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**RELATIONSHIPS BETWEEN BEHAVIOURAL TRAITS, RESIDUAL FEED
INTAKE, AND AVERAGE DAILY GAIN IN GROWING DAIRY HEIFERS
FED LUCERNE CUBES**

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ABSTRACT

Residual feed intake (RFI) is a measure of an individual's efficiency in utilising feed for maintenance and production during growth or lactation. It can be defined as the difference between the actual and predicted feed intake of that individual. Efficient animals eat less than predicted for their body weight and level of performance, and inefficient animals eat more. The objective of this study was to investigate possible relationships between RFI and behavioural traits, such as feeding behaviour, social dominance, and activity in young dairy heifers.

The intakes and liveweights of 1049 growing dairy heifers (6-8 months of age, 195 ± 25.8 kg liveweight) in five cohorts were measured for 42-49 days to ascertain individual RFI. Animals were housed in an outdoor feeding facility comprising 28 pens, each with eight animals and one feeder per pen, and were fed a dried, cubed lucerne diet. An electronic feed monitoring system measured the intake and feeding behaviour of individuals.

Intake was moderately to strongly correlated with RFI for individual cohorts ($r = 0.54-0.74$; $p < 0.001$), indicating that efficient animals ate less than inefficient animals. Several other feeding behaviour traits were related to RFI, but the relationships were weak ($r = 0.14-0.26$; $p < 0.05$) suggesting that feeding behaviour is not a reliable predictor of RFI in growing dairy heifers. Statistical comparison of the extremes of RFI (104 most and 104 least efficient) showed that the most efficient animals (low-RFI) had similar liveweight and average daily gain to the least efficient (high-RFI) ($p > 0.05$) but ate less (mean $\pm$ SED; $6.97 \text{ v } 8.75 \pm 0.10$ kg cubes), had fewer meals ($6.3 \text{ v } 8.2 \pm 0.61/\text{d}$), shorter daily feeding duration ($2.71 \text{ v } 2.85 \pm 0.07$ h), ate longer meals ($35.6 \text{ v } 30.6 \pm 1.54$ min/meal), and ate more slowly ($45.4 \text{ v } 53.0 \pm 1.36$ g cubes/min) than the least efficient animals (all $p < 0.05$). These groups also differed in their feeding patterns over 24 h. Video recordings of 32 animals showed that daily activity included (mean $\pm$ SEM) 15.4 ± 0.5 h lying, 4.8 ± 0.5 h standing, and 2.9 ± 0.1 h feeding. However, neither social status nor activity were related to RFI in this study ($p > 0.05$).

Feeding behaviour explained only a small proportion of the variation in RFI in dairy heifers. Selecting animals for low RFI (efficient) is unlikely to affect social dominance and activity, although these results should be confirmed in a grazing environment representative of most New Zealand dairy farms.

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LIST OF ABBREVIATIONS

ADG	Average daily liveweight gain
ANOVA	Analysis of variance
BW	Breeding Worth
CSV	Computer separated value
d	Day(s)
DI	Dominance Index
DM	Dry matter
EID	Electronic identification
EV	Economic Value
g	Grams
h	Hour(s)
h^2	Heritability
kg	Kilogram(s)
LWT	Liveweight
Min	Minute(s)
n	Number
RFI	Residual feed intake
SD	Standard deviation
SED	Standard error of the difference
SEM	Standard error of the mean
TMR	Total mixed ration

1. INTRODUCTION

Feed is the largest variable cost in dairy production systems, accounting for approximately 50% of the costs of milk production from pasture (Waghorn & Hegarty, 2011). Improving the efficiency of feed utilisation provides an opportunity for reducing costs. Animals that use feed efficiently will require less feed for maintenance and for the same level of production (e.g., growth or milk production), and therefore should be more profitable. Variation in the efficiency of feed utilisation for maintenance or production is known as residual feed intake (RFI), defined as the difference between the actual and predicted feed intake of an individual. The predicted intake is a calculated average value, based on a population with similar characteristics to the animal being measured. Efficient animals will eat less than predicted for their body size and level of production (growth or milk), and will therefore have a negative RFI; inefficient animals will eat more than predicted and will have a positive RFI.

The RFI trait has been studied extensively in beef cattle, and also in other species such as pigs, poultry, fish, and mice (Bordas & Minvielle, 1999; Arthur et al., 2001; Hughes & Pitchford, 2004; Silverstein et al., 2005; Young et al., 2011). However, limited research has been conducted on RFI in dairy cattle. Calculation of RFI in cattle requires measurement of intake and liveweight, usually for 60-80 days, making it expensive and dependent on accurate measurements of these variables. The costs of identifying cattle with high and low RFI has driven research to find phenotypic traits that could be used as indicators of RFI, and more recently, genetic markers. In beef cattle, suggested phenotypic indicators have included blood parameters such as insulin-like growth factor-1 (IGF-1) and glucocorticoid concentrations, carcass characteristics such as backfat thickness, ultrasound measurements, and feeding behaviour (Carstens et al., 2002; Nkrumah et al., 2007; Lancaster, 2008; Montanholi et al., 2010). Phenotypic indicators should contribute to the variation in efficiency of feed utilisation and be relatively easy to measure.

The biological bases and underlying mechanisms affecting RFI have been hypothesised, but are not clearly defined. Understanding the factors associated with efficiency may explain the physiological mechanisms underlying RFI, allowing a more focussed selection for efficiency. However it is equally important that genetic selection for RFI does not inadvertently select for traits that will be of negative economic value or contribute to poor health and welfare of

dairy cattle (Rauw et al., 1998). Therefore, an assessment of the behaviour of individuals with divergent RFI will provide a better understanding of its contribution to RFI, while providing information on potential adverse effects of selection for RFI.

Behavioural traits (e.g., feeding, social dominance, general activity) may be linked with efficiency, and if associations were sufficiently high, could be used as indicators for divergence in RFI. An association between RFI and behaviour may also provide information on the mechanisms regulating efficiency in dairy cattle. Feeding behaviour affects supply of nutrients for maintenance and production, and changes can indicate ill health in dairy cattle (Weary et al., 2009). An understanding of behaviour can also assist in development of management strategies to optimise production, animal health and welfare (Sheahan et al., 2011).

The primary objective of this research was to investigate relationships between RFI and behaviour in growing dairy heifers. Principal calculations were the associations between RFI and feeding behaviour in 1049 animals across five cohorts and comparison of the most and least efficient animals, but other objectives included an investigation of the relationship between average daily gain (ADG) and feeding behaviour, as well as associations between social dominance, general activity and RFI. This study required multiple technologies to be used, including electronic measurement of feed intake and electronic identification of animals when feeding; these data provided behavioural information used for much of the analysis presented here. Data checking and validation was an important component of the analysis. Additional data collection included the use of infrared surveillance video and recording technology for observing activity and social dominance of animals during both daylight and darkness.

Most evaluations were carried out on all 1049 animals in a combined cohort analysis, but the presentation also includes analyses on subsets of those animals, such as at a cohort level, or comparison of groups of the most and least efficient individuals. The visual assessment of social dominance and activity using the video recordings was limited to 32 animals (4 pens in Cohort 5).

This research was part of a larger project conducted by DairyNZ Ltd that identified animals differing in their feed requirements for growth, with the ultimate aim of identifying genetic

markers for RFI. The project was funded by DairyNZ Inc., Livestock Improvement Corporation, New Zealand Trade and Enterprise, and the Ministry of Science and Innovation. A corresponding trial was conducted in Victoria, Australia by the Department of Primary Industries-Victoria and funded by the Geoffrey Gardiner Foundation.

Following this introduction, a review of the literature in Chapter 2 provides background to the research topic. The materials and methods of this research are outlined in Chapter 3, the results are presented in Chapter 4, followed by the discussion and conclusions in Chapters 5 and 6, respectively. Additional data and other material for chapters 3 and 4 are provided in Appendices I and II. Appendix III includes a publication that resulted from an assignment for a course in Animal Welfare Science which was undertaken as part of this MSc degree (Green & Mellor, 2011). This paper was also awarded first prize for Most Commended Paper published in the New Zealand Veterinary Journal in 2011 by the Australian and New Zealand College of Veterinary Scientists. Also included is a publication of initial results of this study which were presented at the New Zealand Society of Animal Production conference in 2011 (Green et al., 2011).

2. REVIEW OF LITERATURE

2.1 The New Zealand dairy industry

The New Zealand dairy industry is a significant contributor to the national economy. It is the country's largest export earner, earning \$NZ 10.4 billion in 2009 (26% of total goods export earnings) (NZIER, 2010). Approximately 95% of dairy products produced in New Zealand are exported, and they account for over one-third of the world trade market in dairy products. This makes New Zealand the largest exporter of dairy products in the world despite producing only 2% of total world milk production (New Zealand Trade and Enterprise, 2007; NZIER, 2010; MAF, 2011).

New Zealand's dairy industry is based on systems that incorporate highly productive pasture grazed year-round by cows of high genetic merit (Holmes et al., 2002). These factors allow production of milk at a relatively low cost compared with many other countries (Figure 2.1), and provide New Zealand with a competitive advantage in the world market. Milk is produced and exported without subsidies or incentives, and the distance from markets and predominance of commodity produce (i.e., milk powder rather than high-value infant formula, for example) requires a low-cost system to remain profitable (ABARE and MAF, 2006).

The number of cows and the milk produced and processed in New Zealand has increased significantly in the last 30 years (Table 2.1). Average herd size has more than tripled in the last 30 years, while number of herds has declined at a rate of 170 herds per season (LIC and DairyNZ, 2011). Average stocking rate has increased over the last 30 years. These figures indicate increasing intensification in the dairy industry.

Jerseys were the dominant dairy breed in New Zealand until the late 1960s, after which Holstein-Friesians and Holstein-Friesian/Jersey crossbreeds became more popular. Holstein-Friesian is now the dominant dairy breed in New Zealand, but there has been a large growth in the number of Holstein-Friesian/Jersey crossbreeds in the last ten years, and together these breeds now comprise almost 80% of the national herd (Figure 2.2) (LIC and DairyNZ, 2011). This shows that New Zealand farmers are very responsive to advances in genetics and

are focussed on breeding the right cow for their system. Therefore, any beneficial traits, such as increased efficiency, are likely to be highly sought after and adopted rapidly.

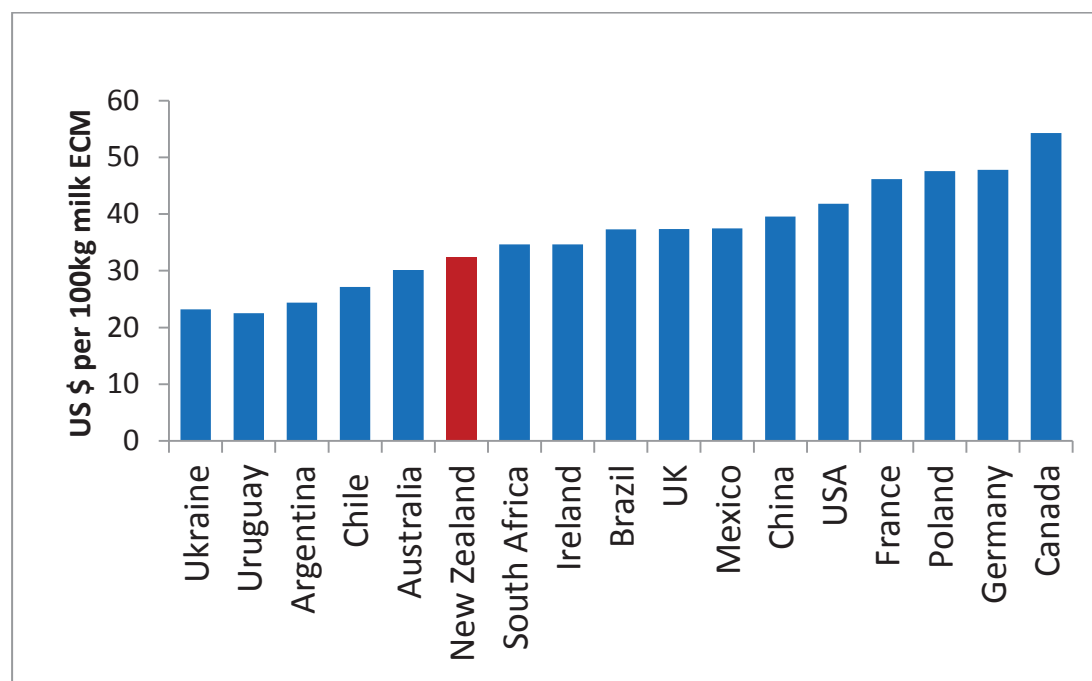


Figure 2.1: Costs of milk production on a typical farm in a selection of countries, averaged over three years from 2008-2010 (IFCN, 2011). ECM: energy-corrected milk.

Table 2.1: New Zealand dairy industry statistics from the 1980/91 and 2010/11 seasons (LIC and DairyNZ, 2011).

	1980/81	2010/11
Milk processed (million litres)	5,868	17,339
Milksolids processed (million kg)	491	1,513
Number of cows (million)	2.0	4.5
Average herd size	126	386
Number of herds	16,089	11,735
Average stocking rate (cows/hectare)	2.07	2.76

The temperate climate of New Zealand makes pastoral farming possible, and pasture comprises a major portion of the dairy cow's diet (Holmes et al., 2002). Management of the dairy farm requires synchrony of cow feed requirements with seasonal pasture growth. Profitability is achieved despite low production per cow relative to overseas total mixed ration (TMR) based systems (Holmes et al., 2002).

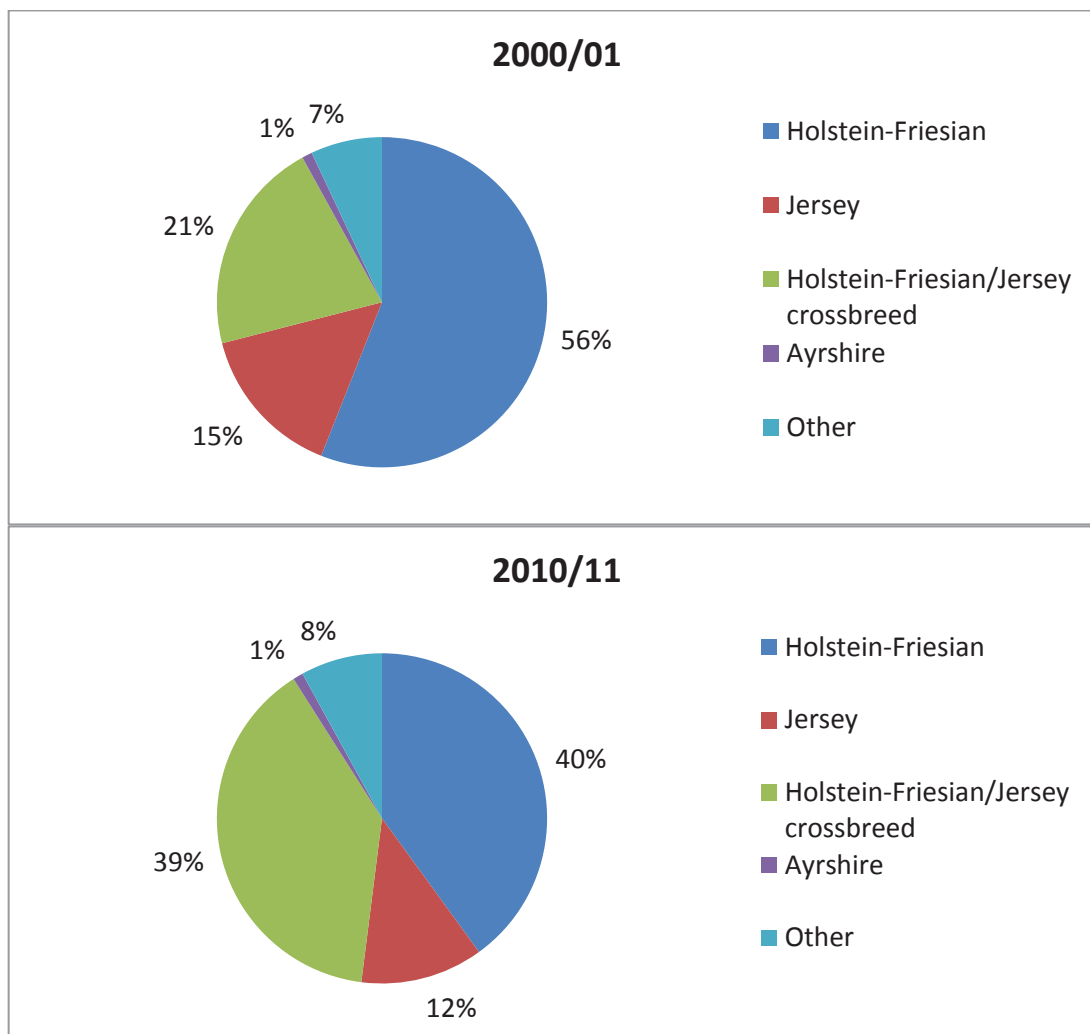


Figure 2.2: Dairy breeds in New Zealand in 2000/01 and 2010/11 (LIC, 2001; LIC and DairyNZ, 2011).

As feed accounts for 50% of costs of milk production from pasture (Beever & Doyle, 2007; Waghorn & Hegarty, 2011), a high utilisation of pasture dry matter (DM) is required. Maximum utilisation of pasture is 80-85% due to the difficulty of harvesting grass lower in the sward and wastage of pasture due to trampling, defecation and urination, but it is essential to achieve a high pasture utilisation and graze to a low residual DM to maintain pasture quality (Waghorn & Clark, 2004). However, dairy cows need to be hungry to achieve this maximum utilisation (i.e., graze to a low pasture residual), so they are rarely “fully fed”. Selective breeding for increased milksolids yields has meant that more feed is required per cow to meet the demands for milk production (Holmes et al., 2002).

2.1.1 Breeding criteria

The New Zealand dairy industry is also successful due to its continual drive to improve animal genetics. Selection in the New Zealand dairy industry is based on breeding objectives that incorporate traits associated with efficient conversion of feed into farmer profit (NZAEL, 2006). Genetic merit or estimated Breeding Value is calculated through the weighting of traits including milk volume, milkfat yield, protein yield, liveweight, cow fertility, somatic cells in milk and residual survival (longevity) from records of the individual animal, the individual's ancestry, and/or its progeny (NZAEL, 2006). As well as these traits, indices for Economic Values (EVs) are also produced for milkfat percentage, protein percentage, calving difficulty, body condition score, and 16 traits other than production which include management, liveweight and conformation traits (NZAEL, 2006). The EVs combine with the seven Breeding Value traits to provide an estimate of Breeding Worth (BW), which ranks animals on their estimated ability to produce efficient, profitable replacements. A positive economic value is placed on protein and milkfat yield, residual survival, and fertility, and a negative value on milk volume yield, liveweight, and somatic cell count (NZAEL, 2006).

An additional index is Production Value, calculated from liveweight and production traits (milk volume yield, milkfat yield and protein yield). The Production Values combine with different EVs to give Production Worth, which reflects production performance and measures the lifetime production of the cow herself (rather than her offspring) (NZAEL, 2006). Lactation Worth, calculated from the same traits as Production Worth but different EVs, ranks a cow's expected ability for milk production in the current lactation only (NZAEL, 2006).

The BW index is an important measure of genetic merit of dairy cows and can be used to compare all dairy cows in New Zealand, regardless of age, breed, or herd. As such, BW can be used as the basis for buying, selling, or culling decisions (NZAEL, 2006). However, a limitation of the BW index is that it does not include traits for feed intake and efficiency of feed utilisation for production (Kolver, 2007; Waghorn & Dewhurst, 2007). Rather, it uses a base unit of feed of 4.5 tonnes dry matter (DM) of average quality pasture per animal per year (NZAEL, 2006). This is not ideal because animals differ in the amount of feed they require, therefore undermining the usefulness of the BW index in relation to individual efficiency of feed utilisation.

2.1.2 Feed intake and utilisation

Dairy cows can have differing energy requirements for maintenance and production, and individuals may vary in their partitioning of energy between maintenance and growth or milk (Herd, 2009). Selecting those individuals that use less feed to achieve the same level of production could increase the efficiency of the whole system (McNaughton & Pryce, 2007), and produce greater profits from fewer cows.

Genetic selection targets animals with high milk production (McNaughton & Pryce, 2007), but the relative intakes of these high producers are not known. The effect of intake on BW is unclear and using an arbitrary intake will limit the effectiveness of BW in selecting individual animals that use their feed efficiently. Therefore, in order to refine breeding criteria, individual intakes must be measured (McNaughton & Pryce, 2007), and this is expected to demonstrate variation between individuals in the efficiency with which feed is utilised for maintenance and production. This divergence in efficiency is known as residual feed intake (RFI) (Herd, 2009).

2.2 Residual feed intake

2.2.1 Concept

The concept of residual feed intake (RFI) is not new; it has been researched in beef cattle (Arthur et al., 2001; Nkrumah et al., 2006), pigs (Young et al., 2011), mice (Hughes & Pitchford, 2004), fish (Silverstein et al., 2005; Grima et al., 2010), and poultry (Braastad & Katle, 1989; Bordas & Minvielle, 1999). It is also sometimes referred to as feed efficiency, feed conversion efficiency, or net feed intake, and was first described by Koch et al. (1963). In the context of this thesis, RFI is defined as the difference between the actual intake and the predicted feed requirements of an animal for a defined size and production (liveweight gain or milk production).

The RFI trait focuses on the variation between animals in their efficiency of energy utilisation for maintenance and growth (Korver et al., 1991). This measure of efficiency differs from other terms used to denote efficiency. For example, output (e.g., milk yield) expressed without reference to feed consumption, or the efficiency of feed conversion to farmer profit (in the context of the farm system), or gross feed efficiency, which is a measure of energy

conversion (megajoules of metabolisable energy) into liveweight gain (Korver et al., 1991; McNaughton & Pryce, 2007).

Predicted feed requirements can be calculated from standard energy requirement formulae for maintenance, production and liveweight loss and gain (e.g., National Research Council, 1996), or by regression of measured data (intake against metabolic liveweight^{0.75} and average daily gain) of the group being tested. Both systems take an average for a population for a defined level of production (Korver et al., 1991; Kolver, 2007; Waghorn, 2009). Efficient animals (negative/low-RFI) eat less than average, and inefficient animals (positive/high-RFI) eat more than average. Individuals that are efficient will contribute to greater system efficiency by requiring less feed for the same level of production (Table 2.2). Therefore, selecting for highly efficient animals (low-RFI) will improve the efficiency of the entire system (Carstens & Tedeschi, 2006).

Table 2.2: Examples of divergence in efficiency of feed utilisation (residual feed intake) in beef cattle.

Type of animal	ADG* (kg/d)	Efficient DMI (kg/d)†	Inefficient DMI (kg/d)	Reference
Steers (7-8 mo, concentrate diet)	1.51	8.00	8.93	Basarab et al. (2003)
Bulls (9 mo, TMR diet)	1.75	9.57	12.0	Fox et al. (2004)
Cows (at maintenance)		13.1	16.5	Basarab (2005)
Progeny	1.30	8.3	9.1	
Growing calves	1.06	8.71	10.61	Carstens and Tedeschi
Finishing calves	1.42	8.44	10.61	(2006)
Steers (concentrate diet)	1.47	9.62	11.62	Nkrumah et al. (2006)
Bulls (corn silage-based diet)	1.41	8.62	10.28	Lancaster et al. (2009)

Abbreviations: ADG, average daily gain; DMI, dry matter intake; TMR, total mixed ration.

*ADG did not differ ($p > 0.05$) between efficient and inefficient groups in all studies.

†DMI differed significantly ($p < 0.05$) between efficient and inefficient groups in all studies.

Divergence in RFI has been exploited in the beef, pig, and poultry industries (Kolver, 2007) but is relatively novel for dairy and milk production (Beever & Doyle, 2007). Studies with

beef cattle in feedlots have shown large differences between individuals in the efficiency with which they utilise their feed for liveweight gain (Herd & Bishop, 2000; Basarab et al., 2003; Arthur et al., 2004). Table 2.2 summarises several studies with beef cattle, to show the extent of divergence in efficiency (high and low RFI).

Heritability is a prerequisite for expression of the trait through selective breeding, and research in the beef industry has indicated that the RFI trait is moderately heritable ($h^2 = 0.14$ to 0.43) (McNaughton & Pryce, 2007). A heritability for RFI of $h^2 = 0.22$ was calculated in a study measuring feed utilisation in 417 growing dairy heifers (Korver et al., 1991), and a value of $h^2 = 0.19$ was calculated during lactation (van Arendonk et al., 1991). Recent calculations from dairy cows evaluated in Australia and New Zealand (including those contributing to this thesis) suggest heritabilities of $h^2 = 0.22$ in Australian heifers and $h^2 = 0.38$ in New Zealand heifers (Pryce et al., 2012). These heritabilities indicate that genetic selection for divergent RFI is possible.

