0.37$, $P < 0.01$), indicating that differences in pre-weaning growth were having a lasting effect on BW until 6 months of age. Raeth-Knight et al. (2009), also reported that calves with greater BW at weaning (day 56) were able to maintain their BW advantage for several months after weaning (day 168) when fed a total mixed-ration. Pre-weaning calf-starter intake was weakly associated with a greater ADG from weaning to 6 months ($R^2 = 0.086$). This result is likely influenced by the lower growth rate in the 5-week post-weaning period for ADLIB calves, which were consuming less pre-weaning calf-starter. A greater pre-weaning calf-starter intake was weakly associated with greater a BW at 6 months ($R^2 = 0.05$), despite pre-weaning MR and calf-starter intake being inversely relate; in this instance it is likely that the lower growth rates 5-week post-weaning for ADLIB calves was affecting BW at 6 months. These results indicate that increasing the pre-weaning growth rate of calves will have positive effects on their BW at 6 months in a pastoral system, and that under the conditions in our study, pre-weaning MR allowance did not affect growth in a 3-month period after weaning.

A positive relationship between β- hydroxybutyrate and early post-weaning growth has previously been demonstrated and plasma β- hydroxybutyrate concentration is considered an indicator of solid-feed intake (Deelen et al., 2016). However, we found no relationship between plasma β- hydroxybutyrate concentration immediately after weaning (day 86 on the study) and ADG from weaning to 6 months or BW at 6 months. In our study, there was no relationship between pre-weaning calf-starter intake to ADG from weaning to 6 months; therefore, it is not surprising that there was no relationship to β- hydroxybutyrate. Any differences in starter intake or rumen development of calves that influenced circulating β- hydroxybutyrate levels at weaning did not affect ADG from weaning to 6 months, or BW at 6 months.

There was large variation in the growth rate of calves from weaning to 6 months, with a range from 0.2 kg/day to 0.9 kg/day. While there was a weak relationship between pre-weaning calf starter intake and growth from weaning to 6 months, a lack of correlation between pre-weaning growth, total DMI and MR intake indicate that other factors have a greater effect on the post-weaning growth of heifers. This could be due to group behaviour that potentially affected intake of pasture, and seasonal effects of pasture quality post-weaning in conjunction with a range of calf ages (by 10 weeks) resulting in calves being given access to pasture at different stages of the season. Less variation has been reported in indoor studies (Raeth-Knight et al., 2009), likely due to a more consistent and even distribution in feed quantity and quality at weaning and after weaning. As with pre-weaning growth rates, variation in ADG after weaning could also be due to differences in the growth potential of different breeds and genetic variation amongst the heifers (Lopez-Villalobos et al., 2000; Berry et al., 2005). However, there was no difference among treatments in our study in circulating total protein, NEFA, β- hydroxybutyrate, glucose or blood urea, indicating that there was no apparent difference in nutrient availability and metabolism at 6 months.

In our study, there was no effect of MR allowance on the growth of the mammary fat pad or the total gland depth, but calves fed the low-allowance of MR had more parenchymal growth than those fed the *ad libitum* MR. Previous studied have reported a positive effect of increased MR intake on the parenchyma development and fat pad mass (Brown et al., 2005a; Geiger et al., 2016) and on parenchyma and total gland mass (Soberon and Van Amburghfil, 2017), while others report no effect of nutrient intake parenchymal mass, but that fat pad mass is increased (Meyer et al., 2006a; Daniels et al., 2009). In agreement with our study, Molenaar et al. (2019) reported a 40% lower ratio of mammary fat pad to parenchyma in calves fed 8 litres/day and those fed 4 litres/day; however, this was due to lower fat pad in high milk fed calves, rather than lower parenchyma as in our study. During lactation, milk yield is proportional to the number of epithelial cells in the mammary gland (Capuco et al., 2003), therefore, increasing the growth of mammary parenchyma is generally considered desirable. However, parenchyma growth requires the mammary fat pad as a matrix for which to grow into (Neville et al., 1998), and to provide hormones and growth factors for development (Hovey and Aimonths, 2010). As such, the effect that growth of mammary parenchyma, mammary fat pad or total growth together may have on future lactation performance is uncertain. It is noted that we used ultrasound to scan and then analysed the images of each quarter while Brown et al. (2005a) and Geiger et al., (2016) euthanised the animals to study mamary gland growth. The discrepancy in our results and previous findings have questioned the validity of using indirect ultrasound scanning to study the mammary gland growth of heifers. Further research is required to refine the use of non-invasive techniques to study mammary gland growth.