Many factors are likely to affect feed utilisation by the animal, such as feed type, physiological status (growth rate, liveweight, lactation, reproduction), maturity, rumen function, efficiency of digestion and absorption, composition of gain, disease status, behaviour and the environment (climate) (Arthur et al., 2004; Waghorn & Dewhurst, 2007). Physiological processes associated with intake, digestion, metabolism, physical activity, and thermoregulation also appear to contribute to variation in RFI (Herd & Arthur, 2009). For example, in beef cattle, six physiological mechanisms accounted for 73% of the variation in RFI (Richardson & Herd, 2004; Figure 2.3). Other reports confirm these results (Basarab et al., 2003; Nkrumah et al., 2004). However, the biological mechanisms and processes for over a quarter of the variation in RFI are not understood (Herd, 2009; Herd & Arthur, 2009).

2.2.2 Measurement of residual feed intake

Calculation of RFI requires the measurement of intake and liveweight gain over a period of several weeks, so that the requirements of individuals can be determined and related to the population average. A regression equation is developed between feed intake, production (i.e., weight change) and metabolic liveweight ($LWT^{0.75}$) over the period of measurement, and the divergence of individuals from the regression enables RFI to be calculated. Although intakes of growing beef animals are commonly measured for 10 weeks, with liveweight measured fortnightly (Archer et al., 1997), estimated standard errors for different weighing

frequencies showed that this period can be reduced without affecting the accuracy of the RFI calculation if the frequency of liveweight measurements is increased (i.e., similar standard error for weighing fortnightly for 10 weeks as for weighing 3 times per week for 7 weeks) (Herd, 2009; Waghorn et al., 2012).

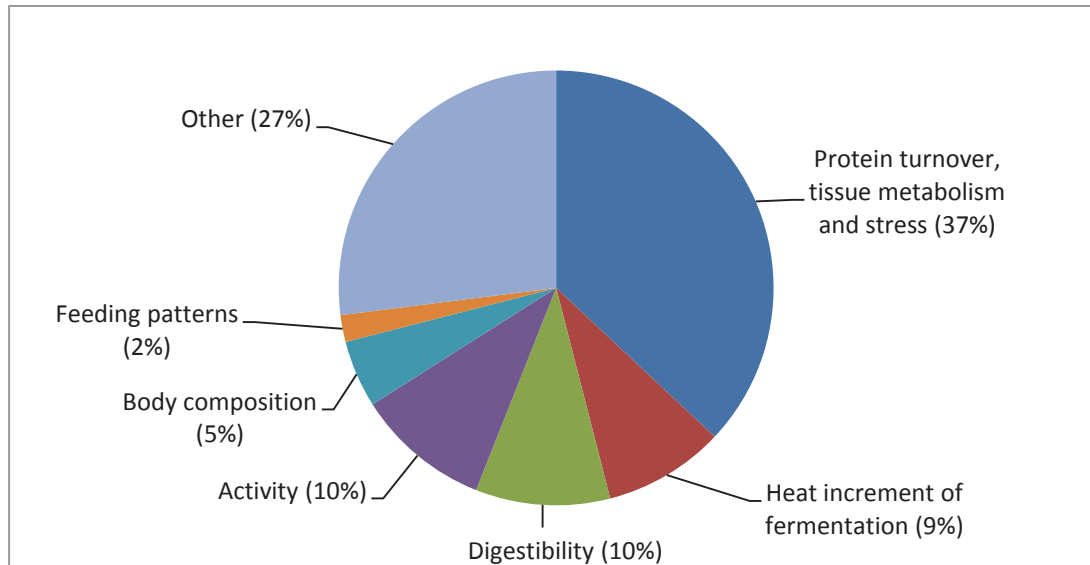


Figure 2.3: Proposed physiological mechanisms contributing to variation in residual feed intake in divergently selected beef cattle (from Richardson and Herd, 2004).

It is not possible to measure RFI from large numbers of animals fed fresh pasture in a confined feeding system. Nor can intakes of grazing cattle be measured accurately, especially without affecting grazing behaviour, which in turn may affect intake (Kolver, 2007). Intakes of grazing animals can be estimated using techniques such as alkane markers (Dove & Mayes, 1996), but this method is labour intensive and its accuracy is questionable (Waghorn et al., 2004). If the animals are confined and eat from feeders with electronic weight measurement, the cutting and feeding of large volumes of pasture is impractical and labour intensive (McNaughton & Pryce, 2007) and changes in pasture quality and moisture content prohibit accurate intake measurements (Waghorn, 2009). Therefore, feeds with a higher DM content are used (e.g., silages or mixed silages with grain), but composition and digestibility of these are quite different to pasture, making results less applicable to animals primarily grazing on fresh pastures. It is important that a feed with similar physical characteristics to those of the animal's lifetime diet is used to determine RFI (Durunna et al., 2011a; Waghorn et al., 2012).

Because intake data must be collected from individual animals for an extended period of time, electronic recording systems are often used to automatically collect these data in a feedlot-type situation. Most of these systems (e.g., INSENTEC, Marknesse, Holland; GrowSafe System Ltd., Airdrie, Alberta, Canada) consist of feed bins mounted on load cells (scales) which record weights continuously. Animals are identified by an electronic tag or transponder usually worn in the ear, allowing changes in feed bin weights to be attributed to the intakes of individual animals (von Keyserlingk & Weary, 2010). In addition to recording intakes of individuals over several weeks, this system can provide continuous information about the time at which individuals eat, their intake rates, and the frequency, size, and duration of meals taken from a feeder within a pen housing several animals (Mendes et al., 2011).

Large quantities of data are collected, and there must be a screening process to ensure all values are valid. Errors may be a consequence of system malfunctioning or animal interference (Casey et al., 2005) as well as environmental factors associated with damp or dusty conditions, wind, or animal movement. Criteria must be developed to detect and manage errors (Casey et al., 2005), usually by removing incorrect values.

Systems for determining RFI are specific to experimental needs, but typically intakes are measured from as many animals as the facilities can accommodate without limiting access of animals to feed (under *ad libitum* regimens). The layout of the facility will influence stocking density and number of animals per feeder which, in turn, will influence feeding behaviour and intake (Pompe et al., 2007; Waghorn & Dewhurst, 2007). A suitable feed must be provided so animals can achieve their daily feed requirements and meet their nutritional needs in a confined system, and the feed should be similar to that fed in a commercial environment. The breed, size and age of the animals will influence grouping and stocking density and the recording system will affect the type and format of data collected and the ease of checking that data daily.

The number of dairy cows that can be measured for RFI is limited because of their high intakes (limiting numbers that can be fed from each feeder), and RFI can also be difficult to calculate in lactating dairy cows because of mobilisation of body tissue. Body weight change may reflect changes in muscle or fat, which differ in their energy yields during mobilisation (Holmes et al., 2002), and also reflect tissue synthesis, making calculation of RFI less accurate

in lactating animals than in growing animals (Pryce et al., 2007). Hence, measurements of RFI are usually done on young, growing animals as they do not have the dynamic changes in energy balance associated with lactation in older cows (McNaughton & Pryce, 2007).

Determination of RFI in growing dairy animals and its application to lactating dairy cows has been justified by the biochemical bases of RFI, and because a significant proportion of feed energy is used for maintenance, even during growth and lactation. In mature dairy cows, about 70% of energy intake is used for maintenance and product synthesis, and only 30% is retained in the product (Waghorn et al., 2012). Differences in energy requirements will apply to both maintenance and product synthesis, but not to the energy in the product, in both young and mature animals (Waghorn et al., 2012). Therefore, it is expected that efficiency for liveweight gain will equate to efficiency for lactation, and there are significant opportunities for selection of efficient (low-RFI) dairy cattle (Nieuwhof et al., 1992; Waghorn, 2009; Waghorn et al., 2012).

The costs and practicality of measuring RFI in large numbers of animals has led to the pursuit of genetic markers for the RFI trait using a subset of the dairy cow population that are representative of the national herd (Pitchford, 2004; McNaughton & Pryce, 2007). A genotype test would enable selection of efficient individuals, but this is only possible if large numbers of animals (approximately 2000) are used to determine RFI and enable marker identification (Pryce et al., 2007). This work is currently underway, and genetic markers will need to be validated once identified.

Other phenotypic traits that are associated with RFI may be used as indicators of RFI. These traits have the advantages of being cheaper and easier to measure than the standard feedlot test. Traits that have been suggested as potential predictors of RFI include blood hormone concentrations, such as Insulin-like Growth Factor I, temperament, and feeding behaviour (Lancaster, 2008; Lancaster et al., 2009; Rolfe et al., 2011). Feeding behaviour can mediate changes in feed intake, and therefore may be important for RFI.

2.2.3 Value of the residual feed intake trait

The RFI trait has the potential to produce significant economic benefits for dairy farmers through a reduction in feed costs while maintaining the same level of production. This is because feed accounts for a large proportion of expenses on New Zealand dairy farms

(Waghorn & Hegarty, 2011), so improved efficiency could have a substantial impact on farmer profit. There may be additional advantages associated with management of dairy herds due to the lower feed requirements of efficient animals compared with untested or inefficient animals, such as increasing stocking rates or keeping the same stocking rate but requiring less feed.

The economic benefits of the RFI trait for the dairy industry will be substantial if the predicted 1-3% gains in efficiency of the national herd can be achieved (Waghorn, 2009). This would allow an additional 40,000 to 120,000 cows to be fed on the same amount of feed. The economic value of the RFI trait for the 2.4 million beef feedlot cattle in Alberta was calculated at \$53-109 million per annum and a larger benefit may be expected for cow/calf operations (Basarab, 2005). The price paid for efficient bulls was \$4338 compared with \$2908 for untested bulls (Basarab et al., 2005). Use of bulls selected for feed efficiency was estimated to increase profitability in beef operations by 9-33% (Archer et al., 2004), and the value of feed efficiency for pastoral beef production was calculated to be \$8.76 per animal (Arthur & Herd, 2005). These figures from the beef industry indicate the significant economic benefits of the RFI trait.

The RFI trait should benefit the genetic improvement of New Zealand dairy cows. Identification of efficient animals through a genotype test or an easily measured correlated trait will enable rapid selection (McNaughton & Pryce, 2007), and could lead to removal of inefficient animals (Kolver, 2007). Because of the extensive use of artificial insemination (73% of cows in New Zealand are bred to artificial insemination, LIC and DairyNZ, 2011), the benefits of efficient bulls can be dispersed quickly throughout the national herd, which will improve the New Zealand dairy industry's international competitiveness. This benefit will also flow into the New Zealand beef industry, as nearly 65% of beef production had a dairy origin in 2003 (Beeby, 2003). This calculation is based on a number of assumptions, but current estimates suggest the dairy industry supplied 46% of export beef in 2010-11, with almost half of that being dairy bulls (Rob Davison, Beef and Lamb NZ, personal communication). RFI is not identified in present selection indices in the dairy industry, but the Australian beef industry now has estimated breeding values for RFI (Kolver, 2007). It may be possible to include RFI in future genetic improvement programs and selection indices. Thus, the gains to be made from the RFI trait are widespread and valuable.

Selection for RFI will reduce feed requirements, but it is equally important to ensure efficient animals have no associated adverse effects (Rauw et al., 1998; Pitchford, 2004; Waghorn & Dewhurst, 2007). It would be unprofitable to improve efficiency while having a detrimental effect on another trait such as fertility or behaviour. Likewise, efficient animals must have at least similar or greater milk production than average or inefficient animals (Waghorn, 2009).

Currently there is little information on the relationship between RFI and health, fertility, and behavioural traits (Pryce et al., 2007). Knowledge of the behaviour and associative traits of efficient animals is necessary to ensure selected individuals have similar or better health and welfare than unselected or inefficient animals (Rauw et al., 1998). Also, an understanding of the behavioural characteristics of efficient animals may aid in their management if they become dominant in the national dairy herd, and this information could be used to reduce stress and improve productivity (Lamb, 1975).

2.3 Behaviour

2.3.1 Concept

Behaviour is the physical response or reaction to internal and external stimuli (Phillips, 2002). Put simply, behaviour is what living beings do. As stated by Lehner (1996), “animals are always behaving. They perform a continuous stream of behaviour from the moment when movement can first be detected in the embryo until their death” (p. 19). Behaviour is elicited by endogenous (animal’s internal environment) and exogenous (external environment) stimuli (Broom & Fraser, 2007).

It is thought that behaviour is influenced by genotype, environment (including experience), the interaction between genotype and environment, and the animal’s anatomy and physiological mechanisms (Lehner, 1996; Ryan & Wilczynski, 2011). The propensity to express behaviour has some genetic components. This is evident in animals that are selectively bred, such as dogs that are bred for specific tasks like herding livestock. The genotype provides the blueprints for the animal’s physiology and anatomy (the nervous system is of particular relevance to the expression of behaviour) (Lehner, 1996), and the biotic and abiotic environment influences behavioural development and expression through injury, disease, climate, and nutrition. Genotype and environment interact closely, making it

difficult to ascribe the origin and development of a particular behaviour to either (Broom & Fraser, 2007).

Behaviour can be divided into a number of different types based on function, such as feeding behaviour, social behaviour, reproductive behaviour, maternal behaviour, learned behaviour, human-animal interaction, or normal activity profiles and patterns (Schütz & Pajor, 2001). This review will focus on feeding behaviour, social dominance, activity and their relationships with RFI in growing dairy heifers.

2.3.2 Feeding behaviour

Feeding behaviour encompasses the activities associated with consuming feed. A cow's daily intake can be divided into several smaller discrete events or "meals" occurring over the course of the day which are separated by periods of no or little feeding activity. This feeding behaviour can be described in different ways, such as intake, time spent feeding, number and duration of meals, and feeding rate (Albright, 1993; Schütz & Pajor, 2001; von Keyserlingk & Weary, 2010). A variety of different factors are known to influence the feeding behaviour of dairy cattle. These include: time of day, feeding system, competition, diet composition, and rate of digestion. Each of these will be considered in more detail.

Cattle feeding behaviour varies over 24 h, and feeding activity is often increased at dawn and dusk (Albright, 1993; Shabi et al., 2005) as well as after provision of fresh feed and upon return from milking (DeVries et al., 2003a; DeVries & von Keyserlingk, 2005). Most feeding occurs during daylight; little feeding occurs at night during darkness (Kyriazakis, 1997; DeVries et al., 2005). For example, in an early study conducted under New Zealand grazing conditions, almost 85% of the total grazing time occurred during daylight hours (Hancock, 1950). Recent research confirmed this, with 73-86% of grazing activity occurring during daylight, and peaks in feeding activity after morning and afternoon milking (Sheahan et al., 2011). Sunrise and sunset appear to be major stimuli for the beginning and cessation of grazing, respectively (Sheahan et al., 2011).

Feeding behaviour is dependent on the feeding system. In a grazing environment, the feeding behaviour of a group of cows is often highly synchronised, with all animals grazing after being given access to a new paddock. A high proportion of pasture is eaten to achieve good profitability or high pasture quality (Waghorn & Clark, 2004), and competition is

intensified by the scarcity of the resource. This necessitates a rapid intake, and animals which arrive later to the pasture or are slow eaters are liable to have a lower quality diet that includes a higher proportion of stem, sheath, dead matter and contaminants compared with those given first access to pasture (Waghorn & Clark, 2004).

In free stall barns, the design of the feed barrier and the space available for cows in these systems can affect feeding and social behaviour (DeVries et al., 2004; DeVries & von Keyserlingk, 2006; Huzzey et al., 2006; Mentink & Cook, 2006). More feeder space will allow more animals to feed simultaneously and increase feeding times. Other feeding systems limit feed access to only one or two animals, which prevents synchrony of feeding behaviour, altering feeding patterns, and may cause increased competition for feed (Gonzalez et al., 2008a).

Gaining access to feed is a high priority for cattle (Val-Laillet et al., 2008a) and competition for feed can alter feeding behaviour. This can occur through increased feeding rates and reduced intakes, particularly in subordinate or lower-ranked animals (von Keyserlingk & Weary, 2010), and these animals will often spend less time eating than dominant or higher-ranked animals (Manson & Appleby, 1990). Competition has been reported to reduce feeding time by 10% and change meal patterns of cattle, resulting in 9% fewer meals than cattle feeding without competition (DeVries & von Keyserlingk, 2009). To maintain dry matter intake in competitive situations, some animals may increase their eating rate or shift feeding times to later in the day (Harb et al., 1985; Gonzalez et al., 2008b; DeVries & von Keyserlingk, 2009). Competition is discussed further in section 2.3.3.

Feeding behaviour is also influenced by the diet. The length and size of feed particles and their composition may influence intake and feeding behaviour (Zebeli et al., 2009; Greter & DeVries, 2011). For example, addition of fibrous feeds with a long particle length can result in selection against these fractions (Bae et al., 1981; Greter et al., 2008; Zebeli et al., 2009). Also, when beef bulls were fed a diet with low energy density they ate for significantly longer per meal (118 vs 85 min) and ate more often (8.7 vs 7.7 meals/day) than bulls fed an energy-dense diet (Lancaster et al., 2009). However, reports concerning diet type and feeding frequency are inconsistent, with some suggestions of increasing frequency with reduced feed particle size (Zebeli et al., 2009) while Durunna et al. (2011b) reported the contrary and Miron et al. (2004) found no difference in feeding frequency between two different diets.

Other dietary factors affecting feeding include moisture content. Fresh forage diets require a large quantity of material to be consumed, but with a relatively low DM intake (Waghorn, 2002). The moisture content of fresh forages is almost double that of TMR (70-90% vs 40-50%), and intakes on fresh forage are typically 15-50% lower than on TMR diets (Waghorn, 2002; Waghorn & Clark, 2004). Cattle must consume a large quantity of fresh forage (>120 kg wet matter of high quality pasture vs 40 kg wet matter of TMR) to achieve high DM intakes (Waghorn et al., 2007). This has implications for feeding behaviour through increased feeding duration and slower DM intake rates with high-moisture feeds compared with low-moisture feeds (e.g., TMR).

Rate of digestion has also been suggested as a factor affecting feeding behaviour. The amount of digesta in the reticulo-rumen and the rate at which feed is broken down by chewing may influence feeding-related activities and dry matter intake (Lindström & Redbo, 2000; Zebeli et al., 2009). Furthermore, the timing and rate of eating can influence rumen function by changing rumen buffering and pH, which in turn can affect cow health, especially when grain is fed (DeVries, 2010).

It is clear that feeding behaviour is influenced by many factors, but provided all animals are treated in the same way, it is possible to compare behaviour within a group. Feeding behaviour is important because changes in feed intake can be mediated by changes in feeding behaviour, and changes in feeding behaviour can be a useful indicator of cow health (Broom & Fraser, 2007; Gonzalez et al., 2008c; Weary et al., 2009; von Keyserlingk & Weary, 2010).

2.3.3 Social behaviour and dominance

Cattle live in groups and engage in social behaviour (Estevez et al., 2007). A characteristic of social groups is some type of social structure or organisation (Broom & Fraser, 2007), which can take various forms depending on the species. Cattle tend to establish hierarchies in which individuals are ranked or have a certain status in relation to other individuals in the group, i.e., dominant or subordinate to another. Hierarchies are usually formed through dominance relationships, determined by animals in the group engaging in agonistic behaviour, which includes “all forms of behaviour by an animal associated with conflict with

another animal” (Broom & Fraser 2007, p. 74). This behaviour is typically more intense when the group is first formed and the hierarchy is being established (Langbein & Puppe, 2004).

Many different definitions of dominance have been used, and there is no consensus on its definition and measurement. Drews (1993) reviewed definitions of dominance and suggested:

“Dominance is an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and that of the loser subordinate.” (p. 308).

This definition implies that dominance is a characteristic of a pair of animals, called a dyad, rather than of the individual. It also requires that animals display agonistic behaviours. Dominance relationships in a dyad may be one-way or two-way (bi-directional), and hierarchies may be linear (e.g., cow A is dominant over B, cow B is dominant over C, and A is dominant over C) or non-linear i.e., be intransitive and contain non-linear circular triads (e.g., cow A is dominant over B, cow B is dominant over C, and C is dominant over A) (Val-Laillet et al., 2008b).

Dominance, as defined above, can be quantified by recording all agonistic interactions between pairs of animals in a group into a matrix with winners of interactions along one side, and losers along the other. However, there is lack of consensus on methods for determining a dominance relationship in a dyad. Some methods require that an animal wins only one more interaction than it loses in order to be considered dominant (de Vries, 1995, 1998). Other methods require the ratio of wins to losses to be statistically different, through use of a binomial sign test or other objective statistical measure (Langbein & Puppe, 2004). This may provide the most accurate test of dominance relationships because a subordinate animal may win one more interaction than it lost over a dominant animal in some circumstances (e.g., more strongly motivated by hunger; Val-Laillet et al., 2008b). However, statistical tests may also lead to a number of interactions being non-significant, or “tied,” in which neither animal in a dyad is considered dominant over the other. Both methods of determining dominance were used in the present study in order to compare their results.

From the dominance relationships, various measures or indices of dominance can be calculated. Indices may be based on the number of animals dominated by an individual (Mendl et al., 1992; Ketelaar-de Lauwere et al., 1996), the number of successful interactions or displacements (Rutter et al., 1987; Zobel et al., 2011), or may rate animals using a complicated method based on the sequence in which interactions occur (e.g., Elo-rating; Neumann et al., 2011). Choice of index will depend on the aim of the study, the research questions to be answered, the characteristics of the species being investigated, and the specific situation in which the group is being observed. For example, a group that has been together for a long time will display less frequent and more subtle agonistic behaviour than a group that has only just been formed (Langbein & Puppe, 2004). Hence, using the number of successful interactions or displacements as the measure of dominance may not truly represent the dominance relationships in the group, as animals of a particular status (i.e., dominant or subordinate) may not engage in such behaviours as frequently once the hierarchy has been established.

Cattle living in groups must compete for access to limited resources such as feed, space or shelter. The forced proximity of animals kept in pens, which results in limitations on space, may increase the frequency and intensity of agonistic and aggressive interactions (Huzzey et al., 2006; Estevez et al., 2007). This was illustrated in a study showing that increasing feeder space from 0.64 to 0.92 m/cow reduced the frequency of aggressive interactions, as well as increasing feeding time (DeVries & von Keyserlingk, 2006). Likewise, when space enabling access to feed was doubled from 0.5 m to 1.0 m per cow, the number of aggressive interactions while feeding reduced by half. The reduction in aggression resulted in a 24% increase in feeding activity at peak feeding times, and this increased feeding was especially noticeable for subordinate animals (DeVries et al., 2004). Even animal position in a pen can be affected by hierarchy, and will in part depend on the location of food, water and resting places, with dominant individuals occupying the most advantageous positions (Estevez et al., 2007).

Clumped resources, such as one feeder for a group of cattle, increases competition and is likely to result in increased agonistic interactions (Estevez et al., 2007). As mentioned earlier, competition changes cattle behaviour. Dominant animals may monopolise access to feed (Estevez et al., 2007), causing subordinate or lower-ranked animals to alter their behaviour and feed at less desirable times (Lamb, 1975; Huzzey et al., 2006; Gibbons et al., 2009). For

example, beef heifers in a highly competitive environment varied in their competitive strategies for access to feed, with positive associations between the number of successful agonistic interactions displayed (indicative of dominance) and dry matter intake ($r^2 = 0.26$), feeding duration ($r^2 = 0.45$), and feeding frequency ($r^2 = 0.49$) (Zobel et al., 2011). Separating dominant and subordinate animals can improve production at pasture or in housed dairy systems where feeding is competitive (Phillips & Rind, 2002). An example of this is separating heifers and cows into different herds.

Competition can affect animal health and performance. Increasing competition for concentrate between heifers resulted in lower rumen pH, greater lactate concentration, and more abscessed livers compared with heifers feeding in an uncompetitive situation (Gonzalez et al., 2008b). The shorter eating times, rapid intakes, and large meal sizes of cattle fed an energy-dense diet in competitive feeding situations can cause reduced rumen pH, which can potentially put cattle at increased risk of ruminal acidosis (DeVries, 2010). Absence of competition allows longer feeding times, which is likely to increase total salivary secretion and lessen the decline in pH, which will benefit rumen fermentation and fibre degradation (Owens et al., 1998; Beauchemin et al., 2008). Heifers fed a ration with higher proportions of forage are less likely to suffer these effects.

Competition may also increase the day-to-day variability in feeding patterns, body weight, and liveweight gain (Longenbach et al., 1999; Gonzalez et al., 2008b; DeVries & von Keyserlingk, 2009). This variability is likely due to higher-ranked animals dominating access to feed and possibly sorting the feed, leaving a feed of lower nutritive quality for the subordinate animals (DeVries, 2010). Competition can have a negative effect on cattle health and performance, especially for lower-ranked or subordinate animals.