Chapter 5. Effect of Pre-weaning Milk Replacer Allowance on Post-Weaning Behaviour of Heifer Calves on Pasture

5.1 Introduction

Feeding calves greater allowances of milk can increase growth rates in the first weeks of life and may lead to improved health and long-term performance (Terré et al., 2009; Soberon and Van Amburgh, 2013). However, increasing the quantity of milk fed to calves results in a reduction in the intake of solid-feed during pre-weaning, which can slow down rumen development and lead to depressed feed intakes and growth rates after weaning, particularly if weaning is abrupt (Khan et al., 2011a). In New Zealand dairy farming systems, young calves are often given access to pasture shortly after they are weaned, or while milk is still being fed. The ability of calves to successfully transition to grazing pasture is important for their performance and growth after weaning. The time spent grazing, ruminating and idling can provide an indication of the ability of calves to consume forage (Aikman et al., 2008). The ability of young calves to rapidly develop the ability to graze has been previously demonstrated by Chambers (1959) in several experiments where calves were given access to pasture shortly after birth, whilst still being fed milk. However, the effect that milk intake may have on the ability of calves to transition to grazing pasture after weaning is not known.

The aim of this chapter was to determine the effect that pre-weaning MR allowance may have on grazing and rumination behaviour of calves after they have been weaned and given access to pasture. It was originally hypothesized that there would be no difference in grazing behaviour between treatments, however, as LA and HA calves consumed more calf-starter post-weaning than ADLIB calves (Chapter 4), it is now hypothesized that LA and HA calves will have more developed rumens, and therefore spend more time grazing and more time ruminating than ADLIB calves immediately after being given access to pasture, but that calves will rapidly adapt, and these differences would disappear within several weeks after being on pasture.

5.2 Methods

This study consists of a treatment period, where calves were fed different MR allowances (outlined in Chapter 4), and the observation period, where calves were outdoors with access to pasture and calf-starter only, and observations took place. The treatment period was from 12 to 93 days of age and calves were kept indoors and fed MR with free access to calf-starter and hay (Chapter 4). Calves remained indoors with access to only calf starter and hay from 93 to 100 days of age and were given access to pasture at 100 days of age. The observation period was from 101 to 127 days of calf-age.

5.2.1 Treatment period

The calves in this study were group-reared using an automatic milk-and starter-feeding system (Zeddy, Palmerston North, New Zealand) as part of the larger cohort of calves previously described in Chapter 4. A subset of heifer calves (Holstein-Friesian x Jersey, n=28) with the same birth date were selected from the 3 MR allowance treatments which were: low allowance (LA; n = 10), MR fed at 10% of their initial BW (taken upon inclusion in the study at 12 ± 2 days of age); high allowance (HA; n = 9), MR fed at 20% of their initial BW; and *ad libitum* (ADLIB; n = 9) MR access.

Calves born on 2 local farms were moved to a dedicated calf-rearing facility at a minimum of 4 days old. Calves were collected within 24 hours of birth and fed 2 litres of first-milking colostrum until 2 days of age, and then manually fed whole milk from a bottle (2 litres morning and 2 litres afternoon) until 11 days of age, at which point they were weighed and applied to treatment groups. From 12 to 93 days of age, a commercially available milk replacer (25% crude protein, 21% crude fat; Ancalf, NZAgbiz Ltd., Hamilton, New Zealand) was diluted in lukewarm water (150 gram/ litre) and fed to all calves via automated milk feeding machines (Zeddy, Palmerston North, New Zealand). Calves were weaned gradually over 14 days, beginning at 79 days of age, by linearly reducing the volume of MR based on each calf's mean consumption in the 3 days prior to the start of weaning. Calves had *ad libitum* access to clean drinking water and to a commercially available pelleted calf starter, (20% crude protein pellets, SealesWinslow Limited, Tauranga, New Zealand) which was also fed via automatic feeders (Zeddy, Palmerston North, New Zealand), along with *ad libitum* access to ryegrass hay from around 3 weeks of age. Intake of hay was not measured. Following weaning, calves remained indoors for a week until 100 days of age with free access to calf-starter and hay, before being moved onto pasture.