2.3.4 Other behaviour and activity patterns

Other behaviours of dairy cattle include activities such as standing, lying, drinking, or locomotion (i.e., walking, movement). Some of these behaviours are highly valued by dairy cattle and appear to be important for normal function. For example, dairy cattle have a strong need to spend a large proportion of time lying, and if they are prevented from doing this, they will give up other activities in order to get that rest (Metz, 1985; Jensen et al., 2005).

Normal activity profiles for dairy cattle depend on the management system, but profiles tend to include lying for an average of 13 hours/day for calves (Weiguo & Phillips, 1991) and 7 to 13 hours/day for lactating dairy cattle, much of that time at night (Arave & Walters, 1980; Thorne et al., 2003; Jensen et al., 2005; Tucker, 2009). Dairy cattle in pastoral systems can spend up to 10 hours per day grazing, while cattle fed in barns spend 4-6 hours per day feeding, or even less on high concentrate diets (Thorne et al., 2003; Gonzalez et al., 2008a; Tucker, 2009). The remainder of the day is spent standing idly and typically 6-8 hours per day is spent ruminating, depending on feed type and availability (Tucker, 2009). Activity is also affected by climate and weather, with more time spent standing and less time spent lying in warm weather (Tucker et al., 2008).

Drinking behaviour depends not only on climate and weather, but also on factors such as time of day, feed type, and physiological status e.g., lactation. Dairy cows fed pasture in late lactation drank 2.4 times/24 h on average, and most drinking occurred during daylight hours (Jago et al., 2005). Cows fed a TMR had greater water intakes than cows grazing grass and were more likely to drink at night (Jago et al., 2005). The high water intakes of cows fed TMR is probably a consequence of the higher DM content (50-60%) of the TMR compared with 10-30% for fresh pasture.

Activities such as standing, walking, and ruminating have an energetic cost, which must be met by the animal's energy intake. An animal that spends more time walking will partition more energy to that activity, meaning that less energy is available for milk production, growth, or other physiological processes. Conversely, an animal that spends more time lying may conserve more energy, thus enabling more energy to be partitioned to production. Therefore, different levels of activity may contribute to differences in RFI.

2.4 RFI and behaviour

2.4.1 Basis for association between RFI and behaviour

Differences in RFI between animals could be partly attributable to behaviour, including effects associated with feeding and general activity. As noted above, there are energetic costs associated with feeding activity, such as time spent feeding and rate of eating; therefore differences in feeding behaviour and activity may contribute to differing energetic efficiency between animals (Richardson & Herd, 2004; Kelly et al., 2010). Herd and Arthur

(2009) suggested that differences in feeding behaviour of beef cattle accounted for only 2% of variation in energetic efficiency, although Lancaster et al. (2009) reported that feed-related activities accounted for 35% of variation in intake, which is a component of RFI. In studies of beef cattle, efficient animals exhibited less feeding-related activity than inefficient animals and were likely to use less energy for feeding (Nkrumah et al., 2007; Kelly et al., 2010; Durunna et al., 2011b).

Social dominance and competition have been shown to affect animal performance (DeVries, 2010) due to effects on intake, but also indicating an energetic cost of the behaviours and potential stress associated with maintaining hierarchies and interacting with animals of different status within the group. Stress has been suggested as a contributor to divergence in RFI, with high and low RFI animals differing in their susceptibility to stress (i.e., likelihood of being affected by particular stressors) (Richardson & Herd, 2004). Variation in the perception of and response to potential stressors, such as agonistic interactions, might influence energy expenditure and therefore RFI. These relationships may differ with the animal's environment, and energetic expenditure associated with agonistic behaviour may be greater for cows held in confinement compared with those grazing pasture, where there is more opportunity to avoid each other.

General locomotive activity could account for 10% of the variation in RFI (Richardson & Herd, 2004), but the energetic cost associated with different activities also depends on the environment in which animals are farmed. For example, grazing dairy cattle will expend more energy on walking than housed cattle. Compared with lying, standing has an additional energetic cost of 10 kilojoules (kJ)/kg liveweight (LWT) when measured over 24 h, and walking has an energetic cost of 30.6 kJ/kilometre per kg LWT in ruminants (CSIRO, 2007). Animals that expend less energy on these activities may use their energy more efficiently for growth or production.

2.4.2 Previous research on associations between RFI and behaviour

Little research has been published regarding the association between RFI and behaviour in dairy cattle, but this has been investigated in beef cattle during the last ten years. Studies with beef cattle suggested that the number of meals per 24 hours accounted for 3-20% of the variation in RFI (Robinson & Oddy, 2004; Nkrumah et al., 2007; Lancaster et al., 2009; Kelly et

al., 2010), and intake (a component of RFI) accounted for 33-66% of the variation (Robinson & Oddy, 2004; Lancaster et al., 2009).

There was also great variation between studies in the contribution of other traits to explaining RFI in beef cattle, such as time spent feeding per day (3-24%) and feeding rate (2-19%) (Robinson & Oddy, 2004; Nkrumah et al., 2007; Lancaster et al., 2009; Kelly et al., 2010; Montanholi et al., 2010), which suggests relationships may be weak. Meal duration (time spent feeding per meal) was negatively associated with RFI (efficient/low-RFI animals had longer meals than inefficient/high-RFI) in one beef study (Montanholi et al., 2010), but positively associated in another (Lancaster et al., 2009). A positive association was reported between meal size and RFI (efficient/low-RFI animals had smaller meals than inefficient/high-RFI) (Montanholi et al., 2010). The variable level of association between studies suggests other factors are affecting behaviour and RFI.

Most studies comparing extremes (i.e., divergent groups) in RFI in beef cattle showed that efficient animals had fewer meals (Nkrumah et al., 2006; Bingham et al., 2009; Kelly et al., 2010), although Dobos and Herd (2008) found no difference in the number of meals per day between efficient and inefficient animals. Most studies showed that efficient and inefficient animals spent a similar time eating (Dobos & Herd, 2008; Bingham et al., 2009; Kelly et al., 2010; Montanholi et al., 2010), except the study of Nkrumah et al. (2006) where efficient animals spent less time eating (and ate less) than inefficient steers. There is no consensus on the relationship between RFI and feeding rate, with some reports of slower eating by efficient animals than inefficient animals (Bingham et al., 2009; Kelly et al., 2010; Montanholi et al., 2010), whilst others found similar rates (Dobos & Herd, 2008; Golden et al., 2008).

Although published studies report conflicting results when relating feeding behaviour and RFI, most of these have been carried out with cattle in confinement and fed diets comprising different ratios of grain and silage. Different outcomes from published studies may be associated with experimental design, diet, and environment, and suggests that behaviour is sensitive to circumstances. The numbers of animals used, the facility or housing setup, the group size and density of the animals, and the diet fed have a large impact on feeding behaviour (Grant & Albright, 2001; Phillips, 2004; Huzzey et al., 2006).

Only one study investigated the association between RFI and feeding behaviour in confinement or grazing behaviour of beef cattle (Trujillo et al., 2011). Average daily eating, ruminating, and idling behaviour were similar for the efficient and inefficient beef calves in confinement, but mornings were characterised by more idling and less eating compared with the afternoon in both the efficient and inefficient groups. There were few differences between efficient and inefficient animals at grazing, except at midday when efficient animals were less likely to graze than the inefficient animals (Trujillo et al., 2011). The authors suggested that differences attributable to RFI may be expressed more strongly at grazing than in confinement because grazing is a more complex event, involving decisions by the animal relating to multiple variables, such as searching, selecting, and harvesting pasture as well as social and environmental conditions.

The relationship between RFI and status within the hierarchy (dominance) does not appear to have been explored, and little information has been published on the relationship between RFI and general activity patterns in cattle, despite its potential contribution to variation in RFI. Inefficient animals may be more excitable or easily stressed than efficient animals (Richardson & Herd, 2004), and this could affect social behaviour, activity, and energy expenditure. Research with poultry showed differing activity patterns between birds of divergent efficiency (Morrison & Lesson, 1978; Katle, 1991). Further research into this relationship in cattle is warranted.

Most published research investigating associations between RFI and cattle behaviour has been conducted with beef cattle. Furthermore, most studies were conducted in housed or feedlot systems with cattle fed concentrates or a TMR. Little research has been conducted on dairy cattle, or on cattle fed a forage as their complete diet.

2.5 Summary and purpose of the proposed study

RFI is an important trait, and selecting for this trait has the potential to provide productive and economic gains on dairy farms. However, identification of animals divergent in RFI involves expensive measurements and procedures that are impractical on a large scale. Other, more easily measured traits may provide indirect predictions of RFI status. A better understanding of the factors associated with RFI and predictors of efficiency in dairy cattle is needed to understand the mechanisms regulating efficiency (Nkrumah et al., 2007; Montanholi et al., 2010). Behaviour is associated with temperament, health, and energy

expenditure, and as well as contributing to divergence in RFI, may provide insights into the biological basis for the variation in RFI (Lancaster et al., 2009).

Very little is known about behaviour and RFI in dairy cattle. Several studies have investigated this relationship in beef cattle, showing variable associations between measures of feeding behaviour and RFI, and although not always consistent, many studies have reported differences in feeding behaviour between beef cattle with divergent efficiency (high and low RFI extremes). These differences may also apply to dairy cattle.

An understanding of the behaviour of dairy cows, and any relationships with RFI, could be used to improve animal management, for example by reducing competition between individuals and optimising the delivery and availability of feed (e.g., time of delivery, size and number of meals) to reduce stress and improve production. It is also important to understand the correlation between RFI and behaviour to ensure that negative or unprofitable traits, such as poor health or welfare, are not associated side effects of selection for efficient animals (Rauw et al., 1998).

The study reported in this thesis involved an analysis of feeding and behavioural data from young dairy heifers to determine relationships with RFI measured during growth. The objective of this study was to determine whether relationships exist between the feeding, dominance status, and activity behaviour and residual feed intake in young dairy heifers.

3. MATERIALS AND METHODS

3.1 Introduction

This study was part of a larger trial designed to identify animals that differ in the efficiency with which they use their feed for growth (RFI). The trial was the responsibility of DairyNZ, and was undertaken alongside similar research in Victoria, Australia (Geoffrey Gardiner Foundation). The trials (Taranaki, New Zealand and Victoria, Australia) utilised young (5-8 month) growing dairy heifers, and efficiency of feed utilisation was determined by measuring feed intakes and liveweight gain for at least 42 days. The measurements reported here were undertaken in Hawera, Taranaki, New Zealand in a purpose-built facility. A total of 1049 individuals in five groups (Cohorts 1-5) were recorded over a three year period. Most cohorts comprised approximately 220 animals distributed across 28 pens (8 animals/pen). Animals were fed lucerne (*Medicago sativa*) cubes imported from Canada.

Measurements of feeding behaviour were carried out using all cohorts and analysis was based on pens, cohorts, and all 1049 individuals. The behavioural characteristics were likely to be affected by the environment and pen design, and may also have been affected by treatment before entering the facility, so details of animals, their procurement and handling prior to efficiency measurements in the facility are summarised here. The facilities are described because the configuration of the pen, feed bin and race providing access to the feed bin are relevant to interpretation of data. The criteria for animal selection, breed, and all aspects of management were the same for all 1049 animals for which data were available.

A major challenge for this study was ensuring accuracy of measurements used in the analyses. This was related mainly to measurement of feed intakes, and although most data appeared accurate, care was taken to check values and ensure incorrect data were removed prior to analyses. Criteria were developed to screen data, and these are described together with a brief overview of the measurement and manipulation of feed weights to achieve a manageable dataset for each animal. Liveweights of animals were also measured, but there were relatively few of these values and they were easily checked. Feed intakes and liveweights were used to determine average daily gain (ADG) and RFI, which have been included in the evaluation and analysis of animal behaviour.

Methods of analysis of feeding behaviour were developed using data collected from the second of the five cohorts of growing heifers (because this was the first full complement of animals), and then applied to the other four cohorts and related to RFI and ADG. As well as feeding behaviour, dominance relationships and activity (time budgets) were measured on a subset of animals in the fifth cohort, and these were related to RFI, ADG, and feeding behaviour to determine if these variables were associated.

3.2 Animals

The animals used in the main trial were procured from 2007-2009 through contracts between Livestock Improvement Corporation (LIC) and Waikato dairy farmers. Holstein-Friesian heifer calves of known parentage (15/16th Holstein-Friesian or higher) and high genetic merit (BW 154, PW 135 or better) were purchased, collected at 4 to 10 days of age from dairy farms in the Waikato, and transported to a commercial calf rearer (M & M Bocock, 183 Parklands Road, Te Awamutu, Waikato, New Zealand) for rearing until weaning. All procedures were approved by the Ruakura Animal Ethics Committee (AEC 11385).

Upon arrival at the rearing facility, calf liveweight, height, length, and girth measurements were recorded and each calf was given a unique electronic identification (EID) ear tag. Blood and tissue samples were collected from each animal to test parentage and check for disease (bovine viral diarrhoea). Calves were fed colostrum and reared on milk and calf meal according to normal farm practice. Milk was initially fed twice daily, then reduced to once daily and milk quantity was gradually reduced from five weeks of age until weaning at approximately 10 weeks of age.

Calves were weighed weekly and vaccinated at 5 weeks of age to provide protection against clostridial diseases. At 5-8 months, they were vaccinated against Leptospirosis and drenched with Oxfen C+ and Tempor (Merial Ancare, Auckland, New Zealand). Gastro-intestinal parasitism was determined from faecal eggs counts taken from a subsample of calves at 10 weeks of age, and all calves received anthelmintic drench when egg counts exceeded 1500/g faeces. Any animals that were unsuitable for the trial (e.g., failed parentage or sick) were not used. After weaning, when the calves reached 95 kg liveweight they were transported to a grazier (Hawke's Bay) and remained as a single group. At about 5-7 months of age, they were transported to the Hawera facility for the trial, and upon completion of measurements at the facility, they were returned to the same grazier and managed as one group.

3.3 The feeding facility at Hawera

Residual feed intake of the dairy heifers was measured in a purpose-built outdoor feeding facility at the Westpac Taranaki Agricultural Research Station in Hawera, New Zealand (Figure 3.1). The facility consisted of 28 pens (each 42 m², housing eight animals) configured in four rows of seven, opening to two races (Figures 3.2 and 3.3; Appendix I, Section 7.1.1, Figures 7.1-7.2). Pens had a concrete apron (12 m²) and post peeling bedding to provide good drainage. Pen railings were steel pipe, with one wall of solid timber which provided wind protection. Shade cloth was attached to the timber wall to provide shelter from the sun (Figure 3.1). The front of the each pen, on the concrete area, comprised two gates, a water trough and feed bin. Gates between the pens could be opened so that animals could be confined onto the concrete area whilst soiled bedding was being removed and clean bedding added when needed (see Appendix I, Section 7.1.1, Figure 7.3). A ball hanging from a chain attached to the side of the pen was provided as a toy to alleviate boredom in the animals.



Figure 3.1: The outdoor feeding facility at the Westpac Taranaki Agricultural Research Station in Hawera, New Zealand. Note solid walls and shade cloth for wind and sun protection.



Figure 3.2: View of one of the races and a row of pens, with a feed bin and set of double gates per pen.

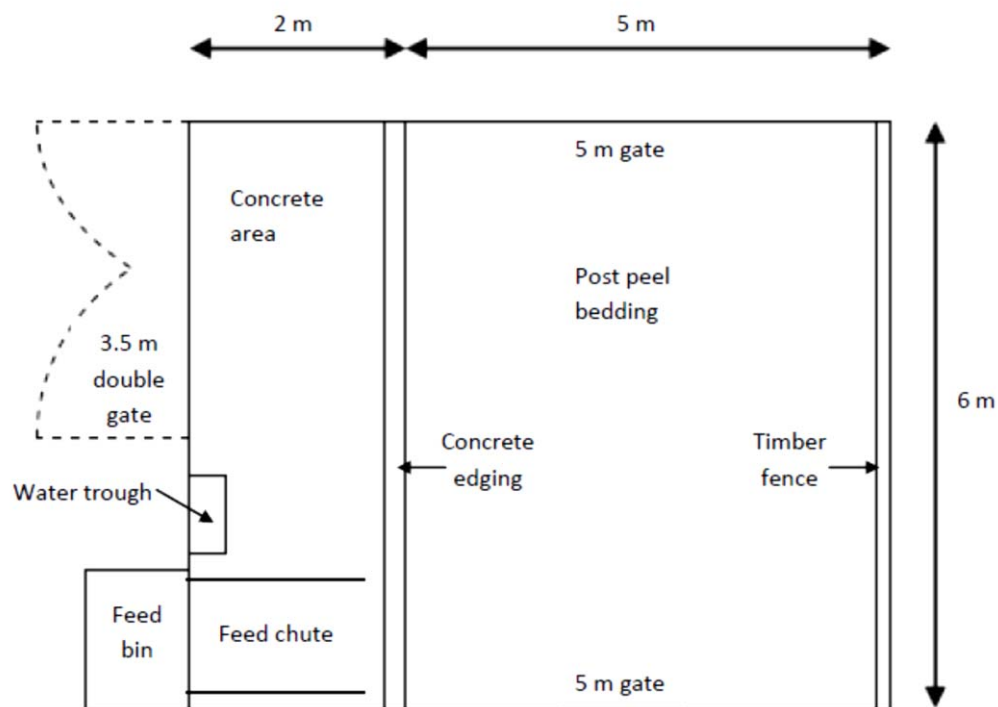


Figure 3.3: Diagram of a pen. Not to scale.

Each pen had one feed bin located outside the front corner of the pen (Figure 3.3) and an EID reader was mounted above each bin. The feed bins, designed and developed for this trial, were manufactured of moulded polythene by Industrial Technical Solutions Ltd, Tauranga, New Zealand, and measured 90 cm high x 90 cm wide x 85 cm deep (Appendix I, Section 7.1.1, Figure 7.4). The base of the bin was 65 x 65 cm and was positioned on a platform over four load cells to enable continuous weighing. A polycarbonate lid and plywood sides around the feed bin shielded it from wind and prevented water entry, which would affect bin weight measurements (Figure 3.4). Access to the feed bin was via a hole in a 22 mm thick plywood sheet that allowed an animal to put its head through to eat (Figure 3.5). A chute leading to the feed bin (2 m length) had adjustable sides, so that only one animal could access the bin at a time (Appendix I, Section 7.1.1, Figure 7.5).



Figure 3.4: The feed bin is outside the pen at the facility, and the sides and lid minimise effects of weather on bin weight measurements. The box to the left houses the electronics that log the feed bin weight and animal EID.



Figure 3.5: An animal entering the feed bin through the access hole.

3.4 Trial design to measure RFI

The feeding facility was built in 2007/08 and the trial commenced in March 2008. A total of five cohorts of weaner dairy heifers were evaluated; one in 2008, two in 2009, and two in 2010 (Table 3.1). The analyses presented here were performed initially on Cohort 2, and most of these analyses were then applied to the other cohorts. Cohort 2 was chosen for initial analyses as this was the first full complement of animals, and cohorts 3-5 had not completed their time in the facility when analyses commenced.

Table 3.1: Number of animals and trial dates for each cohort evaluated in the facility at Hawera.

	Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 5
Number of animals	164	219	219	223	224
Trial start date	18/4/2008	1/2/2009	9/4/2009	22/1/2010	1/4/2010
Trial end date	30/5/2008	19/3/2009	28/5/2009	11/3/2010	20/5/2010

The animals were placed in the facility for an 11-day adaptation period, followed by at least 42 days of measurement during the test period. Prior to entering the pens, they were offered lucerne cubes (Kapt-al Grain & Storage Ltd, Vancouver, British Columbia, Canada) for four days while grazing pasture to allow them to become accustomed to the cubes. Lucerne cubes (22 mm side) were fed as a sole diet during both the adaptation and test period because they were easily managed and had a consistent composition (Table 3.2). Cube composition was analysed by near infrared reflectance spectroscopy (FeedTECH, AgResearch, Palmerston North, New Zealand) and was similar between years. Lucerne was chosen because it is a forage and therefore more relevant to grazed pasture than diets containing grain. Most animals adapted to the cube diet with ease, with some eating within 10 minutes of entering the pens. Any animals not eating from the bins within the first day were given exclusive access to the feed bin and confined in close proximity of the bin to allow them time and uninhibited access to become accustomed to feeding from the bin.

Table 3.2: Mean ($\pm$ standard deviation) composition and predicted metabolisable energy content* of the lucerne cubes fed to the five cohorts of calves.

Chemical component	Mean $\pm$ SD
Dry matter (DM), %	84.6 $\pm$ 1.11
Crude protein, %	18.8 $\pm$ 1.30
Acid detergent fibre, %	28.8 $\pm$ 1.54
Neutral detergent fibre, %	46.3 $\pm$ 4.37
Predicted organic matter digestibility, %	65.9 $\pm$ 2.31
Metabolisable energy, megajoules/kg DM	9.1 $\pm$ 0.43

*Analysed by FeedTECH, AgResearch, Palmerston North, New Zealand.

A pilot study conducted prior to this trial investigated the appropriate number of animals per feeder, and the effects of animal numbers on feeding time and intake. When two groups of heifers were kept at a density of six animals per feeder, the feeders were not fully occupied, indicating there was time to spare. Intakes did not change but animals spent longer eating when stocked at six animals per feeder compared with eight animals per feeder. These results gave confidence that animal intakes were not restricted, and justified the use of eight animals per feeder in the main trial. This was confirmed at the conclusion of Cohort 3, when some animals were retained in the facility for further testing but kept at a lower stocking density per feeder. Intakes were similar for both stocking densities.

During the adaptation and trial periods, the 28 feed bins were filled daily before 0930 h, taking approximately 30 minutes. Bins were filled to provide about 20% more than the expected intake to ensure feed did not run out. The feed bins were emptied and cleaned once a week. Animal access to the feed bins during filling was prevented by a chain placed across the end of the feed chute. Water was available *ad libitum* and a salt block (Dominion Salt Ltd, Mount Maunganui, New Zealand) was placed in each pen to compensate for the low sodium content of the lucerne cubes.

Animals were visually checked daily and feed intakes monitored to ensure all were eating and had good welfare. As well as the intake measurements, individual liveweights were measured three times a week to determine daily gain using a commercial walk-over weigher with a Gallagher SmartScale 500 data collector and EID reader (Smartreader HR1, Gallagher Ltd, Hamilton, New Zealand). A total of 1049 animals were successfully evaluated (Table 3.1) in the trial, and only eight did not adapt to the diet. These animals were removed prior to the start of measurements.

3.5 Electronic recording system

The function and accuracy of data acquisition, and the care taken to ensure data were correct, were important components of this study. Details of data measurement, file structure and screening are presented because the procedures ensured the values used for analysis of feed intake and animal behaviour were robust and reliable.

An electronic system developed by Gallagher Ltd, Hamilton, New Zealand was used to record the intake and identity of animals eating from each of the 28 bins (Figure 3.4). An EID reader (G03103 R series EID reader, Gallagher Ltd, Hamilton), positioned over the feed bin, identified individual animals by their unique EID ear tag as they put their head into the feed bin. Other EID tags were used to identify individual bins when filling. The feed bins were each positioned on four load cells and the weight of the bin was measured 50 times per second, and averaged every second (G01100 SmartScale 300/400 weigh scale, Gallagher Ltd, Hamilton). Intake was calculated from changes in feed bin weight at each feeding event for individual animals. Weighing accuracy for individual feeding events was ± 20 grams.

As well as feed weights, the time that individuals ate from the feed bin was recorded, allowing quantification of time spent eating per day and per feeding event (described in section 3.7; Table 3.3). The bin weight and EID data from all 28 feed bins were logged at one-second intervals onto two computers by purpose-built software. Data were recorded in CSV (comma separated value) files with four file types or levels (Levels 1, 2, 3, and 4). A new Level 1 file was created every hour which contained records of the date, time, bin number, EID and bin weight every second for every bin. Level 2 files summarised the Level 1 data by recording for only the first 20 seconds of each meal to show meal start times. Level 3 files were daily summaries of the individual feeding events for each animal and each pen (i.e., one line logged per feeding event/meal). Data in Level 3 files were the date, start and end time of the feeding event (i.e., meal), bin number, EID, start and end weight of the bin for each feeding event (kg), the amount consumed (kg), meal length (seconds), the interval between meals (seconds), and unaccounted weight (kg). Level 4 files contained the average weight of each bin every 30 seconds, but these data were rarely used.

The Level 3 files provided most information used to evaluate behaviour, and Level 1 files were occasionally interrogated when greater detail was required. Additional data were extracted from the Level 3 files (Feedcheck V1.3) to show the daily activity for all the bins and the daily activity of each animal in each pen. The Feedcheck V1.3 program also produced CSV files with the amount eaten, timing of feed bin use, and weight of the bin throughout the day. Details and examples of the different levels of data and summaries produced are presented in Appendix I, Section 7.1.2.

3.6 Feed intake data collation and sorting

Prior to analysis of feed intake and behaviour (described in section 3.7), the data accumulated in the Level 3 files were checked to ensure values were valid. Factors contributing to aberrant values included occasional electronic failure, usually due to load cell malfunction or water affecting the electronic equipment. Other possibilities were interference caused by close proximity of a second EID tag, EID failure, or loss of ear tags. Data from Cohort 2 were explored in detail and a number of criteria were developed to differentiate “normal” from “unlikely” events. The criteria that were developed, and resolution of problems, are as follows:

- (1) Analyses were applied only to trial days and excluded the adaptation period.

(2) When data were unavailable from a pen (e.g. power outage, load cell malfunction), data from the entire (24 h) day were discarded.

(3) Daily intakes of greater than 15 kg cubes (12.7 kg DM) for individual animals were excluded from the analyses because animals weighing 150-250 kg could not eat that amount (Macdonald et al., 2005). In some cases data were obviously incorrect (e.g., >100 kg), and the errors were attributed to malfunctions in the load cells.

(4) All individual feeding sessions or meals that recorded a negative intake were excluded from the intake calculations, because an animal cannot have a negative intake. Negative values were associated with variation in bin weights and rounding errors, for example when a calf entered the bin and disturbed the cubes without eating any. Therefore, on days when the negative meal weights in 24 h totalled <-0.5 kg (i.e., more negative than -0.5 kg), the intake for that animal on that day was excluded because values may have contained errors. When the intake of negative feeding sessions totalled between -0.5 and 0 kg, these meal weights were not included in the daily intake determination but they were included in analyses of feeding behaviour (e.g., number of feeding events). They were included because the negative value was associated with load cell operation rather than EID reader operation, which provided information on the individual's feeding behaviour.

(5) Where animals had a feeding rate faster than 1 kg cubes in 300 seconds (200 g/min) during a feeding session in which more than 0.5 kg of cubes were consumed, the animal's intake for that day was excluded. This decision was based on examination of plotted eating rates to determine normal ranges and outliers. The hardness of the dry cubes meant that they required significant chewing and salivation, which limited the rate of intake and made it physically impossible to consume a large quantity of dry cubes in a short period. Very fast feeding rates flagged possible errors in data acquisition. Exceptions were made for smaller meals (<0.5 kg) as the calf may have taken a mouthful of cubes and left the bin to chew them, therefore appearing to have a short feeding duration.

(6) Where an animal's EID appeared in a feed bin which was not located in its own pen, the feeding sessions for the second feed bin were excluded, but the feeding sessions in the "home" feed bin were included in analyses. Instances of EID tags appearing in the data for two bins usually occurred when animals were taken out of their pens for weighing. On their way past other pens, the animals would occasionally come close to the feed bin of another pen and their EID was identified by the reader for that feed bin. However, feed was not consumed.

The software logged a meal whenever an animal came within range of the EID reader, regardless of how much they ate. The meal ended when that animal left the feed bin for more than 15 minutes, or when another animal entered the feed bin. However, several definitions of a “meal” have been used in the literature, so a number were trialled in this study to determine whether the definition of a meal would affect the outcomes of the analysis. The definitions of a meal that were tested included:

- ≥ 0.01 kg feed consumed
- ≥ -0.2 kg feed consumed
- > 0 kg feed consumed and ≥ 3 second duration
- ≥ -0.2 kg feed consumed and ≥ 3 seconds duration
- ≥ 60 seconds duration
- ≥ 300 seconds (5 min) duration
- ≤ 2 hours duration
- ≤ 4 hours duration

There was very little difference in the results based on these various definitions, so the first definition (≥ 0.01 kg feed) was used for all analyses.

The criteria used to screen data from Cohort 2, prior to the behavioural analysis, were then applied to the other four cohorts. These criteria enabled errors in the data to be filtered out, providing confidence in the remaining data, which were then used to calculate efficiency of feed utilisation (RFI) and behavioural characteristics. Each cohort was analysed separately due to the differences in age and weight of animals between cohorts.

3.7 Feeding behaviour

The feeding behaviour characteristics determined from the electronically acquired data were: meal frequency per day, total daily feeding duration, daily feeding rate, meal size, and meal duration. A description of each characteristic is given in Table 3.3. Intake and related behavioural traits (feeding rate and meal size) were calculated as kg of feed, rather than DM intake, because this was a behavioural study and the actual weight of feed consumed was more relevant to behavioural traits.

The daily values for each animal for meal frequency, total daily feeding duration, and daily feeding rate were averaged over the whole trial period. Meal size and duration were calculated by averaging the size and duration of meals over a 24 h period, and averaging daily values for individuals over the trial period. These characteristics were related to RFI and ADG.

Table 3.3: Descriptions of feeding behaviour characteristics of individual animals on a daily (24 h) basis. Data used in analyses were calculated by averaging values from the whole 42-49 day trial period.

Feeding behaviour characteristic	Description
Intake	Average kilograms of cubes eaten
Meal frequency	Average number of feeding sessions
Feeding duration	Average number of hours spent with head in the feed bin
Daily feeding rate	Average rate of feeding (grams of feed eaten/minute)
Meal size	Average kilograms of cubes eaten in a feeding session
Meal duration	Average number of minutes spent in a feeding session with head in the feed bin

3.8 Residual feed intake

Residual feed intake (RFI) in this study was calculated as the difference between actual intake and the predicted feed requirement of individual animals. Predicted feed requirements were calculated for each cohort by regressing actual daily feed intake (kg cubes/day) against average daily liveweight gain (ADG; kg/day) and mean metabolic liveweight (LWT; kg^{0.75}). Average daily liveweight gain was calculated by regression analysis of liveweight versus time, over the trial period (Waghorn et al., 2012). The resulting equation was:

$$y = C + b1ADG + b2LWT^{0.75} + RFI$$

Where y is the predicted feed requirements (kg cubes/day), C is the intercept, b1 and b2 are partial regression coefficients, ADG is average daily liveweight gain (kg/day), LWT^{0.75} is metabolic liveweight (kg^{0.75}) at the trial mid-point, and RFI is the residual error (kg/day).

Residual feed intake is determined as the amount actually consumed by a calf (kg cubes/day) minus the calculated (predicted) feed requirement (i.e., the residual from the predicted feed requirement). More efficient animals eat less than their predicted feed requirements (negative values for RFI); whereas less efficient animals eat more than predicted and have positive values for RFI.

3.9 Social dominance

A smaller study was conducted to determine whether social dominance and activity of the heifers related to differences in feeding behaviour, RFI, and ADG. A subset of 32 heifers (4 pens of 8 animals each) in cohort 5 was measured. The study was based on 48 h of video recordings of animals in pens 13, 14, 15, and 16 at the facility. Infrared cameras were placed on top of 3.5 m posts located at each corner of the pens. The video recorder with four colour cameras (XPOSE QV-8100, 4CH H.264 DVR Surveillance Kit; Electus Distribution Pty Ltd) was upgraded with a 640 GB hard drive which was able to store data from the four cameras for the 192 hours of recording. Recording of each pen was carried out sequentially, with 48 h of recording from each of the four pens, one after the other, over a period of 10 days. Animals in each pen were identified by large coloured alpha-numeric symbols on their backs so that individuals could be recognised in the images recorded. The infrared capability of the cameras enabled recording at night.

The analyses were based on social dominance, measured by scoring agonistic interactions between pairs of animals within pens by focal continuous sampling, where all animals were continuously monitored and any occurrences of agonistic interactions were recorded. The heifers were approximately eight months of age and had been together in their pen groups for almost one month when video recordings were made. This allowed sufficient time for dominance relationships within pens to become established before recording began (Langbein & Puppe, 2004).

An ethogram of agonistic behaviours between a pair of animals was developed (Table 3.4). This was based on behaviours observed in the pens, and confirmed by similar behaviours listed in ethograms in previous studies with cattle (e.g., Beilharz & Mylrea, 1963; Dickson et al., 1967; Kondo & Hurnik, 1990; Huzzey et al., 2006; Val-Laillet et al., 2008b). The purpose of the ethogram was to categorise the typical agonistic behaviours so that interactions could be quantified. This ethogram allowed different types of interactions to be captured, ranging

from overt agonistic displays (e.g., bunts), through to more subtle displays (e.g., threats) which are often more prevalent when a group of animals have been together for some time (Langbein & Puppe, 2004). The animal initiating the agonistic behaviour was called the initiator, and the other the recipient.

Table 3.4: Ethogram of initiator and recipient behaviours used to score agonistic interactions between animals housed in pens of eight.

Behaviour	Description
Initiator behaviours	
Head-to-body bunt (HB)	Initiator pushes head, often with force, against the body of another animal (the recipient)
Head-to-head bunt (HH)	Initiator pushes head, often with force, against the head of the recipient, usually facing each other (head-on)
Push (P)	Initiator pushes against the recipient with any part of its body except its head
Threat (T)	Initiator tosses head at, walks forcefully towards, runs or lunges at the recipient, but does not make contact with the recipient
Recipient behaviours	
Retreat (R)	Recipient moves away from the initiator in response to any of the initiator behaviours above
Aggressive response (AR)	Recipient responds to initiator with an aggressive behaviour, such as those listed above as initiator behaviours. In this situation, it is necessary to specify which animal won the contest (i.e. the animal which caused the other to retreat).

Analysis of all interactions was undertaken for the whole pen, and a zone of about 1.5m radius at the entrance to the feed chute was also considered separately. This “feed zone” was easily recognised in the images as a darker patch on the bedding due to increased traffic in this area from animals waiting to feed. An animal with at least two legs within 1.5 m of the end of the chute was considered to be in the feed zone.

When an interaction occurred, the following were recorded: the time of the interaction, the identity of the initiator and recipient of the agonistic behaviour, the type of agonistic behaviour (from the ethogram), and the location (i.e., which zone the interaction occurred in). An interaction was recorded only if a winner and loser of the encounter could clearly be established. An interaction was not recorded when the recipient had at least two legs within the chute because the recipient could not see the initiator, and the response was not necessarily related to the identity of the initiator. Interactions involving more than two individuals were dealt with by separating the interactions into the relevant pairs of animals. So, for example, if animal A threatened animals B and C simultaneously, this would be treated as two separate interactions i.e., A – B and A – C.

All the recorded interactions were transformed into a matrix, with winners in rows and losers in columns, as indicated in the example (Table 3.5). An animal that won an interaction had one point scored in the cell where its row (winner) met the loser's column. So, using an example from Table 3.5, calf 3510 won five encounters against calf 3191 and lost one encounter against 3191. If an animal won all interactions against its penmates, there would be no entries in its own column (e.g. calf 3191 won all interactions against its penmates except for the five interactions it lost to 3510).

Table 3.5: An example of a matrix developed from one pen observed for 48 h. All animals are listed in both the rows and columns to indicate incidence of winning and losing, respectively. Each number in the body of the table is the number of interactions in which the calf in the row (left side) “defeated” the calf in the column (top).

		Losers							
		3191	3395	3436	3510	3296	3324	3498	3444
Winners	3191	-	3	6	1	2	3	15	11
	3395	0	-	3	0	7	2	10	15
	3436	0	0	-	1	6	18	12	10
	3510	5	8	11	-	7	15	16	11
	3296	0	0	1	2	-	1	0	1
	3324	0	0	0	0	2	-	2	2
	3498	0	0	1	0	2	0	-	0
	3444	0	0	0	0	5	1	16	-

The dominance relationship between each pair of animals was determined using two methods because there is no standard procedure in the literature.

1. The first method required an animal to win only one interaction more than it lost in a pair to be considered dominant (based on de Vries, 1995); hereafter called the 'majority criterion'.
2. The second method was a two-tailed binomial test which determined an animal to be dominant over another if the number of interactions won differed significantly from $p = 0.5$ (based on Lehner, 1996; Langbein & Puppe, 2004); hereafter called the 'binomial criterion'.

Both methods were used to calculate a dominance relationship for each pair of animals, and the two methods were compared. If an animal had the same number of wins and losses against another animal, or if the number of wins and losses were not statistically different (for the binomial criterion), then that relationship was considered a tie. Once dominance relationships between pairs of animals were determined, a dominance index (DI) was calculated for each method for each animal:

$$\text{Dominance Index (DI)} = \frac{\text{Number of animals that "animal A" is dominant over}}{\text{Total number of animals that "animal A" interacted with}}$$

An animal was given a value of 0.5 for each tied relationship in this equation. So, in a pen of eight animals, if animal A was dominant over four others, tied with one other, and subordinate to/dominated by two animals, then the DI for animal A in that pen would be $4.5/7 = 0.64$.

One observer (TG) scored all the agonistic interactions recorded between pairs of animals recorded from videos. Observer consistency was evaluated by repeat scoring three hours of video on four occasions over the 48 h of recordings. A Pearson correlation coefficient (r) was calculated, giving a within-observer reliability of 0.98.

Analysis of social dominance (using values calculated from the DI) involved correlations with RFI, ADG, LWT, feeding behaviour, and activity (section 3.10). The two derivations of DI were analysed separately.

3.10 Activity time budgets

In addition to the agonistic interactions, activity time budgets of the animals in the four pens were recorded from the 48 h of video recordings of each pen. Every 10 minutes for 48 h, each animal was identified and their activity/behaviour at that point in time was recorded using scan instantaneous sampling. Activities recorded were lying, standing, feeding, drinking, walking/moving, and using the salt block. Rumination was also recorded alongside the other activities (e.g. ruminating while standing, referred to as standing ruminating; and ruminating while lying, referred to as lying ruminating) at each 10-minute scan between 0700 and 1800 h (daylight hours). Reduced video quality during night recording prohibited recording of rumination at night. The 10-minute scan data were used to calculate the proportion of time each animal was observed spending on each activity per 24 h. These proportions were then averaged across the two 24 h periods, giving a daily value for each activity.

Variables analysed included either time spent lying, drinking, feeding, standing, walking, using the salt block, or ruminating (while lying and standing). These were related to indices of performance and feeding behaviour (RFI, ADG, feed intake, time spent feeding, feeding rate, and the number, size and duration of individual meals) and LWT.

3.11 Statistical analysis

3.11.1 Summary of the variables considered in this study

The variables described in sections 3.7, 3.8, 3.9, and 3.10, and summarised in Table 3.6, were used in correlation analyses to determine relationships between performance measures, feeding behaviour, dominance, and activity.

Table 3.6: Summary of the variables used in correlation analyses with performance measures, grouped by type: feeding behaviour (all 1049 animals), dominance index (32 animals), and activity (32 animals).

Performance	Dominance Index
Residual feed intake	Majority criterion
Average daily liveweight gain	Binomial criterion
Liveweight	
Feeding behaviour	Activity
Intake	Lying
Meal frequency	Standing
Feeding duration	Walking
Intake rate	Drinking
Meal size	Feeding
Meal duration	Using the salt block
	Lying ruminating
	Standing ruminating

3.11.2 Cohort correlations

Correlations between variables were developed using the data collected from the 219 animals in Cohort 2, and these methods were applied to the other four cohorts. Correlations using all animals in each cohort were calculated by regression analysis for each cohort using GenStat (Payne et al., 2009). Correlations were calculated for both ADG and RFI with each feeding behaviour characteristic (intake, meal frequency, feeding duration, feeding rate, meal size and meal duration) for each cohort.

3.11.3 Comparison of top 10% and bottom 10% animals

The performance and feeding behaviour of the 10% most (low-RFI) and 10% least efficient (high-RFI) individuals from each cohort were compared using analysis of variance (ANOVA) in GenStat. The cohorts were combined in a pooled within-cohort analysis (i.e. cohort included in the model), which allowed an overall comparison of the 10% most and 10% least efficient animals of all cohorts, presented in chapter 4. Comparisons using ANOVA were also made for the most and least efficient groups (10% of each) from individual cohorts, and these results are presented in Appendix II, Section 7.2.2. This analysis provided a numerical summary of

divergence and illustrated average values of RFI, ADG, LWT, intake and feeding behaviour for the most (low-RFI) and least (high-RFI) efficient groups.

In total, 208 animals were included in this analysis of extremes: 32 in Cohort 1 (16 low-RFI and 16 high-RFI), and 44 in each of the remaining cohorts (22 low-RFI and 22 high-RFI in each of cohorts 2-5). These animals were retained, mated, calved and were used for further research (e.g., postpartum liveweight change, methane production) as part of the on-going research.

3.11.4 Temporal feeding patterns

Analyses included the time of day that animals consumed their feed. The 24 h day was divided into eight 3-hour time periods (0000-0300, 0300-0600 h, etc.) and average feeding behaviour was summarised for each of these periods. Initial evaluation with Cohort 2 indicated differences between the 10% most and 10% least efficient groups, which prompted an evaluation of the 10% most and 10% least efficient animals in all cohorts using a pooled within-cohort analysis (as described in section 3.11.3). Cohorts were combined for simplicity and brevity and these results are presented in chapter 4, whilst the evaluations of each cohort separately are presented in Appendix II, Section 7.2.3.

A repeated measures analysis of data was conducted using AREPMEASURES procedure in GenStat, with time included as a factor, to determine whether there were differences in feeding behaviour between the most and least efficient animals ($n = 208$; 10% most and 10% least efficient animals in each cohort combined) during a 24 h day. All variables had significant interactions between time and efficiency group ($p < 0.001$), so this interaction was then explored at each 3-hour time period. The mean intake, meal frequency, and feeding duration of the 10% most efficient (low-RFI) and 10% least efficient (high-RFI) animals in each cohort were compared in each 3-hour time period using ANOVA in a pooled within-cohort analysis to determine feeding patterns over a 24 h day. The feeding patterns were also compared within each group (i.e., the change in feeding activity of each group over 24 h), hence two standard errors of the difference (SED) were calculated. Correlations of mean intake, meal frequency, and feeding duration in each of these periods were calculated against RFI and ADG for all five cohorts ($n = 1049$), but these are not presented as they showed similar patterns to those shown in the comparison of the most and least efficient animals (Section 4.6).

3.11.5 Dominance and activity

Dominance indices (DI) and activity profiles were calculated for a subset of animals ($n = 32$) in Cohort 5, as described in sections 3.9 and 3.10. The number of interactions per pen, and the zone and time of day (in 3-hour time periods) at which these interactions occurred were calculated over the 48 h of recording. As well as daily activity, proportions of time spent in each activity in 3-hour time periods were calculated. Correlations between variables of DI, activity, feeding behaviour, and performance were derived for each pen (GenStat), because the DI and activity of each animal was dependent on the presence and behaviour of its penmates. The slopes of the correlations for each pen were compared for each variable, and when there were no statistically significant differences ($p > 0.05$) between the regression slopes of individual pens, the slopes were pooled to give one correlation for all pens. These pooled slopes were used in this analysis where appropriate.

To determine whether there were differences in activity between animals of differing dominance status, animals were grouped into three dominance categories based on their DI:

Low:	DI < 0.4
Medium:	DI 0.4-0.6
High:	DI > 0.6

A repeated measures analysis of data was conducted using AREPMEASURES procedure and splines in GenStat, with time included as a factor, to determine whether there were differences in activity between the three dominance categories within pens ($n = 8/\text{pen}$) during a 24 h day.

4. RESULTS

4.1 Description of the cohorts

All cohorts completed the trial period successfully, and data enabling calculation of ADG, RFI, and feeding behaviour were collected. The animals adapted to the cube diet easily and the feed bins were in use for approximately 22.5 hours per day. Tables 4.1 and 4.2 summarise each of the five cohorts. Most analyses were undertaken with individual cohorts because of differences between them in age, liveweight, and season/year of testing, but the heifers were the same breed, similar BW, fed the same diet, and managed in the same way.

Due to delays in implementing recording systems in the new facility, Cohort 1 had a longer adaptation period (49 days) and spent 91 days in the facility, compared with 60 days for the other cohorts, and therefore Cohort 1 had a higher liveweight at the end of the measurement period than the other cohorts. Mean birth dates of heifers in Cohorts 3 and 5 were about three weeks later than Cohorts 2 and 4, but trial start dates of Cohorts 3 and 5 were 70 days later, so animals were older and heavier than those in 2 and 4 at the start of their measurement periods.

Table 4.1: Number of animals, days in the facility, trial length, average age (days) and average liveweight (kg) when entering and leaving the facility, for each cohort (mean $\pm$ standard deviation).

	Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 5
Number of animals	164	219	219	223	224
Days in the facility	91	60	60	60	60
Trial length (days)	42	47	49	48	48
Age on entering facility	214 $\pm$ 6.5	186 $\pm$ 4.8	234 $\pm$ 7.3	176 $\pm$ 9.7	227 $\pm$ 11.2
Liveweight on entering facility	167 $\pm$ 15.1	142 $\pm$ 13.7	155 $\pm$ 12.3	145 $\pm$ 11.9	151 $\pm$ 8.8
Liveweight on leaving facility	256 $\pm$ 28.3	191 $\pm$ 19.3	218 $\pm$ 16.6	201 $\pm$ 15.6	209 $\pm$ 13.2

Table 4.2: Means and standard deviations (SD) for residual feed intake (RFI), average daily liveweight gain (ADG), liveweight (mid-point of the regression over the 42-49 day trial), and feeding behaviour characteristics in each cohort of animals, with an overall average.

	Cohort 1		Cohort 2		Cohort 3		Cohort 4		Cohort 5		Average
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
RFI (kg cubes/d)	0.00	0.53	0.00	0.42	0.00	0.52	0.00	0.47	0.00	0.56	0.00
ADG (kg/d)	0.89	0.13	0.80	0.12	0.91	0.14	0.93	0.11	0.87	0.12	0.88
Liveweight (kg)	238	18.9	172	17.1	194	15.9	180	14.2	190	12.0	195
Daily intake (kg cubes)	9.44	0.95	6.86	0.78	8.27	0.78	7.53	0.78	7.78	0.75	7.98
Meal frequency (/d)	12.1	6.71	4.7	1.31	6.6	2.20	5.9	3.13	6.8	4.22	7.2
Feeding duration (h/d)	2.62	0.44	2.90	0.43	2.79	0.43	2.83	0.45	2.82	0.37	2.79
Feeding rate (g cubes/min)	62.2	12.4	40.8	7.85	51.1	9.13	45.9	8.72	47.2	7.01	49.4
Meal size (kg cubes)	1.01	0.39	1.64	0.38	1.44	0.30	1.53	0.42	1.54	0.49	1.43
Meal duration (min)	17.3	7.56	42.0	11.3	29.8	7.57	34.8	10.8	34.0	11.4	31.6

The distribution of data from each cohort is presented in Figures 4.1-4.9 for each variable. By definition, average RFI should be zero, but the spread of efficiencies indicates that a few individuals in Cohorts 1, 3, 4 and 5 had very low RFIs (Figure 4.1) and appear to be outliers suggesting some intake was not measured. RFI of most individuals ranged from -1.5 to +1.5 kg cubes/day. Average daily gain was relatively consistent across cohorts, with most individuals ranging from 0.5 kg/day to 1.2 kg/day (Figure 4.2), and individual liveweight (mid-point of each trial) ranging from 137 to 292 kg (Figure 4.3).

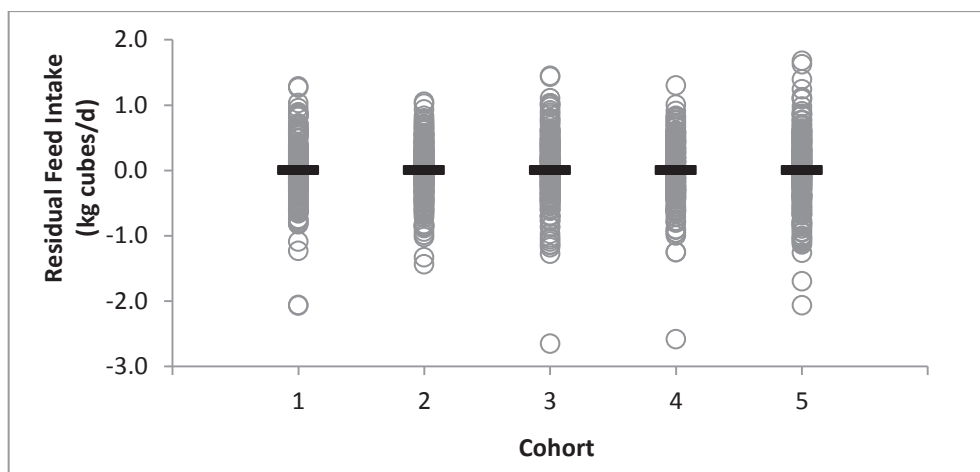


Figure 4.1: Distribution of residual feed intake data for individuals (open circles) in each cohort. The mean is indicated by the solid bar.