5.2.2 Observation period

Upon being moved outdoors 1-week after weaning at 100 days of age, calves were kept as a single mob and set-stocked in an area of approximately 2 hectares. Calf starter remained available *ad libitum* from automatic feeders for a further week on pasture and was then gradually reduced to zero over 2 weeks, and fresh water was always available from a drinking trough.

Observations to monitor behaviour were made on 4 days over a 4-week period, beginning 1 day after calves were moved onto pasture at 101 days of age, and then weekly at 108, 122 and 127 days of age. Observations on these days are referred to as week 1, week 2, week 4 and week 5 respectively. Calves were uniquely marked with different colours and numbers using stock marker to allow easy identification and recorded at 5-minute intervals by 3 observers from 8am to 4pm. Observers attempted to scan and record calves in the same order to ensure a consistent 5-minute gap between observations, and binoculars were used where necessary for identification of calf and behaviour. Calves were recorded as either grazing (actively consuming pasture), ruminating (visible jaw movement, not consuming pasture), idling (sitting or standing stationary whilst not visibly ruminating or grazing), active (moving, with no visible rumination), drinking water (actively consuming water) or eating calf starter (head inside feeding stall). Total time spent drinking water and consuming calf starter was negligible and not different among the 3 treatments and has not been presented.

BW of all calves were recorded using a digital weigh scale monitor (Gallagher TW1 Data Monitor, Hamilton New Zealand) attached to a double load-bar scale (Technipharm, Rotorua, New Zealand) at the beginning of the observation period (100 days of age) and at the end of the observation period (126 days of age). Average daily gain during the observation period was calculated with these weights and the precise number of days between weights. Blood samples for β- hydroxybutyrate analysis were collected from the jugular vein of calves (LA; n = 9, HA; n = 6, ADLIB; n = 9) at the beginning of the observation period (100 days of age), and during week 4, after calf-starter weaning (121 days of age). A 10-ml blood sample was collected in evacuated tubes (Vacutainer, EDTA; Becton-Dickinson, Wellington, New Zealand). Blood samples were centrifuged (20 minutes at 1300 *g*) and 3 sub-samples were stored at about -80°C until analysis. Analysis of β-hydroxybutyric was carried out using an enzyme kinetic assay (Randox Laboratories Ltd, United Kingdom). Pasture samples were collected by pluck sampling on the same day, and composition determined according to the methods of AOAC

(1990). Pasture components were determined by manually separated and weighing each fraction after drying. Pasture mass was measured using a rising-plate meter.

5.2.3 Statistical analysis

Behaviour parameters and BW data were analysed with the PROC MIXED procedure in SAS (v9.4, SAS Institute Inc, Cary, NC, USA), with pre-weaning treatment as a fixed effect and calf nested within treatment as a random effect. A general linear model was used to analyse β-hydroxybutyric, ADG, MR intakes and calf starter intakes, with pre-weaning treatment as a fixed effect.

5.3 Results and Discussion

5.3.1 Pasture composition, calf-starter intakes and calf growth

Herbage mass was high throughout the study period (Table 9), and would have ensured that pasture availability was unrestricted to calves, but pasture quality and quantity deteriorated over the 4-week period, as indicated by increasing neutral-detergent fibre and decreasing organic matter digestibility, crude protein, metabolizable energy (Table 9) and decreasing leaf:stem ratio (Table 10). The change in pasture composition due to selective grazing and the hot and dry conditions experienced. This may have affected the ADG of calves, particularly after week 4 when calf-starter feeding was stopped.

Table 9. Pasture chemical composition (% DM) and herbage mass of pasture grazed by calves over the 4-weeks of the study.