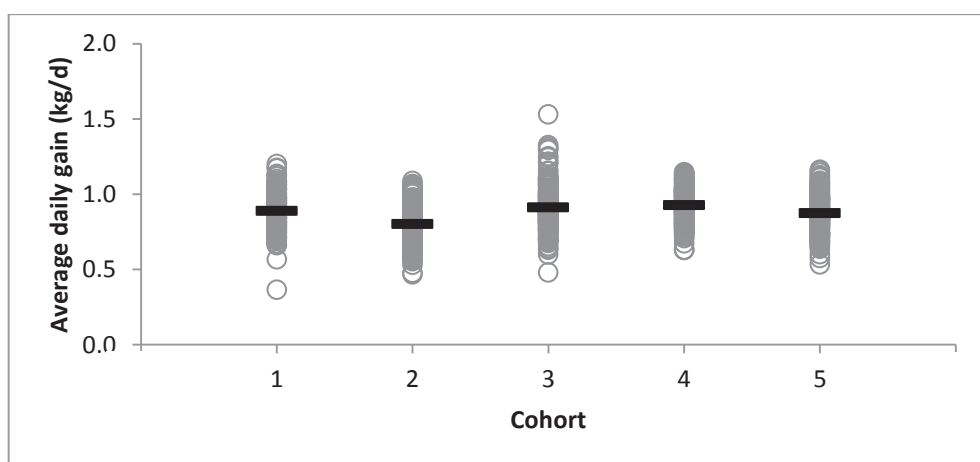


Figure 4.2: Distribution of average daily liveweight gain data for individuals (open circles) in each cohort. The mean is indicated by the solid bar.

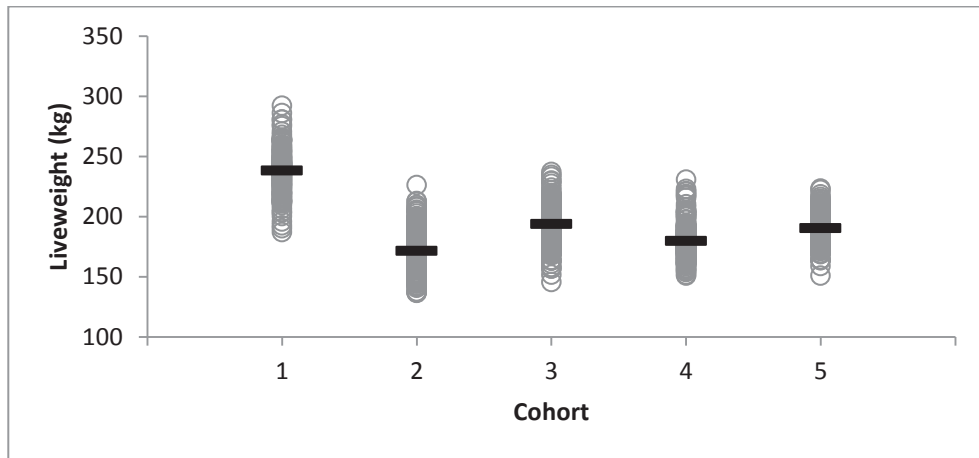


Figure 4.3: Distribution of liveweight (mid-point of each trial) data for individuals (open circles) in each cohort. The cohort mean is indicated by the solid bar.

4.2 Feeding behaviour of the animals

Feeding behaviour was investigated in terms of intake, meal frequency, feeding duration, feeding rate, meal size, and meal duration. Mean intakes of individuals ranged from 4.9 to 11.8 kg/day across all cohorts (Figure 4.4). Animals in Cohort 1 had an average intake of 9.4 kg cubes/day and the other cohorts had average intakes ranging from 6.9 to 8.3 kg cubes/day (Table 4.2; Figure 4.4). Within each cohort, some individuals initiated a large number of meals, resulting in a skewed distribution (Figure 4.5). For example, Cohort 1 had a relatively high average meal frequency per day (12), with several animals having 30+ meals per day. The average feeding duration per day ranged from 2.6 to 2.9 h/animal across cohorts, but from as little as 1.6 to over 4.5 h for some individuals (Figure 4.6), suggesting a large range in behaviour of individuals. Feeding duration and intake were used to determine daily feeding rates, which averaged 49.4 g cubes/minute across all cohorts (Table 4.2; Figure 4.7) but ranged from below 30 to more than 70 g/minute for individuals. The dry matter content of the cubes was 85%, so mean DM intake rate was 42.0 g/minute.

Meal size (kg cubes/meal) varied in relation to meal duration, with values ranging from 0.2 to over 3 kg/meal for some individuals (Figure 4.8), and meal duration also had large ranges (4-87 min) (Figure 4.9). Meal size and meal duration appeared to be inversely related to meal frequency. Hence animals in Cohort 1 had a high average meal frequency (12), but a small average meal size (1 kg cubes) and short meal duration (averaging 17 minutes), whereas other cohorts had a low meal frequency (5-7) and numerically higher average meal size and duration of 1.4-1.6 kg cubes and 30-42 minutes respectively (Table 4.2).

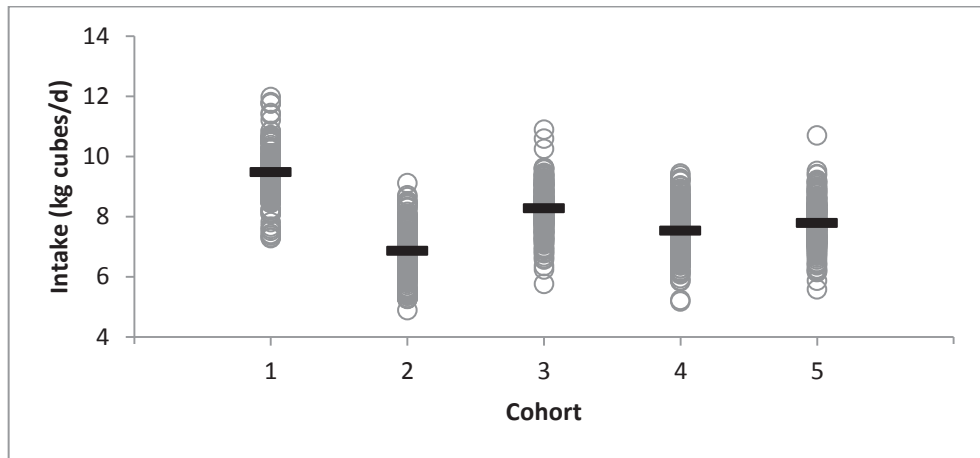


Figure 4.4: Distribution of intake data for individuals (open circles) in each cohort. The mean is indicated by the solid bar.

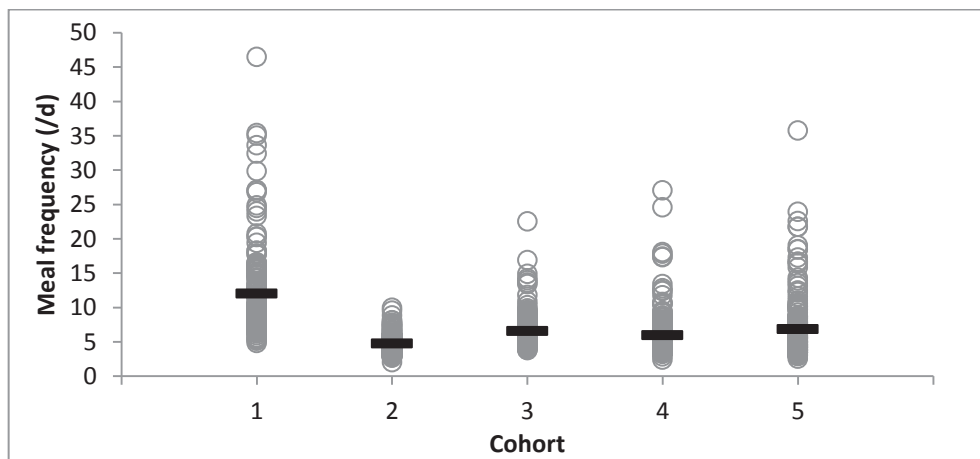


Figure 4.5: Distribution of average meal frequency per day for individuals (open circles) in each cohort. The mean is indicated by the solid bar.

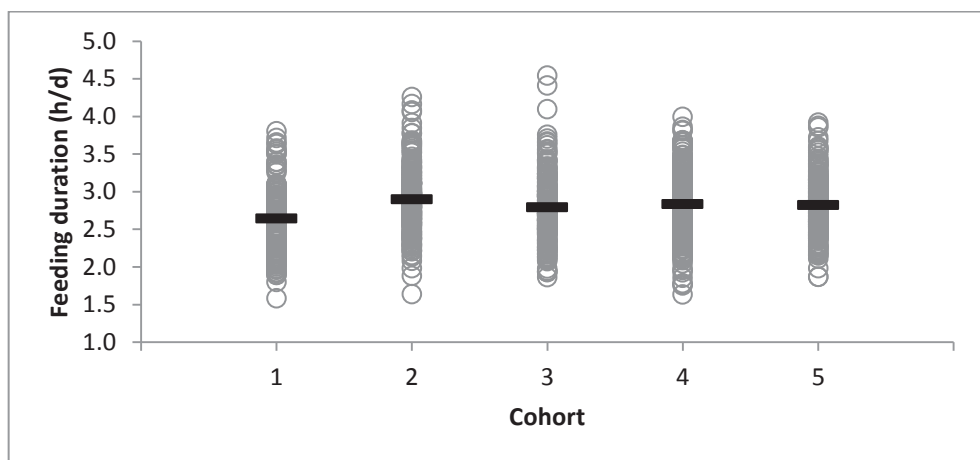


Figure 4.6: Distribution of average feeding duration per day for individuals (open circles) in each cohort. The mean is indicated by the solid bar.

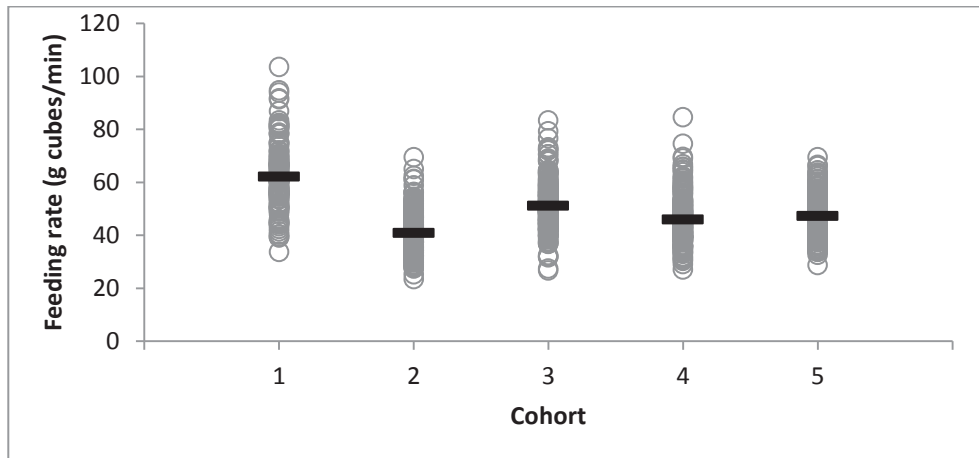


Figure 4.7: Distribution of average daily feeding rate for individuals (open circles) in each cohort. The mean is indicated by the solid bar.

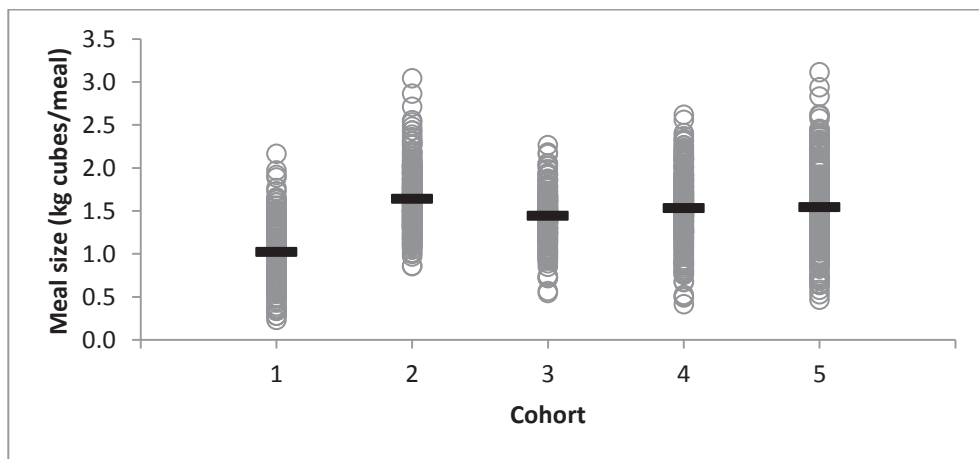


Figure 4.8: Distribution of average meal size for individuals (open circles) in each cohort. The mean is indicated by the solid bar.

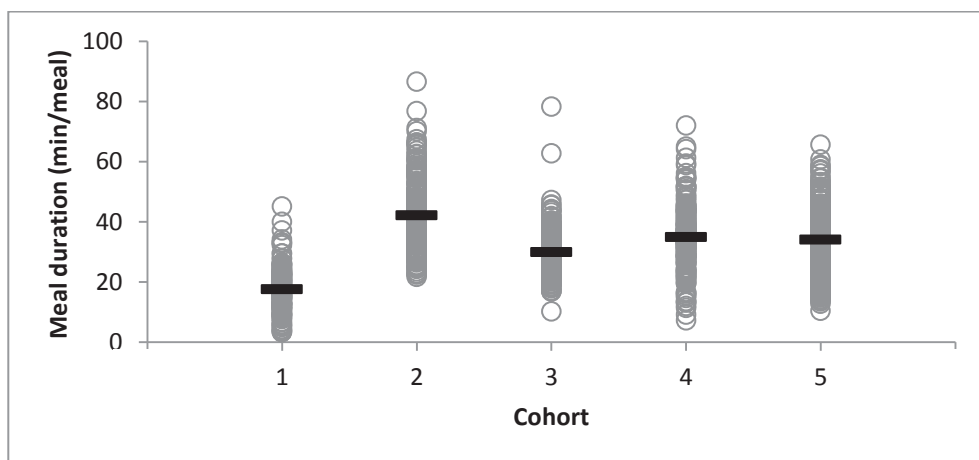


Figure 4.9: Distribution of average meal duration for individuals (open circles) in each cohort. The mean is indicated by the solid bar.

4.3 Correlations between feeding behaviour and ADG of animals from all cohorts

Daily intake was positively correlated with ADG and this was consistent across all cohorts (Table 4.3), indicating that faster growing animals had greater intakes than slower growing animals. Correlations between ADG and the remaining feeding behaviour characteristics were inconsistent between cohorts, but tended to be positive for meal frequency and daily feeding duration. This suggests that faster growing animals tended to have more meals per day and spend more time feeding per day than slower growing animals. Feeding rate and ADG were positively correlated ($p < 0.01$) for all cohorts except Cohort 3; in general, faster growing animals ate faster than slower growing animals. Meal size and duration were not related to ADG (Table 4.3).

Table 4.3: Correlation coefficients (r) between average daily liveweight gain and feeding behaviour for each cohort of animals.

	Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 5
Daily intake (kg cubes)	0.43***	0.67***	0.25***	0.60***	0.45***
Meal frequency (/d)	-0.03	0.19**	0.17*	0.13*	0.13
Feeding duration (h/d)	-0.03	0.00	0.20**	0.16*	0.09
Feeding rate (g cubes/min)	0.23**	0.40***	-0.01	0.21**	0.21**
Meal size (kg cubes)	0.17*	0.11	-0.11	0.03	-0.05
Meal duration (min)	0.02	-0.20**	-0.07	-0.10	-0.12

N.B. Symbols following the correlations indicate the level of statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4.4 Correlations between feeding behaviour and RFI of animals from all cohorts

The correlations between RFI and daily intake of cubes were positive and are summarised in Table 4.4, showing that efficient animals (low-RFI) ate less feed than inefficient animals (high-RFI). Intake had the strongest relationship with RFI of all the behavioural characteristics measured (Table 4.4), but most correlations between RFI and the behavioural variables were weak, although many were statistically significant. The r^2 values were mostly below 0.05 for meal frequency, daily feeding duration, feeding rate, meal size, and meal duration, suggesting that the proportion of variation in RFI explained by these relationships was low.

Statistically significant correlations between feeding rate and RFI (Table 4.4) were evident across cohorts and indicate that efficient animals ate more slowly than inefficient animals. Meal frequency and RFI were weakly correlated for all cohorts except Cohort 3, which had a weak negative relationship (Table 4.4); in general, efficient animals usually had fewer meals per day than inefficient animals.

Correlations between RFI and the remaining feeding behaviour characteristics (daily feeding duration, meal size, and meal duration) were inconsistent, with some cohorts having statistically significant correlations and others not (Table 4.4). In general, feeding duration (h/d) tended to have a weak positive relationship with RFI. Cohort 3 had a statistically significant relationship between RFI and meal size, but this was not observed in the other cohorts. There was a weak negative correlation between RFI and meal duration in Cohorts 4 and 5 but no correlation between these variables in the other cohorts (Table 4.4). Correlations between RFI and feeding behaviour variables for Cohort 2 have been plotted to provide a visual summary of these relationships for this cohort, and are presented in Appendix II, Section 7.2.1, Figure 7.10.

Table 4.4: Correlation coefficients (r) between residual feed intake and feeding behaviour in each cohort of animals.

	Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 5
Daily intake (kg cubes)	0.63***	0.54***	0.61***	0.60***	0.74***
Meal frequency (/d)	0.18*	0.23***	-0.14*	0.17*	0.21**
Feeding duration (h/d)	0.11	0.17*	0.06	0.14*	0.26***
Feeding rate (g cubes/min)	0.20*	0.18**	0.21**	0.16*	0.24***
Meal size (kg cubes)	0.00	-0.02	0.26***	-0.04	-0.04
Meal duration (min)	-0.08	-0.16	0.00	-0.20**	-0.14*

N.B. Symbols following the correlations indicate the level of statistical significance: * $p < 0.05$,

** $p < 0.01$, *** $p < 0.001$.

4.5 Comparison of the 10% most and 10% least efficient animals (RFI extremes) from all cohorts

A comparison of the 10% most efficient and 10% least efficient (i.e., inefficient) animals from all five cohorts is summarised in Table 4.5, and data for individual cohorts are presented in Appendix II, Section 7.2.2, Tables 7.1-7.5. The divergent groups had a similar weight and ADG, but RFI was significantly different between the two groups (Table 4.5). The most efficient animals (low-RFI) ate 1.78 kg cubes/day less (20% less) than the least efficient animals (high-RFI), and also had fewer meals, spent less time eating, had a slower feeding rate, and spent longer feeding at each meal than the least efficient animals (all $p < 0.05$). Meal size of the 10% most and 10% least efficient was similar ($p > 0.05$; Table 4.5).

Table 4.5: Mean values of the 10% most ($n = 104$) and 10% least ($n = 104$) efficient animals in all cohorts for residual feed intake (RFI), average daily liveweight gain (ADG), liveweight (mid-point of the regression over the trial period), and feeding behaviour.

	10% most efficient	10% least efficient	SED	p value
RFI (kg cubes)	-0.96	0.82	0.05	<0.0001
ADG (kg/d)	0.86	0.87	0.02	0.585
Liveweight (kg)	193	194	2.24	0.680
Daily intake (kg cubes)	6.97	8.75	0.10	<0.0001
Meal frequency (/d)	6.3	8.2	0.61	0.002
Feeding duration (h/d)	2.71	2.85	0.07	0.026
Feeding rate (g cubes/min)	45.4	53.0	1.36	<0.0001
Meal size (kg cubes/meal)	1.44	1.48	0.06	0.470
Meal duration (min/meal)	35.6	30.6	1.54	0.001

4.6 Temporal feeding patterns of the 10% most and 10% least efficient animals (RFI extremes) from all cohorts

Analysis of feeding behaviour included an evaluation of the 10% most efficient and 10% least efficient animals in all cohorts by assessing their intake, meal frequency, and feeding duration during eight x 3-hour periods (commencing 0000 h) over the trial period (42-49 days). The results of the combined cohort analysis are presented in Figures 4.10-4.12, and the feeding

patterns of the 10% most and 10% least efficient animals in individual cohorts are presented in Appendix II, Section 7.2.3, Figures 7.11-7.15.

Comparisons of the 10% most efficient and 10% least efficient animals combined from each cohort indicated statistically significant differences ($p < 0.05$) between groups at certain times of day (Figures 4.10-4.12). From 0600 h to midnight, the most efficient animals ate less than the least efficient animals (Figure 4.10). The most efficient animals also had fewer meals between 0600 and 2100 h than the least efficient animals (Figure 4.11). During the early hours of the morning (0000-0600 h), the most efficient animals spent more time eating than the least efficient animals, but this pattern was reversed between 1200 and 1800 h when the most efficient animals spent less time eating than the least efficient animals (Figure 4.12). These differences in feeding activity were greatest in the afternoon.

Generally, the most efficient group had a consistent intake and meal frequency throughout 24 h, whereas the least efficient group had a higher intake and meal frequency during daylight, particularly during the afternoon, and lower during the night (Figures 4.10-4.11). The most efficient animals spent more time feeding at night than during daylight, but the least efficient were the opposite, with more time spent feeding during the afternoon than at other times of the 24 h day (Figure 4.12).

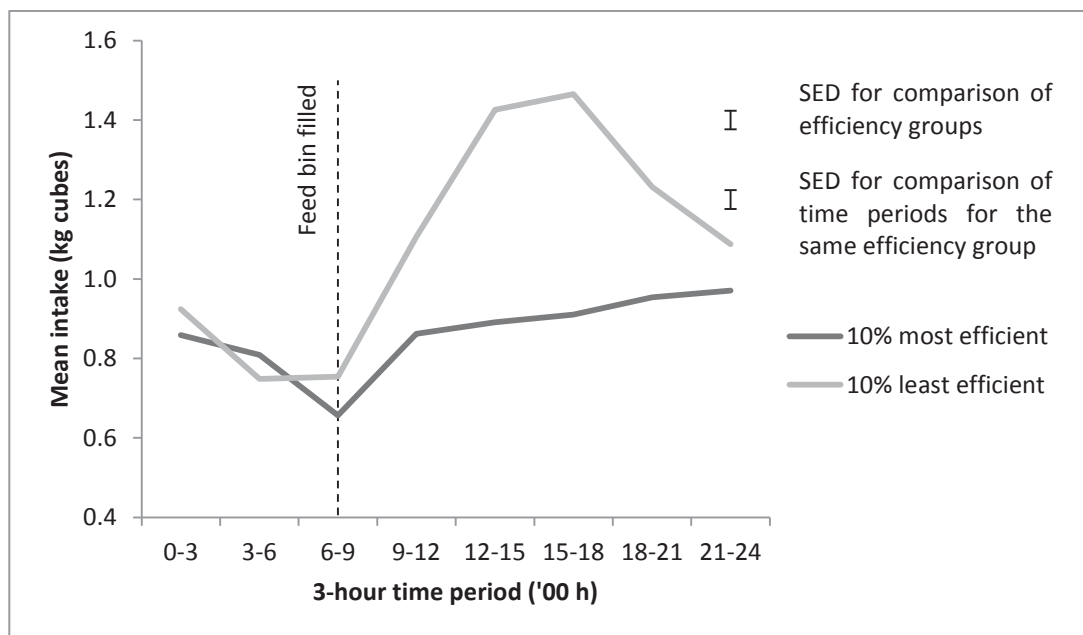


Figure 4.10: Mean intake per 3-hour time period (commencing midnight) of the 10% most efficient animals ($n = 104$) and the 10% least efficient animals ($n = 104$) from all cohorts. Error bars indicate the standard error of the difference (SED).