Week	NDF %	ADF %	CP %	OMD %	ME, MJ/kgDM	Herbage mass (kgDM/ha)
1	52.0	27.5	15.0	70.2	10.3	5549
2	52.6	28.7	11.2	70.0	10.3	3654
3	56.2	32.3	8.5	66.7	9.8	3037
4	53.5	30.1	11.5	66.7	9.9	3662
5	59.4	34.0	9.7	59.3	9.0	3257

NDF = neutral detergent fiber; ADF = acid detergent fiber; CP = crude protein; OMD = organic matter digestibility; ME = metabolizable energy

Table 10. Botanical composition (percentage of dry matter) of pasture grazed by calves over the 4-weeks of the study and leaf:stem ratio of grass species.

Week	Grass leaf %	Grass stem %	Clover %	Other %	Dead material %	Leaf:stem ratio
1	29.9	64.8	1.0	4.0	0.4	0.46
2	18.0	68.9	1.2	9.9	2.1	0.26
3	9.1	77.1	0	2.5	11.3	0.12
4	11.3	63.2	0	11.7	13.9	0.18
5	17.3	72.4	0	4.9	5.4	0.24

At the beginning of the study (100 days of age), ADLIB calves tended ($P = 0.087$) to be heavier than HA and LA calves (Table 10). In the overall study that included data from 198 calves (Chapter 4), ADLIB calves were heavier than LA and HA calves at 100 days of age. By week 5 of the current study, ADLIB calves were heaviest ($P < 0.05$), and HA and LA calves had similar BW. There was no difference in ADG between the treatments (Table 11), though the low number of calves in this study relative to chapter 4 may have reduced the chances of detecting a difference.

Table 11. Mean (± standard error) body weight and plasma β-hydroxybutyric at the beginning (100 days of age, 1-week post-weaning) and end of the study (121 days of age, 6 weeks after weaning), and average daily gain over the 4-week study period

	Milk replacer allowance[1]			
Item	LA	HA	ADLIB	*P*-value
Pre-weaning milk intake (litres/day)	3.6 ± 0.3[c]	6.2 ± 0.3[b]	9.3 ± 0.3[a]	<0.001
Initial body weight (kg)	94.7 ± 4.5	93.1 ± 4.7	104.6 ± 4.7	0.16
Final body weight (kg)	109.5 ± 4.5[b]	111.7 ± 4.7[b]	124.5 ± 4.7[a]	0.07
Average daily gain (kg/day)	0.57 ± 0.10	0.72 ± 0.10	0.76 ± 0.10	0.36
Initial β-hydroxybutyric (mmol/litre)	0.31 ± 0.05	0.25 ± 0.06	0.27 ± 0.05	0.69
Final β-hydroxybutyric, (mmol/litre)	0.26 ± 0.03	0.22 ± 0.03	0.26 ± 0.03	0.45

[a,b]Means with different superscripts within each row are significantly different at $P < 0.05$.
[1]Calves were fed milk replacer at 10% initial body weight (LA), 20% initial body weight (HA) or *ad libitum* (ADLIB).