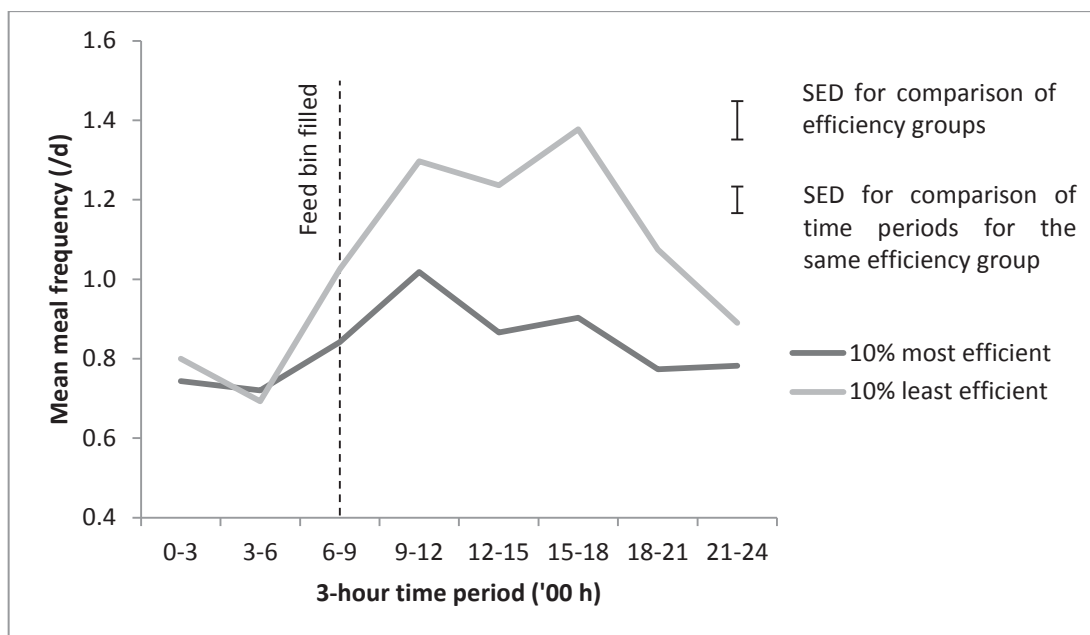


Figure 4.11: Mean meal frequency per 3-hour time period (commencing midnight) of the 10% most efficient animals (n = 104) and the 10% least efficient animals (n = 104) from all cohorts. Error bars indicate the standard error of the difference (SED).

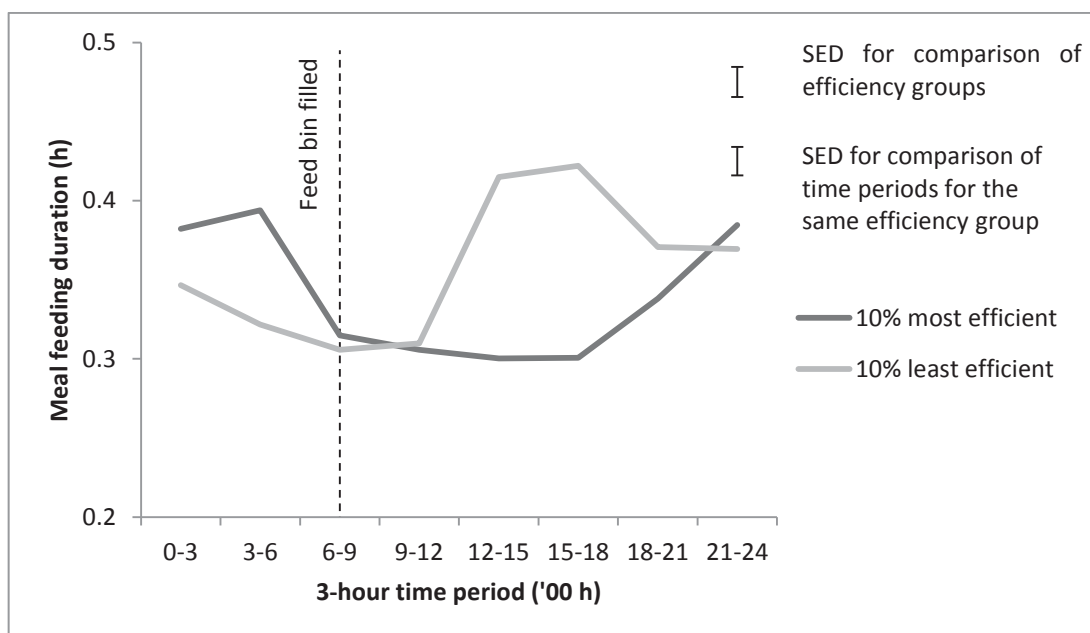


Figure 4.12: Mean feeding duration per 3-hour time period (commencing midnight) of the 10% most efficient animals (n = 104) and the 10% least efficient animals (n = 104) from all cohorts. Error bars indicate the standard error of the difference (SED).

4.7 Social dominance in a subgroup of animals

Evaluations made over 48 h in each of four pens animals in of Cohort 5 are presented in terms of agonistic interactions in the feeding zone (within a 1.5 m radius of the end of the chute) and outside of this zone, summarised in Figure 4.13. Other than correlations using the dominance indices, statistical analyses of agonistic interactions were not undertaken because data were collected from only four pens and small numbers of animals ($n = 32$). Therefore, results presented here are a descriptive analysis only, but show several patterns, such as increased agonistic behaviour during daylight hours.

Pens differed in the total number of agonistic interactions, with Pen 13 having the most (235) and pen 15 the least (116). A greater percentage of agonistic interactions occurred outside the feed zone (70-76%) than inside the feed zone (24-30%) in all of the four pens (Figure 4.13). Few agonistic interactions occurred between 0000 and 0600 h in any of the four pens observed (Figure 4.14). The greatest number of interactions occurred between 0900 and 1800 h (daylight hours).

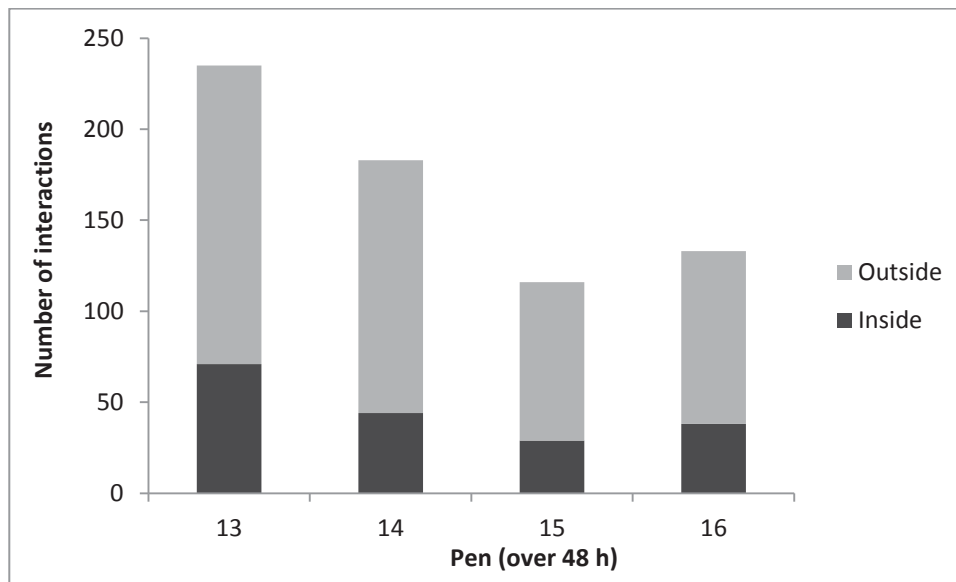


Figure 4.13: Number of agonistic interactions occurring in each pen over a 48 h period. Interactions occurring outside the feed zone are indicated as light grey, and inside the feed zone is indicated as dark grey.

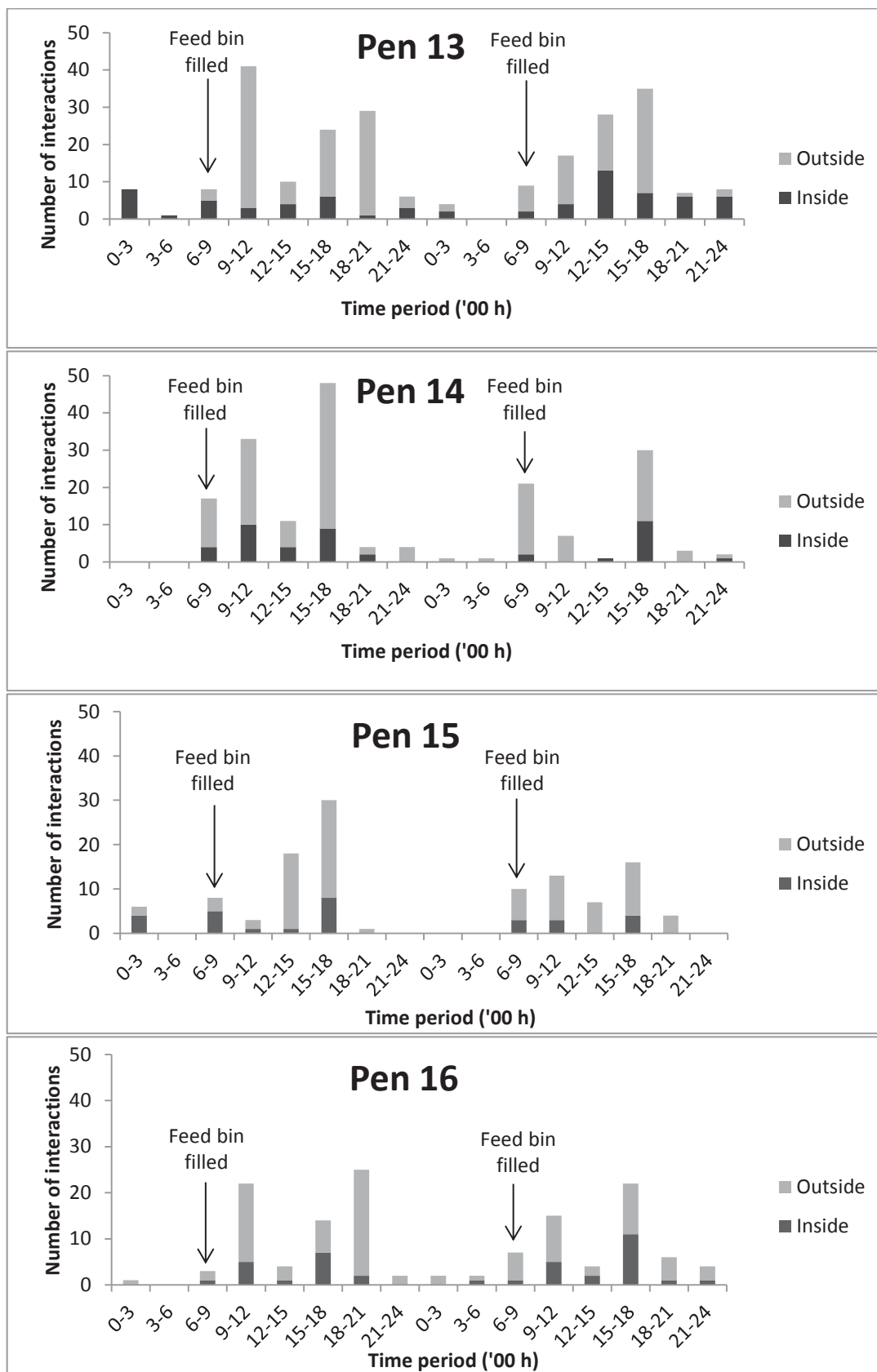


Figure 4.14: Number of agonistic interactions occurring in 3-hour time periods (commencing midnight) over 48 hours in four pens. Interactions occurring outside the feed zone are indicated as light grey, and inside the feed zone is indicated as dark grey.

Overall, values calculated using the two methods of dominance index (DI) used to evaluate social dominance were positively correlated ($r^2 = 0.57$, $p < 0.05$; Figure 4.15), indicating good agreement between the two criteria used (majority DI and binomial DI). However, there were some large differences between the DI derived for some animals. For example, one animal received a DI of 0.00 when calculated by the majority criterion and a DI of 0.43 when calculated by the binomial criterion.

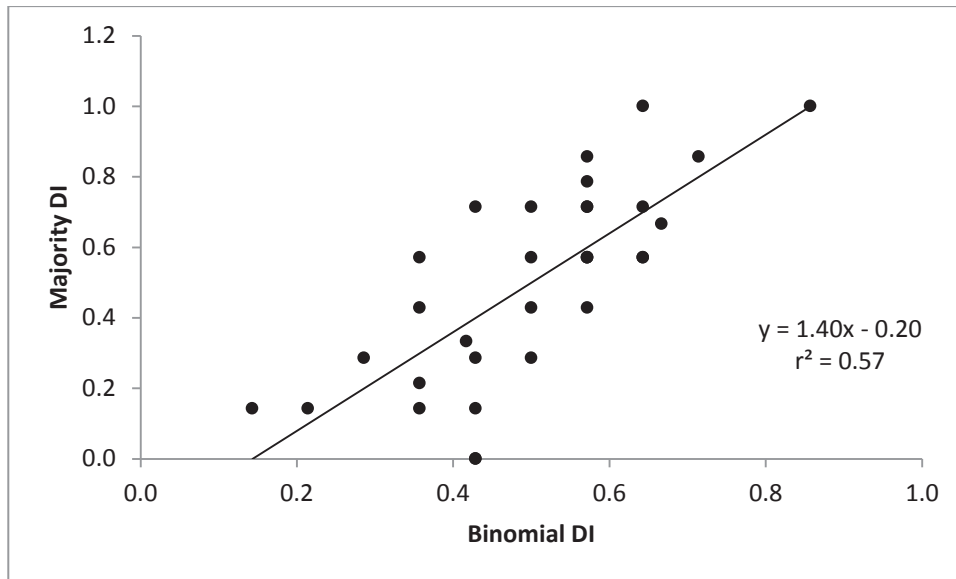


Figure 4.15: Correlation between the majority dominance index (DI) and binomial dominance index used in this study to calculate social dominance of individual animals.

The DI of individual animals were not related to their RFI, ADG, LWT, feeding behaviour (intake, time spent feeding, feeding rate, and number, size, and duration of meals), or general activity (lying, standing, drinking, feeding, using the salt block, walking and ruminating; see section 4.8 below) for either the majority or binomial DI (Table 4.6; all r values < 0.33 ; all p values > 0.05).

A repeated measures analysis using splines showed, in general, no statistically significant ($p < 0.05$) interaction of dominance group with time i.e., no evidence that the activity pattern through time differed for different dominance groups.

Table 4.6: Correlation coefficients (r) of the majority dominance index and binomial dominance index with performance, feeding behaviour, and activity.

	Majority	Binomial		Majority	Binomial
RFI	-0.04	-0.11	Lying	-0.06	0.03
ADG	0.15	0.05	Standing	0.00	0.03
LWT	0.26	0.08	Drinking	0.33	0.26
Intake	0.19	-0.01	Feeding	-0.04	-0.12
Meal frequency	0.10	-0.04	Salt block	0.21	-0.02
Feeding duration	0.06	0.02	Walking	-0.29	-0.20
Feeding rate	0.04	0.02	Lying Ruminating	0.00	0.13
Meal size	-0.05	-0.12	Standing Ruminating	0.06	0.01
Meal duration	-0.21	-0.19			

NB: all $p > 0.05$

4.8 Activity in a subgroup of animals

Average activity proportions presented here are a descriptive analysis only, but show general patterns over the course of a day (24 h). On average, in the four pens observed for 48 h, animals spent a large proportion (0.64) of their time lying each day (Table 4.7). Standing (0.20) and feeding (0.12) were the next most common activities per day. Very little time was spent walking/moving or drinking (0.01). Proportion of time spent ruminating during daylight (0600-1800 h) averaged 0.24 (Table 4.7).

Profiles of activity averaged in 3-hour time intervals over 24 h showed that animals spent a greater proportion of time lying overnight (between 2100 and 0600 h) than during the day (Table 4.7). The proportion of time spent standing varied over 24 h, with the greatest proportion occurring between 0600 and 0900 h due to pen cleaning. Proportion of time standing in the evening was low. Feeding and drinking activity was generally regular across 24 h and average salt block use was greatest between 0900 and 1200 h (Table 4.7). The period from 0600-0900 h had lower proportions of ruminating than other times during daylight, but recording of rumination was only able to begin at 0700 h when visibility improved. Average activity profiles of each pen over 24 h are presented in Appendix II, Section 7.2.4, Figures 7.16-7.17.

Table 4.7: Average proportions of time spent in each activity in each 3-h time period (from midnight), averaged across all animals in 4 pens (n = 32). NB: rumination was recorded from 0700 to 1800 h only.

Time	Lying	Standing	Walking	Feeding	Drinking	Salt Block	Ruminating*
0-3	0.76	0.10	0.00	0.12	0.01	0.01	-
3-6	0.79	0.07	0.00	0.12	0.01	0.01	-
6-9	0.41	0.46	0.01	0.09	0.01	0.03	0.12
9-12	0.58	0.24	0.01	0.12	0.01	0.04	0.28
12-15	0.68	0.16	0.00	0.13	0.01	0.02	0.29
15-18	0.56	0.27	0.01	0.12	0.01	0.03	0.28
18-21	0.66	0.19	0.00	0.13	0.01	0.02	-
21-24	0.73	0.12	0.00	0.13	0.01	0.02	-
Average	0.64	0.20	0.01	0.12	0.01	0.02	0.24

*Rumination was measured at the same time as other activities (e.g., an animal could be lying and ruminating).

Pooled pen measures of activity (n = 32; 4 pens; 8 animals/pen) were not correlated (all $p > 0.05$) with performance indices, feeding behaviour, or dominance indices, except for the following. Time spent lying was moderately positively related to meal size ($r = 0.40$; $p = 0.031$), and time spent lying and ruminating was positively related to total time spent eating ($r = 0.37$; $p = 0.046$), although ruminating was only recorded from 0700-1800 h. Salt block use was positively related to meal size ($r = 0.42$; $p = 0.022$) and time spent drinking was negatively related to meal duration ($r = -0.37$; $p = 0.048$).

Relationships existed between time spent feeding (as measured by 10-minute scans) and the following variables: RFI ($r = 0.43$; $p = 0.019$), feeding rate ($r = -0.61$; $p < 0.0001$), and total time spent feeding as measured by the automatic recording system ($r = 0.77$; $p < 0.0001$). The strong and statistically significant correlation between time spent feeding as measured by 10-minute scans on video and the automatic recording system gave confidence in the accuracy of both methods for measuring behaviour.

5. DISCUSSION

The primary aim of this study was to investigate relationships between residual feed intake (RFI) and behaviour of growing dairy heifers, particularly feeding behaviour, social dominance, and general activity. Knowledge of behavioural differences between animals of divergent RFI can provide insight into potential mechanisms underlying RFI and sources of variation in performance (Nkrumah et al., 2007). Furthermore, it is essential to investigate relationships between RFI and other traits such as behaviour to ensure that selection for RFI will not have any associated adverse effects, as well as to aid in development of good management practices for efficient animals.

The descriptive statistics and correlations between RFI, average daily gain (ADG), and behavioural variables of animals from all five cohorts (n = 1049) are discussed in sections 5.1 – 5.4. This is followed in sections 5.5 – 5.6 by a discussion of the results from the 10% most and 10% least efficient animals (n = 208) drawn from all cohorts, and sections 5.7 – 5.8 refer to the subgroup of animals (n = 32) from Cohort 5 used to study dominance and activity. The remaining sections (5.9 – 5.11) discuss some other factors that may be contributing to RFI, and the limitations and implications of this study.

5.1 Animal performance, feeding facility, and data collection and analyses

The animals used in this study showed good performance, making them appropriate subjects for a study relevant to the New Zealand dairy industry. The heifers adapted to the cube diet and pen feeding facilities quickly, allowing consistent data collection over the whole study period. The feeding facility and diet enabled good rates of gain (ADG; 0.88 kg/d), slightly higher than the 0.77 kg/d reported for Holstein-Friesian animals of a similar age fed *ad libitum* on high quality pasture and silage (Macdonald et al., 2005). Average liveweights were similar to those reported for animals of the same age (Macdonald et al., 2005).

Most RFIs ranged from about -1.5 to +1.5 kg/d. This indicated that the most efficient individuals ate 1.5 kg less feed than predicted, and the least efficient individuals ate 1.5 kg more feed than predicted, leaving a difference of 3 kg feed between the most and least efficient individuals. This range in RFI is slightly smaller than those reported in studies with beef steers (-2.1 to +1.8 kg feed/d) (Basarab et al., 2003; Basarab, 2005), although the beef

animals were older and larger than the dairy heifers used in the present study and therefore had higher intakes and greater scope for variation in intakes. The large divergence in RFI in both this and other studies (Table 2.2) indicates that there is potential to improve individual efficiency of feed utilisation. The RFI trait is heritable ($h^2 = 0.38$, Pryce et al., 2012), so selection will contribute to greater efficiency of the whole dairy system either through reduced feed requirements or increased stocking rates.

Large quantities of data were collected from the animals in the facility, making it important to screen data carefully to identify potential errors arising from automated collection of data from electronic ear tags and load cells under feed bins. Criteria for data screening can identify and remove errors, but there must be a balance between removing erroneous data and potentially removing accurate data. Most errors were associated with feed bin weights (e.g., problems with load cell malfunction) rather than animal identification, which has also been reported from similar electronic recording systems (Casey et al., 2005). The criteria used in the present study to screen and sort the data were developed to address these potential errors and were similar to some of the 16 criteria used by Casey et al. (2005) to identify and sort errors from automatically-recorded swine feeder data. Care was taken in this study to ensure accurate data were not removed in this process.

5.2 Feeding behaviour

Feeding behaviour can be affected by the diet, animals, feeding systems, and facilities where measurements are made. In general, the feeding behaviours measured from heifers in the feeding facility were similar to reports from other studies where animals were fed dry/conserved diets in confinement. The average intakes measured in this study (6.86-9.44 kg cubes/d; 5.83-8.02 kg DM/d) were similar to intakes measured in other studies on growing dairy and beef heifers (6.18-8.12 kg DM/d) fed total mixed ration (TMR) diets in confinement (Greter et al., 2008; Kelly et al., 2010). The animals in this study spent, on average, 2.79 h/d feeding, which is similar to other reported values in growing dairy heifers fed a lucerne cube diet (Williams et al., 2011) and also observations in both dairy cow and beef studies with TMR diets (2.83 h/d, Shabi et al., 2005; 2.59 h/d, Montanholi et al., 2010). Most of the animals measured here had 6-7 meals per day, which is similar to other reports (Tolkamp et al., 2000; DeVries et al., 2003b), although animals in Cohort 1 had an average of 12 meals per day. Cohort 1 spent much longer in the facility than the other cohorts and this may have affected their feeding behaviour.

Average meal size (1.4 kg cubes) and meal duration (32 min) in this study were similar to values for dairy heifers and cows fed silage or TMR diets (meal size: 0.9-1.6 kg; meal duration: 24-43 min) (Deswysen et al., 1993; Romney et al., 2000; Greter et al., 2008). The daily feeding rate of 49.4 g cubes/min measured in this study was in agreement with those reported for dairy heifers on a TMR and straw diet (Greter et al., 2008) and lower than the 67.0 g DM/min found in beef cattle (Montanholi et al., 2010), probably because these beef steers were older and larger than the heifers in the present study and thus capable of consuming more in the same period of time.

Feeding behaviour is likely to differ depending on the diet and feeding method, and the use of cubes as a sole diet in this study differs from other evaluations where silage/grain mixtures were fed (e.g., Greter et al., 2008; Kelly et al., 2010; Montanholi et al., 2010). Fibrous feeds are bulky and take longer to consume and digest than less fibrous concentrate-based feeds. For example, cows spent more time (463 vs. 348 min/d) eating long lucerne hay than silage (Brouk & Belyea, 1993). However, when fibrous feeds are chopped, as in this study and others with feeds of short fibre length, a rapid consumption of DM is possible.

The feeding system is likely to affect feeding behaviour, but the need to measure feed intake accurately precluded the use of either grazing or fresh forage feeding. In the current study, one feed bin was shared between eight animals, thus restricting access. Hosseinkhani et al. (2008) evaluated feeding systems with 36 non-lactating cows fed a TMR from either their own bin (one cow/bin) or a shared bin (two cows/bin). Cows that had to share and compete for feed access had an increased feeding rate and ate fewer meals (which tended to be larger and longer) than cows that did not have to share bins (Hosseinkhani et al., 2008). Dry matter intake was not different but daily distribution of that intake differed with competition (Hosseinkhani et al., 2008). Other studies also reported an increase in feeding rate from 43 to 71 g DM/min when cattle that had been fed from individual feeders were fed in groups or when number of feeders was reduced (Harb et al., 1985). The behaviour of animals in the present study was likely to be affected by the feeding system, with faster feeding rates and altered timing of meals due to sharing one feeder between eight animals.

Interpretation of behavioural data needs to take into account the effect that the system can have on feeding behaviour, and there can be great variability in feeding behaviour between

individual animals. When given the choice, cattle often feed in synchrony (Tucker, 2009), so the feeding behaviours observed in systems where they must take turns at the feeder may not be the animal's preferred behaviour, but rather an adaptation to suit the feeding system. Intake level is often consistent over time, but the feeding pattern to achieve that intake may differ between animals (Nielsen, 1999). For example, Friggens et al. (1998) found a five-fold range in meal size and frequency between cows, and this was even larger in the current study, with a 13-fold range in meal size and a 23-fold range in meal frequency between individuals. This variation in feeding behaviour between individuals allows investigation of relationships between behaviour and other variables, such as RFI and ADG.

5.3 Feeding behaviour and ADG of all cohorts

Achieving a high ADG is one of the main aims of livestock farming. In young growing animals, ADG will largely be determined by intake, which is affected by feed availability and quality (Waghorn & Clark, 2004). Relationships between feeding behaviour and performance (e.g., ADG) can now be investigated easily with electronic feed monitoring systems.