5.3.2 Behaviour of calves during the observation period

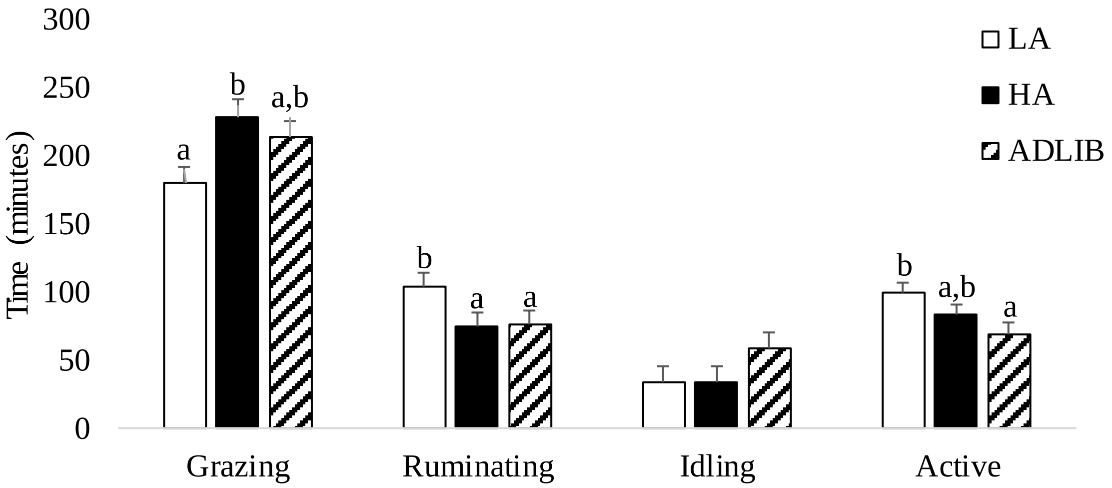
In our study, scanning and recording intervals of 5 minutes were used to monitor behavior, which have previously been demonstrated to result in reliable estimates of the time spent grazing, ruminating and resting in grazing calves (Hirata et al., 2002). It was expected that LA calves would have better developed rumens at weaning due to greater pre and post-weaning calf-starter intake (Khan et al., 2011a), and we speculated that they would spend more time grazing than HA or ADLIB calves. On the first observation at 101 days of age, however, LA calves spent less time grazing than HA, but the same time as ADLIB calves ($P < 0.05$; Figure 7), while LA calves spent more time ruminating than HA and ADLIB calves ($P < 0.05$). Plasma β-hydroxybutyric levels were not different between treatments at the start or end of the observation period (Table 11), which could indicate that there was no apparent difference in rumen development between treatments (Quigley et al., 1991). Pre-weaning calf-starter intake was inversely associated to MR intake (chapter 4; Khan et al., 2011), and calf-starter intake remained greater in LA calves compared to HA and ADLIB calves during the 1-week period after weaning that calves remained indoors (ADLIB = 1.0 ± 0.1 kgDM, HA = 1.19 ± 0.1 kgDM, LA = 1.56 ± 0.1 kgDM; $P < 0.05$). The LA calves might then have been less motivated to consume pasture, although there was no difference in calf-starter intake on the observation day, or over the following 2 weeks. Increased intake of calf-starter prior to the grazing period in LA calves could have increased their development of rumination and feed intake behaviour (Khan et al., 2016). This may have led to LA calves spending more time ruminating, therefore having less time to graze during the observation period.

Differences in concentrate intake between calves fed *ad libitum* or restricted milk intakes do not persist for more than a week after weaning (Miller-Cushon et al., 2013), and calves in our study were not observed at pasture until 1-week after weaning. During this time, differences in calf development that may have affected grazing behaviour may have been overcome. Additionally, the hay that was provided to calves before weaning may have aided the adaptation of calves to grazing pasture, as the provision of cut ryegrass to housed calves before weaning has been shown to result in greater grazing times when calves were given access to pasture *in-situ* (Phillips, 2004). Greater differences might have been seen among treatments in grazing behaviour if calves were not provided a source of forage prior to going out onto pasture.

In our study, it was apparent that calves had largely synchronous behaviour. Social interaction and learning are important in developing the foraging ability of young herbivores (Launchbaugh and Howery, 2005), and calves have been shown to spend more time grazing and have greater pasture intake when in groups rather than individually (Phillips, 2004). To more accurately determine the impact of milk allowance on grazing and rumination time, it may therefore be necessary to keep animals from different treatment groups separate to avoid the effect of peer-learning (Costa et al., 2016).

A diurnal grazing pattern is commonly observed in cattle; the most significant grazing event is in the early evening/late afternoon and the other major event occurs in the early morning (Gregorini, 2012). As our observation period was from 8 am to 4 pm, the main grazing events may not have been observed, although excluding week 2, calves still spent most of their time grazing (Figure 8). It could be assumed that any differences in grazing behaviour among treatments would be consistent throughout the day, although a longer period of observations would allow greater accuracy.