The coefficients for the correlations between feeding behaviour and ADG reported in this study (Table 4.3) varied between cohorts, and relationships that were statistically significant were generally not as strong as those reported in other studies with beef cattle (Schwartzkopf-Genswein et al., 2002; Lancaster et al., 2009; Montanholi et al., 2010). For example, the weak to moderate positive relationship between intake and ADG varied from $r = 0.25$ to 0.67 for the five cohorts, whereas Lancaster et al. (2009) reported a correlation of $r = 0.66$, $p < 0.05$, in 341 growing bulls. A relationship between intake and ADG was expected because animals need energy to grow and eating more provides more energy for growth, although some of the energy eaten is used for other processes (e.g., maintenance) which will reduce the correlation coefficients. The relationships between other behavioural traits and ADG are not as direct and less well understood.

Correlations between meal frequency and ADG were lower than with intake, and also varied in strength between cohorts, indicating that this relationship is unlikely to be very important. The majority of beef research has not shown significant relationships between ADG and meal frequency (Schwartzkopf-Genswein et al., 2002; Lancaster et al., 2009; Kelly et al., 2010; Montanholi et al., 2010). This contrasts with a survey which found that increasing feeding frequency from 1 or 2 meals to 4 meals/day increased ADG by 16.2% in cattle fed a

concentrate-based diet (Gibson, 1981). It is possible that the relationship between meal frequency and ADG may be more important in situations where animals have few meals per day, e.g., changing meal frequencies from 1 to 4 meals/day is likely to have a greater impact on animals than changing from 6 to 7 meals/day. This is particularly important when applied to pastoral systems, where animals are typically given one or two breaks of pasture per 24 h and have two major grazing events in the early morning and late afternoon/early evening (Gregorini, 2012).

Feeding rate was weakly to moderately correlated with ADG in the present study, which was similar to two beef studies ($r = 0.26-0.32$, $p < 0.05$, Lancaster et al., 2009; Montanholi et al., 2010), although another beef study found no relationship (Kelly et al., 2010). Most studies with beef cows showed weak to moderate relationships between ADG and daily feeding duration, meal size, and meal duration ($r = 0.14-0.38$, $p < 0.05$; Schwartzkopf-Genswein et al., 2002; Lancaster et al., 2009; Montanholi et al., 2010) although such relationships were not evident in the results of the research presented here. The variable results reported in the literature may be due to differences in study designs, and suggest that, overall, feeding behaviour is not a good predictor of ADG.

5.4 Feeding behaviour and RFI of all cohorts

Apart from intake, which is a component of RFI, the correlations between RFI and feeding behaviour variables in this study (Table 4.4) were weak ($r = 0.00-0.26$) despite many being statistically significant. No published studies on behaviour and RFI in dairy cattle were found, but a substantial literature is available for growing beef cattle. The summary in Table 5.1 shows that many published relationships were stronger than those measured here.

Of all the behavioural variables measured, intake had the strongest relationship with RFI in both this study and others, ranging from $r = 0.43-0.74$ in the present study and those on beef cattle (Robinson & Oddy, 2004; Basarab, 2005; Lancaster et al., 2009; Kelly et al., 2010), indicating lower intakes of efficient animals. However, the remaining behavioural traits showed variable levels of association with RFI, both between cohorts in the present study and between other studies on beef cattle (Table 5.1). The weak to moderate associations reported in this and other studies, between feeding behaviour characteristics and RFI, suggest that these behaviours are not primary drivers of efficiency and, on their own, explain only a small amount of the variation in RFI between animals. Other factors, such as digestion and

metabolic processes like protein synthesis and cellular ion fluxes, may explain a larger portion of differences between individuals with divergent RFI (Herd & Arthur, 2009). Behavioural traits are not independent of each other (e.g., meal frequency, duration, size, feeding rate) so it is not appropriate to combine these factors in a multiple regression analysis. The large number of animals used in the analyses in this study may have contributed to measures of statistical significance for relationships between RFI and behaviour despite low correlation coefficients, but relationships show similar patterns in all studies (Table 5.1), though at different levels.

Table 5.1: Correlation coefficients (r) for RFI and feeding behaviour characteristics from published studies on beef cattle.

	Robinson and Oddy (2004)	Nkrumah et al. (2007)	Lancaster et al. (2009)	Kelly et al. (2010)	Montanholi et al. (2010)
Intake (kg DM/d)	0.57*		0.60*	0.47*	
Meal frequency (/d)	0.18*	0.18*	0.26*	0.45*	0.15
Feeding duration (min/d)	0.16*	0.49*	0.41*	0.06	0.24*
Feeding rate (g DM/min)	0.14*			0.26*	0.44*
Meal size (g DM)					0.41*
Meal duration (min)					-0.15

* $p < 0.05$

Differences in the relationships between behavioural traits and RFI in various studies may be a consequence of the systems employed to measure the associations, including feed/feeding, the animals, and the analyses of observations, which are summarised in Tables 5.2 and 5.3. For example, differences in the numbers and type of animals used, the facility or housing setup, group size, and the diet fed may have a large impact on feeding behaviour (Tables 5.2 and 5.3) (Grant & Albright, 2001; Phillips, 2004; Huzzey et al., 2006). Most correlations reported from studies with beef cattle were stronger than those found in this study, possibly due to differences between dairy and beef breeds or the physiological status of the animals in different studies (e.g., gender, age – growing or mature). For example, this study used dairy heifers, whereas many of the other studies used beef steers (Tables 5.2 and 5.3). Other research has shown gender effects on intake, feeding duration, and meal frequency of heifers compared with steers (of the same breed), and under both *ad libitum* and restricted feeding (Schwartzkopf-Genswein et al., 2002). Gender and feeding systems may affect relationships between RFI and behaviour and account for some of the differences between studies.

Table 5.2: A summary of animals and diets used in studies on residual feed intake with beef cattle.

Type of animal	Number of animals	Diet	Age (d)	Initial LWT (kg)	ADG (kg/d)	Reference
Crossbred beef steers	148	Concentrate-based	235	291	1.52	Basarab et al. (2003)
Crossbred beef steers and bulls	150	Corn-based	248	325	1.42	Nkrumah et al. (2004)
Tropically adapted & temperate steers & heifers	1481	Grain-based	477-673	300-400	1.15-1.73	Robinson and Oddy (2004)
Crossbred beef steers	464	Corn- or barley-based	252	353	1.46	Nkrumah et al. (2007)
Crossbred Angus steers, 2 experiments	Expt 1: 80 Expt 2: 40	Roughage-based Corn-based, no roughage	325 325	324 325	1.45 1.50	Golden et al. (2008)
Angus bulls	341	Corn silage-based	310	371	1.44	Lancaster et al. (2009)
Brangus heifers	115	Roughage-based	236	269	1.08	Bingham et al. (2009)
Crossbred beef heifers	86	70:30 concentrate: corn silage	247	192	1.51	Kelly et al. (2010)
Crossbred beef steers	91	Corn silage-based (grower); high moisture corn-based (finisher)	-	313	1.64	Montanholi et al. (2010)
Pregnant crossbred beef heifers	73	Grass silage	635	548	0.46 (0.09)*	Lawrence et al. (2011)

- indicates data not available

*conceptus-adjusted ADG in brackets

Table 5.3: Experimental details of studies measuring behaviour in cattle.

Breed	Age (d)	Type of facility	Time in facility (d)	Behavioural method	measurement	No. animals /pen	No. animals /feeder	Reference
Tropically adapted and temperate beef steer and heifers	477-673	Feedlot	53-57	Automated self-feeder, 2 min meal interval*		12	12	Robinson and Oddy (2004)
Angus beef steers	-	9 pens, 1 feeder/pen	72	Automated self-feeder, 5 min meal interval		8	8	Dobos and Herd (2008)
Crossbred Angus beef steers	325	Partially covered pens (8x18 m)	123	GrowSafe ¹		10	-	Golden et al. (2008)
Holstein dairy heifers	226	2 pens in barn	21	Insentec ² ; 21 min meal interval		3	1	Greter et al. (2008)
Holstein dairy cows (non-lactating)	Parity 2.4	Free-stall barn	23	Insentec; 16.7 min meal interval		9	1 or 2	Hosseinkhani et al. (2008)
Brangus beef heifers	236	20 pens, Calan-gate feeders ³	70	Video recordings for 28 days; 5 min meal interval		6	1	Bingham et al. (2009)
Angus beef bulls	310	2 x 2ha pens, 9 feeders/pen	70-84	GrowSafe; 5 min meal interval		-	6-8	Lancaster et al. (2009)
Crossbred beef heifers	247	1 large pen (21x17m), 15 feeders	82	Insentec; meal = >100 g consumed		86	5-7	Kelly et al. (2010)
Crossbred beef steers	-	Indoor pens	140	Insentec; 7 min meal interval		12-15	3-4	Montanholi et al. (2010)

- indicates data not available

* The interval used by the automatic feed monitoring system to define when a meal has ended i.e., if an animal returned to the feed bin within this interval (without another animal having entered), that would be considered a continuation of the meal.

¹ GrowSafe Systems Ltd, Airdrie, Alberta, Canada. ² Insentec, BV, Marknesse, The Netherlands. ³ American Calan Inc., Northwood, New Hampshire, USA.

5.5 Comparison of the RFI extremes from all cohorts

Comparisons of the 10% most ($n = 104$) and 10% least ($n = 104$) efficient animals (RFI extremes) in this study showed similar liveweight and ADG, which was anticipated as RFI is independent of level of production (Herd & Arthur, 2009). However the groups differed in their intake (kg cubes/d), feeding duration (h/d), meal frequency (meals/day), meal duration (min/meal), and feeding rate (g/min), with no difference in meal size. These results complement studies on beef cattle which demonstrate differences in the feeding behaviour of the most efficient and the least efficient (inefficient) animals, although findings are not consistent.

In this study, the most efficient animals ate 20% less than the least efficient individuals (Table 4.5), and similar responses have been reported with beef animals (Golden et al., 2008; Bingham et al., 2009; Durunna et al., 2011b). Daily feeding duration also differed, with the most efficient animals spending less time eating per day than the least efficient animals, and this was also evident in some beef studies (Nkrumah et al., 2006; Durunna et al., 2011b), although others did not find differences between groups (Dobos & Herd, 2008; Kelly et al., 2010; Montanholi et al., 2010). The difference in feeding duration of the most and least efficient animals was only 8 min, so is unlikely to be important biologically. Like the dairy animals in this study, the most efficient beef animals had fewer meals per day than the least efficient animals (high-RFI) (Nkrumah et al., 2006; Golden et al., 2008; Bingham et al., 2009; Kelly et al., 2010; Durunna et al., 2011b), although Dobos and Herd (2008) found no differences in meal frequency.

Eating fewer meals corresponds with a lower feed requirement, if meal size is similar as in this study, so time spent eating should be reduced, unless efficient individuals eat more slowly. The most efficient animals ate about 15% more slowly than the least efficient animals in this study with dairy animals (Table 4.5), and similar findings have been reported with some studies of growing beef cattle (Bingham et al., 2009; Kelly et al., 2010; Montanholi et al., 2010), but not in others (Dobos & Herd, 2008; Golden et al., 2008; Durunna et al., 2011b).

There is little published in the literature comparing meal size and duration of animals with divergent RFI. Meal size did not differ in this study, but one beef study reported that the most efficient animals had smaller meals (of similar duration) than the least efficient animals

(Montanholi et al., 2010). In accordance with their slower feeding rate, meal duration was about 15% longer for the most efficient than the least efficient animals in this study, whereas Lancaster et al. (2009) found that the most efficient beef animals had shorter meals than the least efficient.

Again, the differences among studies may be due to experimental design, facilities and measurement of behaviour, such as the definition of behavioural characteristics and even the determination of a meal by the automatic recording system. For example, the system used in this study determined a meal as having ended when it was separated by an interval of 15 min from the next time that individual entered the feed bin, whereas other studies have used intervals of 5, 7, or 21 min (Table 5.3). These different definitions of a meal could alter the number, size, and duration of meals of animals in each of these systems, and thus the method by which behaviour is measured can affect the outcome of the study.

It is unclear from this study why the most efficient animals had fewer, longer meals per day and a slower feeding rate than the least efficient animals. Longer meals and slower feeding rates by the most efficient animals should encourage increased saliva production, thus improving rumen buffering and pH (Beauchemin et al., 2008). This feeding pattern may improve digestion and health of these animals, providing benefits that may contribute to efficiency. However pH change will not be as important to animals in the present study because they were fed a forage-based diet (lucerne cubes). Lower feeding activity by the most efficient animals may reduce energy expenditure on feeding, especially as less feed is consumed and has to be digested, allowing more of the feed energy to be used for production (Nkrumah et al., 2007; Durunna et al., 2011b).

In summary, this study found differences in feeding behaviour between the most and least efficient animals. The most efficient ate less, spent less time eating, had fewer meals, ate more slowly, and had longer meals than the least efficient animals. However, it was not clear whether differences in feeding behaviour were driving differences in RFI or whether RFI was affecting behaviour.

5.6 Temporal feeding patterns of the RFI extremes from all cohorts

The temporal feeding patterns of the 10% most and 10% least efficient individuals from all cohorts summarised in Figures 4.10-4.12 showed average intakes, meal frequencies and daily

feeding duration per 3-hour time period over 24 h. Animals occupied the feeders most of the time (about 22.5 h/d) and access to cubes was prevented during filling and cleaning (0800-0900 h), after which some competition for access to the feed was evident. The stimulus to feed that is associated with delivery of fresh feed in barns (DeVries & von Keyserlingk, 2005) or provision of new pasture, causing periods of increased feeding activity at certain times of day, probably has little relevance to differences in behaviour of animals with divergent RFI unless it is related to dominance within pens.

There were significant differences in feeding behaviour between the divergent groups, particularly during daylight hours and early evening, when the most efficient (low-RFI) animals had lower intakes, fewer meals, and less total time spent feeding than the least efficient animals (high-RFI/inefficient). Studies with growing beef cattle also demonstrated differences in eating patterns associated with RFI, but these occurred at night; the most efficient beef animals consumed less feed at night than the least efficient animals, whereas intakes were similar during daylight hours (Montanholi et al., 2010; Lawrence et al., 2011). In contrast, no differences were observed between the most and least efficient animals by Golden et al. (2008), but most feeding occurred between 0900 and 1800 h in their system. However, they used small numbers of animals in their comparison of RFI extremes (n = 6-9 animals per efficiency group) compared with this study (n = 104 animals per efficiency group) which may have limited their ability to detect statistically significant differences.

The lower meal frequency of the most efficient animals during daylight/early evening hours (0600-2100 h) in this study corresponds with a beef study which showed a numerically lower frequency ($p < 0.10$) of visits to the feeder for the most efficient versus the least efficient beef steers throughout the day (Montanholi et al., 2010). The most efficient steers also had 15% fewer visits to the feeder overnight (2000-0800 h) (Montanholi et al., 2010). In the present study, despite longer individual meals, total daily feeding duration was less for the most efficient than the least efficient group (Table 4.5) and this was due to less time spent eating by the most efficient animals in the afternoon (1200-1800 h), although they spent more time eating in the early hours of the morning (0000-0600 h) than the least efficient animals.

There are no other comparable studies, and the reasons for the lower feeding activity of the most efficient animals in the afternoon are unclear, but they did spend more time eating

between midnight and sunrise, when ruminants are usually resting (Hancock, 1950; Albright, 1993). In grazing situations, cattle tend to eat in the early morning after sunrise and late afternoon before sunset and avoid eating during the hottest part of the day (Hancock, 1950; Albright, 1993; Sheahan et al., 2011).

There may be physiological aspects of efficiency that affect the distribution of meals over 24 h, for example factors associated with rumen function and animal health. Spreading feeding activity more evenly over 24 h, as the efficient animals in this study appeared to do, may change volatile fatty acid production and affect animal performance through provision of a more constant supply of energy and amino acids for absorption (Deswysen et al., 1993). There is limited research investigating feeding patterns over 24 h in animals of divergent efficiency. The findings from the present study merit further research into feeding patterns during the day, and effects on performance. This may be particularly important for grazing dairy cattle, where access to fresh pasture typically occurs only once or twice per day.

5.7 Social dominance in a subgroup of animals

Social dominance measured in four pens of heifers (32 animals) from Cohort 5 over 48 h was not correlated with RFI or any of the other variables (ADG, LWT, feeding behaviour, or activity), i.e., there were no indications of dominance by efficient animals. No other studies were found investigating the relationship between dominance and RFI. Some research has investigated relationships between RFI and temperament or docility, finding no phenotypic relationships (Nkrumah et al., 2007; Kelly et al., 2010). While temperament relates to an animal's behavioural response to handling, it may also modulate the response of the animal to social situations and its environment (Sebastian et al., 2011).

Although this study used only 32 animals, the number of agonistic interactions in each pen ranged from 58-118/24 h, and most occurred during daylight hours, when there were also differences in intake and meal frequencies between efficient and inefficient animals. Few agonistic interactions occurred at night, especially between 0000 and 0600 h when three-quarters of the animals were lying down (Table 4.7).

Dominance is important in confined situations, and other research reported that although dominance was not related to time spent lying, feeding, or the number of visits to an automatic milking system, dominant cows did not have to wait as often to enter the milking

system as cows of lower status (Ketelaar-de Lauwere et al., 1996). Dominant heifers may have had priority of access to feed in this study, but this could not be determined because of the layout of the feeding area and the difficulty in deciding whether an animal had left the feeder because of a dominant animal or because they had finished feeding.

A greater number of agonistic interactions occurred outside the feed zone than inside. This was probably because the area outside the feed zone was considerably larger, but more interactions might have been expected in the feed zone if there had been competition for access to feed. However, animals did not appear to engage in many agonistic interactions over feed access, perhaps because the chute leading to the feed bin prevented recognition of, and full access to, the individual that was feeding. Some attempts to displace the feeding individual were observed, but these were not analysed as the feeding animal could not see who was attacking it or retreat without displacing the initiator of the attack (feeding individual had to back out of the chute to engage in interactions). Hence, only interactions at the entrance to the feed chute were used in calculation of dominance indices.

Although not captured by the division of zones in this study, there were a large number of interactions occurring near the salt block (in the three pens with a salt block remaining), which contributed to the larger number of interactions outside the feed zone. This indicates that the salt block was also a valuable resource to these heifers and that the location of interactions will depend on the layout of the pen and resources, such as water, salt block or shade.

A strong relationship between the two dominance indices indicates that both methods achieved a similar final value for most animals. However, there were large differences (e.g., 0-0.4) for a few animals. Of the two methods, the binomial criterion was preferred because it provided a statistical test for asymmetry in dyadic relationships (i.e., whether or not one animal in a pair was dominant over the other) (Langbein & Puppe, 2004). Lack of an objective statistical method was seen to be a limitation of the majority criterion, although this does not necessarily reflect lack of biological significance. However, recordings made in a relatively short period of time may not provide an accurate estimate of the dominance relationship between a pair of animals, especially when one animal wins only one more interaction than the other animal (Langbein & Puppe, 2004). Determination of dominance through indices is only one way of inferring relationships between individuals, but animal

groups and societies are highly dynamic, making quantification difficult (Neumann et al., 2011).

Individual interactions are likely to be influenced by the situation in which they occur at that point in time. For example, if a subordinate animal is hungry because other animals have prevented it from accessing feed, it may have a stronger motivation to access the feed and present itself more forcefully in an encounter with a higher-ranking animal (Val-Laillet et al., 2008b). If this animal wins the encounter, and this encounter is the only one observed between this dyad, then the subordinate animal would be incorrectly considered dominant under the majority criterion. Many dyads are bi-directional (two-way), where both animals win one/some interactions over the other, but the dominant individual is the consistent winner in repeated agonistic interactions (Drews, 1993; Val-Laillet et al., 2008b). The binomial criterion has the limitation that fewer dominance relationships between dyads are clarified, as the dominant animal must win several (usually at least 3) encounters over the subordinate animal to be considered dominant. This results in more tied relationships. Therefore, both methods have limitations, but the binomial criterion is a more rigorous and objective statistical method to test dyadic asymmetry of the outcome of wins and defeats than the majority criterion (Langbein & Puppe, 2004).

Social dominance and hierarchies can be calculated in many different ways with different indices, and they do not all represent the same thing. While the best efforts were made to choose the most appropriate dominance indices in this study, other methods may have yielded different results and revealed a relationship between dominance status and RFI. There is a lack of published literature relating dominance and RFI, and although the numbers of animals used to investigate this relationship in the present study were small, results indicate that selecting for efficiency will probably not affect dominance.

5.8 General activity in a subgroup of animals

The general activity of the 32 animals measured in the 4 pens over 48 h was not related to RFI or any of the other variables measured in this study (ADG, LWT, feeding behaviour, or dominance indices) except for a few feeding behaviour variables. Although published research relating RFI and activity in cattle is limited, one beef study reported that high, medium, and low RFI groups of beef heifers spent similar amounts of time standing, lying, or

active (Lawrence et al., 2011). These animals were in late stages of gestation which may have affected the results.

Relationships between activity and RFI have been found in other species. Poultry which spent more time resting and less time standing used feed more efficiently for egg production (Morrison & Lesson, 1978). Physical activity was the most important factor contributing to energetic efficiency in poultry (Katie, 1991), accounting for 80% of the genetic variation in RFI (Luiting et al., 1994). It is possible that activity may not be an important contributor to efficiency in cattle, particularly in confined systems, although it could be more important in a grazing environment (Trujillo et al., 2011) especially as locomotive activity has been suggested to account for 10% of the variation in RFI (Richardson & Herd, 2004). The limited space for the heifers evaluated here (5 m²/animal) restricted their activity, but there is greater opportunity in pastoral systems for some animals to be more active than others, for example through expending more energy on searching for and harvesting grass, interacting with other animals, and being generally more restless. Therefore, there may be greater variation between animals in their activity and thus energy expenditure in pastoral systems. The number of animals used in the present study may have been too small to determine relationships, and further research could be conducted on larger numbers of animals to investigate the relationship between activity and RFI, especially in pastoral systems.

The proportion of time spent lying (0.64), standing (0.20), and drinking (0.01) per day by the heifers in this study was similar to values reported for Friesian heifer calves (lying: 0.66; standing: 0.19; drinking: 0.01) housed in conditions similar to the present study i.e., a feedlot situation with eight animals and one feeder per pen (Gonzalez et al., 2008a). Additional feeding stations resulted in animals spending more time lying and less time standing, probably due to a reduction in the time spent standing while waiting for access to occupied feeders as competition for access to feed diminished (Huzzey et al., 2006; Gonzalez et al., 2008a).

The animals in all pens spent a large proportion of time standing between 0600 and 0900 h. This was because they were confined to the concrete area of the pen during cleaning of the bedding, which usually occurred between 0800 and 0900 h each morning. The high proportion of time spent lying at night and early morning is consistent with other reports of cattle behaviour (Miller & Wood-Gush, 1991; Overton et al., 2002).

The infrared cameras proved useful for recording during darkness, but visibility was greatly reduced compared with daylight recordings (e.g., 5 m distance at night compared with 10 m distance during daylight) so time spent ruminating was only analysed between 0700 and 1800 h. Because ruminating could not be recorded over a complete day (24 h), this information is of limited use. However, the infrared cameras used in this study were a suitable option for observation of more obvious, “larger-scale” behaviours, such as feeding, standing, lying, or walking, at night. The cameras and recording equipment were low cost (about \$1000, including wiring and hard drive) and provided a viable option for studying animal behaviour in confined spaces, especially when compared with costly and tiring 24 h observations by people.

5.9 Other factors that may be contributing to RFI

Any process that affects energy supply to the animals’ tissues, or utilisation by tissues, can affect RFI, and energy requirements may be interpreted in terms of either maintenance or production. A number of processes that may influence RFI were suggested by Herd et al. (2004) and these can be considered in terms of feeding and digestion, which affects nutrient supply, or the routes by which the energy derived from feed is used (Waghorn & Dewhurst, 2007). Energy which is not stored in product (liveweight gain or milk) is lost as heat, so inefficient animals will probably generate more heat than inefficient individuals. This would be beneficial in cold conditions, and detrimental in a hot environment. Other potential differences between efficient and inefficient animals include ion transport and protein turnover (synthesis and degradation) because these processes use a significant portion of feed energy (Archer et al., 1999; Basarab, 2005), especially in young animals (Baldwin, 1995).

Variations in efficiency are a combination of biochemistry associated with energy capture and utilisation, and physiology, which affects requirements for growth (including the composition of production), activity and behaviour. Potential factors that may be contributing to variation in RFI were outlined in Chapter 2, so will not be repeated here. It is clear that no single factor is responsible for efficiency, and even seasonal effects on intake may be important (Mujibi et al., 2010). Further research is required to better understand the underlying mechanisms contributing to RFI, particularly in dairy cattle.