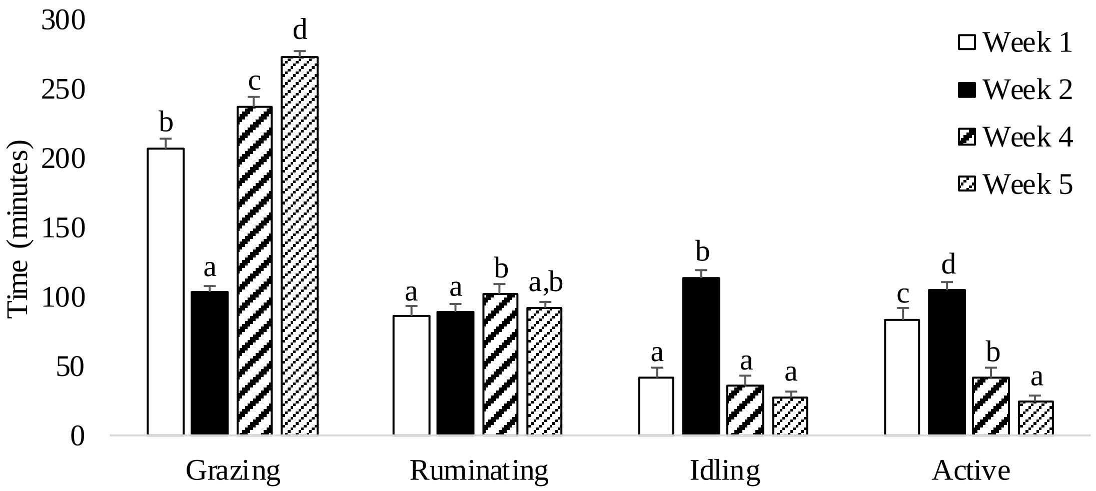
Figure 7. Mean time (and standard error represented by bars) spent on each activity (grazing, ruminating, idling or active) on the first observation day, one day after calves were given access to pasture



[a,b]Values with different superscripts within each activity are significantly different at $P < 0.05$. Total observation length was 8 hours (480 minutes).

LA = low allowance; HA = high allowance; ADLIB = *ad libitum* milk replacer.

Figure 8. Mean time (and standard error represented by bars) spent on each activity (grazing, ruminating, idling or active) by all calves on each observation day. Calves were observed for 8 hours per day



[a,b,c,d]Values with different superscripts within each activity are significantly different at $P < 0.05$. Total observation length was 8 hours (480 minutes) on each day.

Calves were given access to pasture one day prior to the observation day at week 1, and calf-starter access was removed one day prior to the observation day of week 4.

LA = low allowance; HA = high allowance; ADLIB = *ad libitum* milk replacer

Excluding week 2, mean total grazing time by all calves increased every week, and was 274 ± 7 minutes on the observation day of week 5, compared to 207 ± 7 minutes in week 1 (Figure 8). While pasture covers remained high throughout the observation period, it was likely that calves were selectively grazing preferable areas and species (Gibb et al., 1997). The reduction in leaf:stem ratio and increasing dead material after week 2 (Table 10) suggests that calves would have had to increase their grazing time to compensate for decreased bite size and biting rate (Cosgrove and Edwards, 2007). The reason for the low grazing time in week 2 is uncertain and requires further investigation. Measuring actual pasture intakes would provide a more accurate representation of grazing behaviour in the calves according to milk allowance and pasture factors.

Chapter 6.0 General Discussion

The first objective of this study was to determine the effect of a low, high or *ad libitum* MR allowance on pre-weaning concentrate intake, total nutrient intake and growth. As hypothesised, calves that consumed more MR had less calf-starter intake, as indicated by the inverse relationship between MR and calf-starter intake (R^2 = 0.33). Despite this inverse relationship, calves that were allocated to higher MR allowances consumed more energy, protein and total DM; total pre-weaning DMI in ADLIB calves was 18% greater than HA and 38% greater than LA calves. Therefore, calves that consumed more MR had greater pre-weaning growth rates. Milk replacer intake had a positive relationship to pre-weaning ADG (R^2 = 0.36), and pre-weaning ADG was 0.70 kg/day for ADLIB, 0.60 kg/day for HA and 0.53 kg/day for LA calves. The effect of MR allowance on total nutrient intake and growth before weaning is consistent with other studies investigating the effect of milk allowance (reviewed by Khan et al., 2011b) and indicates a direct nutritional response on ADG in the pre-weaning period.

We have demonstrated that crossbred dairy heifer calves are able to safely consume far greater milk allowances than typically provided (10-20% of initial BW) when fed *ad libitum* via automated milk feeders. It was expected that *ad libitum* intakes of calves would be lower in our study than in those from North America or Europe due to lower initial BW (37 kg *vs* 43-45 kg; Borderas et al., 2009a; Welboren et al., 2019). Maximum daily milk intakes of 10-16 litres/day have been reported in the literature for *ad libitum* milk fed calves (Borderas et al., 2009a; Frieten et al., 2017; Welboren et al., 2019). The maximum intake of ADLIB calves in our study was 13.6 ± 0.25 litres/day, compared to the maximum daily allowance of ~8 litres/day for HA calves. Differences in intake by calves in other studies could also be ascribed to the duration of milk-feeding (Kehoe et al., 2007) climatic conditions (Khan et al., 2011b) or age of introduction and training to the feeders (Fujiwara et al., 2014; Medrano-Galarza et al., 2018a).

A second objective of the study was to determine the effect of pre-weaning milk allowance on calf-starter intake and growth immediately after weaning, and on grazing and rumination time on pasture. Feeding high milk allowance is often viewed as unattractive due to the perceived growth slump after weaning, but we have demonstrated that with gradual weaning implemented with automatic feeders (linearly reducing MR intake over 14 days) HA calves experienced similar calf starter intakes and growth in the 5-week post-weaning period as LA calves. However, in our study, ADLIB calves had lower calf starter intakes and lower growth rates in the post-weaning period than HA and LA calves, as well as higher circulating NEFA than LA calves, indicating that the weaning method did not foster sufficient starter intake and rumen development for *ad libitum* MR fed calves. Additionally, the difference in grazing and ruminating times among calves reared on different treatments suggests that MR allowance may have also affected grazing behaviour and pasture intake for up to 2 weeks after weaning.

Two further objectives of this study were to investigate the effect of pre-weaning milk allowance on the pre-weaning mammary gland development of heifer calves, and on BW up to 10 months of age in a pastoral system. We demonstrated that calves that had a higher growth rate before weaning were heavier at 6 months of age, but there was no difference among treatments in BW at 10 months of age. Literature suggests that it will have a positive effect on lactation performance (Soberon and Van Amburgh, 2013; Gelsinger et al., 2016), but in contrast to others (Brown et al., 2005a; Soberon and Van Amburgh, 2017), mammary gland development of calves measured through ultrasound in our study was not enhanced with greater MR allowance. While we have demonstrated in this study that improving pre-weaning growth rate can contribute to improved calf BW at 6 months of age in a pastoral system, the difference among treatments was small (7-9 kg of BW) and was lost by 10 months of age. Therefore, it is unlikely that there would be a difference among treatments in the age at which heifers attain puberty and in their reproductive performance. However, the differences created in pre-weaning ADG warrants further research to evaluate the performance of the heifers reared during the first lactation.

To implement enhanced milk feeding systems, it may be necessary to utilise automatic feeding machines. While such systems may be cost-efficient in year-round calving systems, each feeder can only support a limited number of calves, and so the ratio of feeders to cow numbers required is far greater in seasonal calving systems. In our study, total MR consumption per calf was 290.5 litres for LA, 518.8 litres for HA and 722.1 litres for ADLIB calves, and total pre-weaning calf starter consumption per calf was 34.3 kg for LA, 21.9 kg for HA and 11.4 kg for ADLIB calves. At NZ$0.77/litres for MR (Farm Source, 2019a) and NZ$1.135/kg of calf starter (Farm Source, 2019b), the total pre-weaning feed cost per calf on our study was $235 for LA, $421 for HA and $569 for ADLIB calves. Further evidence of production benefits from feeding more milk to calves in NZ systems is therefore required to justify the expense of the additional milk or MR, as well as the cost of automatic feeding machines which may be necessary for the successful application of enhanced milk-feeding programmes.

In our study, calves were kept indoors and not given access to pasture until after the cessation of MR feeding. However, in NZ, calves are often given access to pasture while they are still being fed milk. Previously, Macdonald et al. (2008) demonstrated that when calves were given free access to concentrate and to pasture after 3-4 weeks of age, there was no difference in concentrate intake between calves fed at a different milk allowance, but energy balance calculations indicated that calves fed less milk consumed more pasture (Macdonald et al., 2008). No difference in pre-weaning growth rate between calves fed a low or high allowance of milk was reported by Cardoso et al. (2015), although calves fed the high milk allowance reached the pre-determined weaning weight earlier (90.6 ± 1.7 days *vs* 84.8 ± 1.8 days); these authors stated that calves appeared to show a strong preference for pasture over concentrate. This suggests that the effect of milk allowance on the total feed intake and growth of calves that are provided with milk, concentrate and *in-situ* pasture simultaneously may differ to when calves are only given access to milk and concentrate, as in our study.

6.1 Limitations

In our study, we aimed to assess the effect of MR allowance on the total pre-weaning feed intake. However, in NZ, calves are often given access to pasture before weaning, and as previously discussed, the effect of milk allowance on the intake of concentrate may be different when calves are grazing pasture. However, accurately measuring the pasture intakes of grazing animals is difficult and was beyond the scope of this study. Additionally, calves are often weaned when they reach a set BW, but in our study, they were weaned at a set age. Calves that are fed more milk will reach their weaning age earlier due to greater growth rate but will have lower solid-feed intake and likely less rumen development, thereby affecting their weaning transition. We could expect to see different results in pre and post-weaning feed intake and growth rate if calves were weaned at a set BW. Therefore, our study may not accurately depict the effect of pre-weaning milk intake on total feed intake and growth before and immediately after weaning under typical management in NZ.

6.3 Industry Implications and Future Research

Greater BW of calves at 6 months of age could have positive effects on the future lactation performance of heifers (McNaughton et al., 2019). This could contribute to improved efficiency of production and lower culling rates, thereby improving farm financial outcomes and decreasing the environmental impacts of greater cow numbers. However, further research is required to determine the effect that milk allowance, and pre-weaning growth rate may have on the future lactation performance of NZ heifers in a pastoral system. While we demonstrated benefits to feeding greater MR allowances on calf growth and BW after weaning in a pastoral system, the cost of this is high and requires justification.

In contrast to other studies where calves were slaughtered, pre-weaning mammary parenchyma growth was reduced with *ad libitum* MR allowance. These results require further investigation using slaughter studies, and validation of non-invasive techniques for measuring mammary gland growth in calves is necessary.

This research also has implications to the beef industry. With the increased scrutiny on unwanted 'bobby' calves in NZ, there is a requirement to utilise these animals for beef production, and a possible solution could be to slaughter these animals earlier than is traditional (Pike et al., 2019). To make this a viable solution, calves will need to be grown faster, and we have demonstrated that feeding greater milk allowances improves weight gain of calves before weaning, and that a post-weaning growth check can be avoided in calves fed a high milk allowance. For the beef industry to capitalise on this, further research on post-weaning rearing strategies that allow the weight advantage of high milk-fed calves to be maintained are required. However, the economic feasibility of feeding high allowances of milk must also be considered.

Improved weaning methods are required if calves are to be fed *ad libitum* MR allowances. Possible methods should involve altering the intake of calves according to their individual intakes of solid-feed (de Passillé and Rushen, 2016; Benetton et al., 2019), or gradually adjusting milk allowance based on previous intakes (Welboren et al., 2019). However, these methods require the use of both automatic milk feeders and automatic calf starter feeders, which represent a high cost to the farmer.

In Chapter 5, it was demonstrated that pre-weaning milk allowance may have an effect on the grazing behaviour of calves after they have been weaned. This has implications for heifer rearing in NZ where calves are provided access to pasture during or immediately after milk feeding, as milk allowance may affect calf performance after they are weaned. Further research is required to better understand the effect that milk allowance may have on pasture intakes of calves before and immediately after weaning, accounting for the effect that peer-learning, pasture quality and species may have on grazing behaviour. Additionally, forage sources for rearing calves requires further investigation, as early weaning of lambs onto pastures or forages with high nutritive value has been shown to maintain growth rates compared to lambs still obtaining milk (Cranston et al., 2016), and McCoard et al. (2019) demonstrated that calves can be successfully reared on a forage diet with no concentrate.

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