5.10 Limitations of the present study

The measurements of animal behaviour in this and other studies are affected by the feeding systems and housing of the animals (e.g., Tables 5.2 and 5.3 for examples of different systems), so it is important to consider facility design and operation as well as animal welfare in behavioural evaluations such as this. A potential limitation affecting both behaviour and daily gain in this study was the number of animals having access to feed from a single feeder in each pen. Preliminary studies with fewer animals per feeder (6/feeder) showed that intake was not affected by adding two more animals per pen (Waghorn et al., 2012). However other studies suggest that increasing the numbers of animals per feeder alters feeding behaviour, with shorter feeding times and faster feeding rates likely in pens with eight, compared with six, animals per feeder (Gonzalez et al., 2008b). The feeder in the present study was used for almost all of the available time, and a study with pigs showed that, when there was no time constraint and feeders were not always occupied, feeding rates were faster in groups with more pigs even though intakes were unaffected (Nielsen et al., 1995).

A system where only one of eight animals can feed at any given time will modify the feeding behaviour of the whole group by preventing behavioural synchrony and social facilitation of feeding events, compared with animals that can access feed simultaneously. These modifications caused by the system may result in somewhat artificial behavioural measures, especially in relation to grazing, but also in relation to other studies or systems. However, many behavioural studies with cattle are undertaken in systems similar to that used here (Tables 5.2 and 5.3), because they enable feed intakes to be measured. Behaviour was compared between individuals that were treated in the same way, and can be compared with other studies conducted in similar systems (which are akin to a feedlot environment).

The results presented in this study do not indicate whether the differences in behaviour of high and low efficiency heifers are a cause or a consequence of divergence for RFI. In other words, it was not clear whether differences in behaviour resulted in differences in efficiency, or whether efficiency (and the other factors affecting efficiency) was driving behaviour. However, the differences demonstrated here provide an avenue for further research investigating the role of behaviour in efficiency, which may lead to a better understanding of the underlying mechanisms associated with individual differences.

The small numbers of animals used in the investigation of social dominance and activity patterns may have prevented demonstration of statistically significant relationships with RFI, and a study of the relationships between these variables using larger numbers of animals may be warranted. Technology allows activity to be monitored automatically on large numbers of animals (e.g., pedometers), and this could be undertaken in a grazing environment, especially where there is some competition for feed. However bigger groups sizes will make it more difficult to determine dominance relationships between all individuals in a group.

It is important to appreciate that both the diet and the environment where this study was conducted will limit the application of findings to New Zealand's dairy herd. The design of the feeding facility was driven by the need to measure intake accurately, and this could not have been done in a pastoral situation. Steps were taken to ensure some similarities with normal feeding, such as the cubes being a forage (rather than grain) with a suitable particle length to ensure normal rumen function, but efficiency and behaviour still need to be investigated in a grazing system if possible.

5.11 Implications of findings

The implications of the research presented in this thesis are:

1. Biological basis of RFI – feeding behaviour appears to account for only a small proportion of the variation in RFI, and the relationships between behaviour and RFI do not appear to be very biologically meaningful. It was not clear from this study whether differences in feeding behaviour contributed to differences in efficiency or whether it was the animal's efficiency that led to it exhibiting different patterns of behaviour. Many factors contribute to variation in RFI, as discussed earlier, and this study suggested that behaviour had only a small contribution.
2. Predictive ability of traits – published studies have suggested that feeding behaviour traits may be useful predictors of RFI, but in this study feeding behaviour was a weak predictor of RFI. Intake was positively and strongly correlated with RFI and this was consistent across all five cohorts tested, however, it is also a component of RFI. Feeding rate was positively correlated with RFI across all cohorts, however this relationship was weak ($r = 0.16-0.24$) and would be difficult to apply for identification of efficient individuals, especially under different circumstances (e.g. pasture

feeding). Correlations between RFI and the other feeding behaviour traits (number of meals, feeding duration, meal size, and meal duration) were inconsistent, suggesting that they are not accurate predictors of RFI in young dairy heifers in the situation where measurements were made. In addition, social dominance and activity do not appear to be useful as predictors of RFI for young heifers in pens.

3. Management implications – knowledge of animal behaviour will assist farmers in the management of efficient animals, especially as selection will increase their proportion in herds. However, the small differences in the behaviour of efficient and inefficient animals suggests the main benefits of this research will be in management of all animals, and would be especially useful in design of feedlot or indoor systems. An important observation was the willingness of animals to eat during the night, which contrasts with accepted observations that cattle eat mainly during daylight hours. Further research is required to measure behaviour of efficient and inefficient cattle while grazing to confirm the differences measured here. This information could be used to develop feeding systems that would promote efficiency in dairy animals in New Zealand. The results of this study suggest that selecting for RFI will not cause adverse changes in feeding behaviour, social dominance, or activity in dairy cattle.

6. CONCLUSIONS AND FUTURE RESEARCH OPPORTUNITIES

The primary objective of this study was to investigate relationships between RFI and a number of behavioural variables, especially those associated with feeding. Correlations using all 1049 animals showed statistically significant, but weak, relationships between RFI, ADG and all behavioural variables. This analysis suggests that feeding behaviour accounted for a small amount of the variation in RFI and ADG of dairy heifers, and that selection for divergence in RFI is unlikely to result in unwanted behaviour. There are likely many factors contributing to differences in efficiency, including physiological processes such as digestion, thermoregulation, and protein turnover, with feeding behaviour being only one of the many factors.

Differences in feeding behaviour did exist between the RFI extremes (most efficient and least efficient animals). The most efficient animals ate less, spent less time feeding, had fewer meals, ate more slowly, and had longer meals than the least efficient animals. It was not clear from this study whether differences in feeding behaviour contributed to differences in RFI or whether an animal's RFI was affecting behaviour.

Interesting feeding patterns over 24 h were found in the most and least efficient animals. The most efficient ate less and had fewer meals during day time hours and early evening than the least efficient animals. The most efficient animals spent less time feeding in the afternoon compared with the least efficient group, but this pattern was reversed in the early hours of the morning (midnight to 6 am). The reason for the difference is unknown, nor the significance in relation to RFI. Future research could explore this more extensively.

RFI was not related to social dominance in this study, suggesting that selecting for efficient animals is unlikely to cause changes in social hierarchy in cattle groups. Furthermore, RFI was not consistently related to activity patterns in this study, although the analysis may have been constrained by the restricted opportunity for expression in the facilities. Behaviour may be more significant in pastoral systems where animals must walk greater distances, interact with each other, and compete for pasture. The role of activity in RFI warrants further investigation in grazing animals.

The most and least efficient animals from the present study were retained for further research, including reassessment for efficiency during lactation. Whether or not these animals retain the same efficiency status and magnitude of divergence in efficiency as milking animals, as they had during growth, is an important avenue of research. The next step should be to evaluate groups of animals with divergent RFI when grazing pasture.

7. APPENDICES

7.1 Appendix I

The following provides additional information to compliment the Materials and Methods chapter (chapter 3) by showing details of the facility and detailing the data measured by the system, and its presentation for analysis.

7.1.1 Feeding facility



Figure 7.1: View of one of the rows of pens in the purpose-built facility at Hawera, New Zealand.

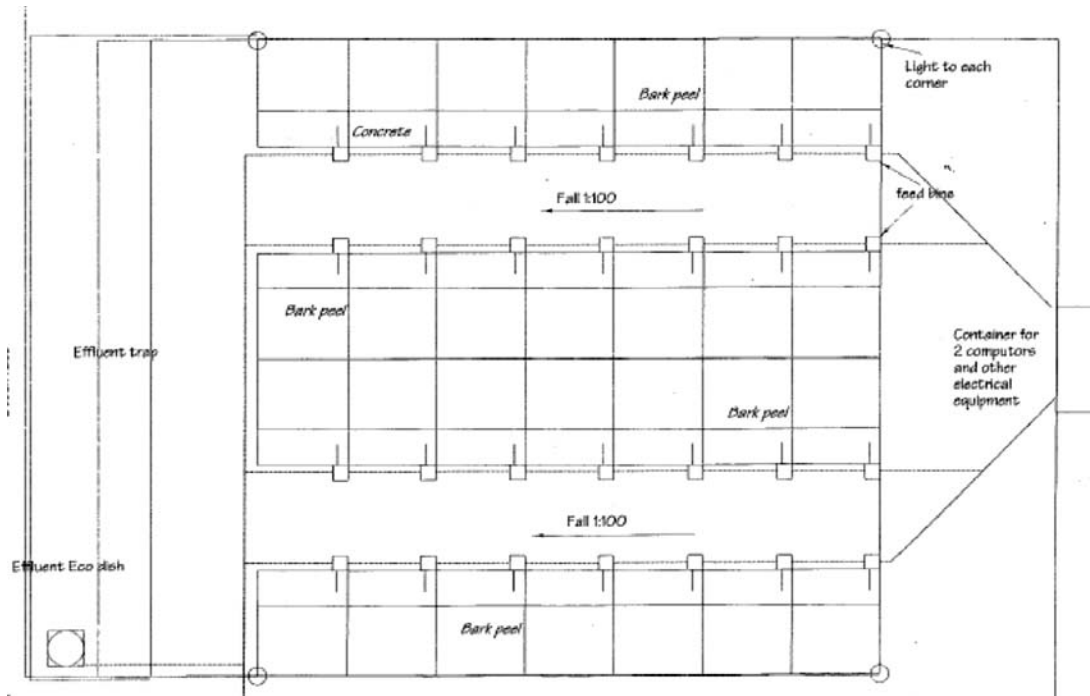


Figure 7.2: Diagram of the feeding facility, with four rows of seven pens opening to two races.



Figure 7.3: Animals are shut into the concrete area of the pen while soiled bedding is removed from the facility.



Figure 7.4: The feed bin sitting on load cells that weigh the bin continuously.



Figure 7.5: Entrance to the feed bin is via a hole in a plywood sheet. A feed chute formed by plywood sheets leading up to the bin (can be seen through hole for head) allows only one animal access to the feed at a time.

7.1.2 Electronic recording system

Multiple levels of data were produced. The data collected every second was recorded in a CSV (computer separated values) file, called a Level 1 file. Two Level 1 files were created every hour for 14 bins each and logged onto two computers. Each Level 1 file was about 4 MB in size and contained records of the date, time, bin number, EID and bin weight every second for every bin. An example of a Level 1 file is shown below:

Date/Time, Bin, EID/Weight

```
2007/12/19 00:00:01.87,R001,0,  
2007/12/19 00:00:01.89,S001,+074.06,  
2007/12/19 00:00:01.90,R002,000102858659,  
2007/12/19 00:00:01.92,S002,+091.74,  
2007/12/19 00:00:02.87,R001,0,  
2007/12/19 00:00:02.89,S001,+074.07,  
2007/12/19 00:00:02.90,R002,000102858659,  
2007/12/19 00:00:02.92,S002,+091.75,
```

The data were then smoothed and filtered by software provided by the manufacturers (Gallagher Ltd, Hamilton, New Zealand) to provide summary information of feeding events. Level 2 files were produced every day, and logged 20 lines per feeding session (i.e., the first 20 seconds of each meal) with the same information as in the Level 1 file. Therefore, the size of the file was dependent on the amount of feeding activity. An example of a Level 2 file is shown below:

Date/Time, Bin, EID, Weight

```
2007/12/18 23:59:56.93,2,0,91.71  
2007/12/18 23:59:57.92,2,0,91.71  
2007/12/18 23:59:58.92,2,000102858659,91.71  
2007/12/18 23:59:59.92,2,000102858659,91.71  
2007/12/19 00:00:00.92,2,000102858659,91.72  
2007/12/19 00:00:01.92,2,000102858659,91.74  
2007/12/19 00:00:02.92,2,000102858659,91.75  
2007/12/19 00:00:03.92,2,000102858659,91.77  
2007/12/19 00:00:16.89,1,0,74.09  
2007/12/19 00:00:17.89,1,0,74.10  
2007/12/19 00:00:18.89,1,0,74.10  
2007/12/19 00:00:19.89,1,0,74.09  
2007/12/19 00:00:20.89,1,0,74.09  
2007/12/19 00:00:21.89,1,0,74.11
```

Level 3 files were produced every day and summarised the individual feeding events that occurred that day for each animal and each pen (i.e., one line logged per feeding session). Data presented in Level 3 files were the date, start and end time of the meal, bin number, EID, start and end weight of the bin for each meal (kg), the amount consumed (kg), session length (seconds), the interval between sessions (seconds), and unaccounted weight (kg). An example of a Level 3 file is shown below:

Date/Time(Start), Date/Time(End), Bin, EID, Start Weight, End Weight, Consumed, Session Length(sec), Session Interval(sec), Unaccounted Weight

```
2007/12/18 23:38:34.89,2007/12/19 00:01:16.89,1,000102858801,74.73,74.03,0.70,1362,3558,0.01
2007/12/18 23:59:59.92,2007/12/19 00:23:14.92,2,000102858659,91.71,90.99,0.72,1395,712,-0.03
2007/12/19 00:36:47.92,2007/12/19 00:47:58.92,2,000102858914,91.02,90.65,0.37,671,813,-0.03
2007/12/19 00:50:26.89,2007/12/19 01:04:16.89,1,000102859389,74.01,73.66,0.35,830,2950,0.02
2007/12/19 01:04:41.89,2007/12/19 01:12:35.89,1,000102858981,73.64,73.41,0.23,474,25,0.02
2007/12/19 01:21:00.89,2007/12/19 01:32:18.89,1,000102859072,73.40,73.00,0.40,678,505,0.01
2007/12/19 01:23:06.92,2007/12/19 01:42:04.92,2,000102858659,90.67,90.18,0.49,1138,2108,-0.02
```

Level 4 files contained the average weights of each bin every 30 seconds. A new Level 4 file was created each day and was about 1.3 MB in size. An example of a Level 4 file is shown below:

Date/Time, Bin, AvWeight

```
2007/12/19 00:00:08,1,74.13
2007/12/19 00:00:08,2,91.72
2007/12/19 00:00:39,1,74.17
2007/12/19 00:00:39,2,91.74
2007/12/19 00:01:10,1,74.21
2007/12/19 00:01:10,2,91.70
2007/12/19 00:01:41,1,74.04
2007/12/19 00:01:41,2,91.77
2007/12/19 00:02:11,1,74.02
2007/12/19 00:02:11,2,91.67
```

Additional summaries of the data were extracted from the Level 3 data using a program called Feedcheck V1.3, creating a folder (named with the date (yymmdd) e.g., 090119) which contained 80+ files. Two of these files were summary files (one for each set of 14 pens). The summary files contained a summary of the daily activity of all the bins and a summary of the daily activity of each animal in each pen. The bin summary displayed how many EID tags

were detected in each bin, the feed amount (kg; net of feed added and eaten from the bin), feed count (number of feeding events in that bin), feed duration (hours; daily bin occupation time), and feed (kg) unaccounted for by feeding sessions. The information for each animal in each bin included a number identification of the animal for graphing purposes, animal EID, feed count (number of feeding events), feed amount (kg; daily intake), and feed duration (length of time each animal spent eating). An example of the summary file is shown below.

Summary Report for 080518

Bin	Unique EIDs	Feed Amount	Feed Count	Feed Duration	Feed Unaccounted
Bin 001	9	-2.74	94	21.64	0.12
Bin 002	9	-7.55	103	20.36	0.24
Bin 003	9	1.28	146	18.73	2.23
Bin 004	9	10.32	151	20.06	0.21
Bin 005	9	13.17	59	22.22	-0.70
Bin 006	9	8.69	105	19.82	0.26
Bin 007	9	11.68	86	17.67	0.19
Bin 008	9	10.92	97	20.67	4.58
Bin 009	9	11.27	69	21.60	0.02
Bin 010	9	12.92	58	21.71	-0.56
Bin 011	0	0	0	0	0
Bin 012	9	9.96	74	20.69	0.12
Bin 013	8	0.26	73	19.87	0.36
Bin 014	0	0	0	0	0

Processing Local 080518.A.L3.CSV for Bin 001

Bin	Graph ID	EID	Feed Count	Feed Amount	Feed Duration
Bin 001	9	Tag 106314622	1	-77.2	1.43
Bin 001	1	Tag 94246653	10	10.55	2.58
Bin 001	8	Tag 94323945	7	7.93	2.51
Bin 001	6	Tag 94247117	14	8.52	2.30
Bin 001	3	Tag 94324352	12	9.84	2.08
Bin 001	5	Tag 94323991	11	9.4	2.27
Bin 001	7	Tag 94246593	13	8.48	2.03
Bin 001	4	Tag 94324010	12	10.12	3.70
Bin 001	2	Tag 94247090	14	9.62	2.75

In addition to these summary files, the Feedcheck V1.3 program also produced three files for each bin. These three files were in CSV format and contained data on the amount eaten from each bin, the timing of feed bin use, and the weight of the bin throughout the day that could be graphed to show data for each bin (e.g., Figures 7.6-7.9).

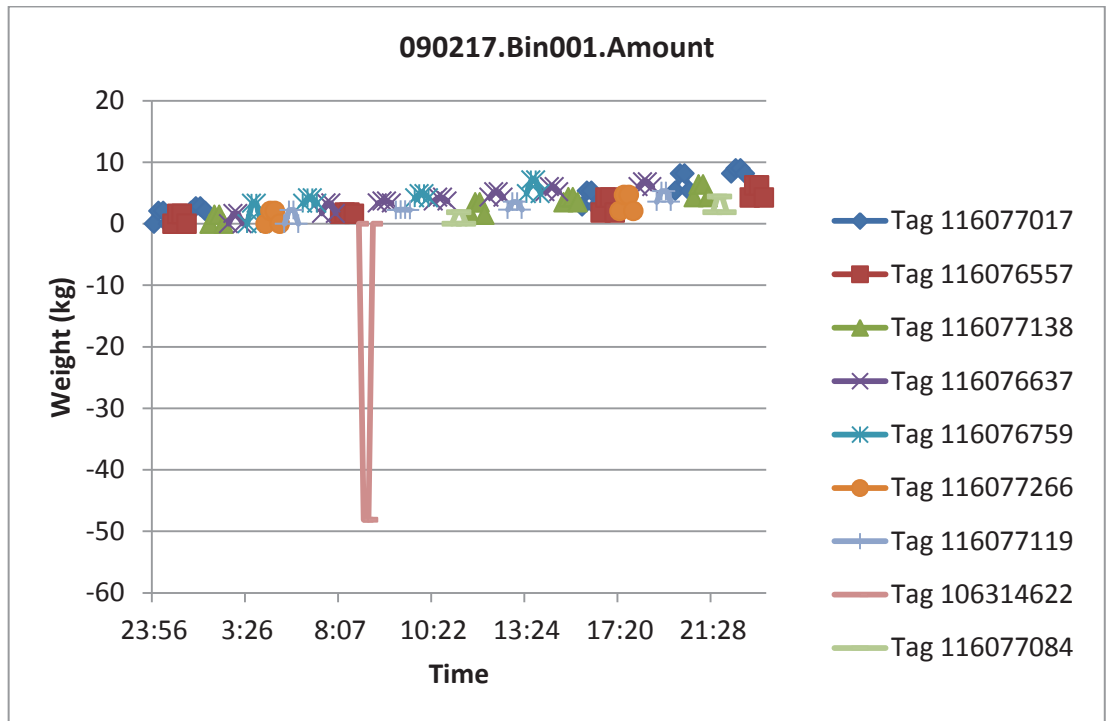


Figure 7.6: Bin weight over 24 h showing the filling event (0815-0900 h). Individual tag data are expanded and presented in Figure 7.7.

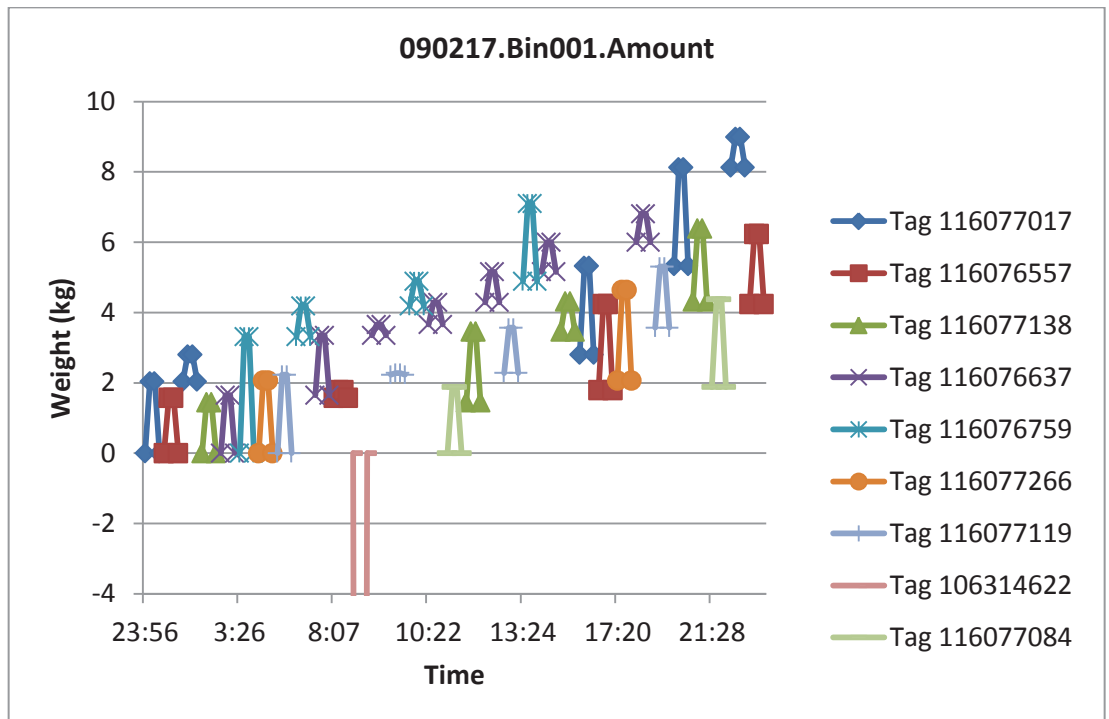


Figure 7.7: Weight of cubes consumed by individual animals at feeding events from one bin.

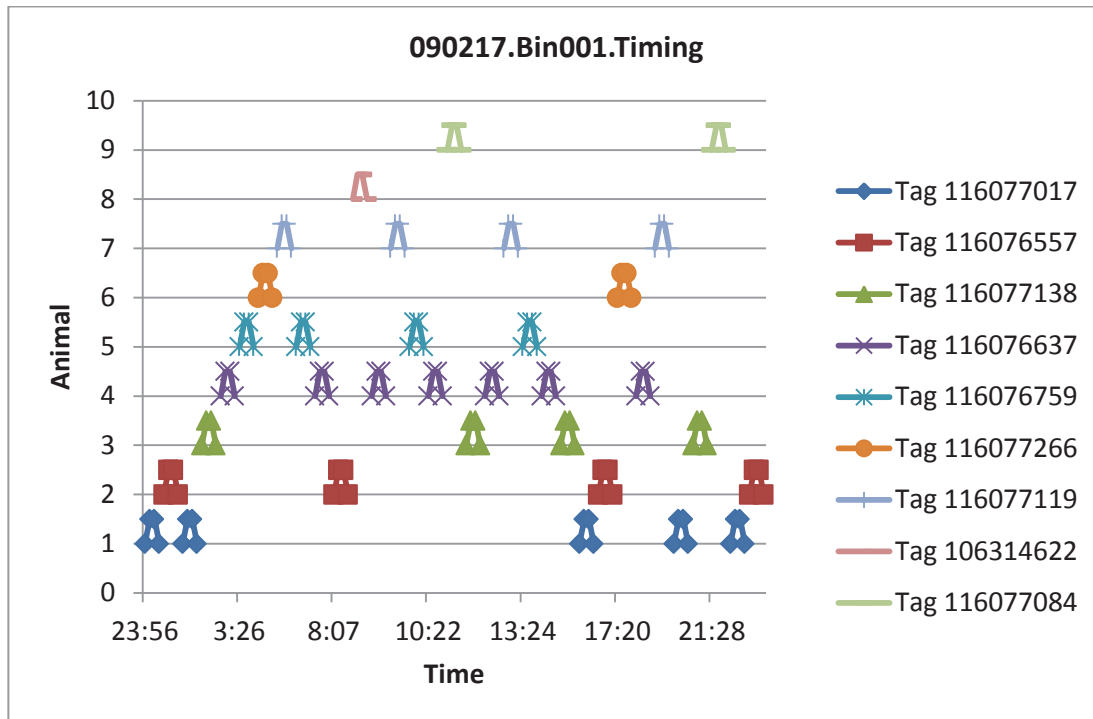


Figure 7.8: Timing of feeding sessions for each animal identifiable by tag number (row) and colour in a pen.

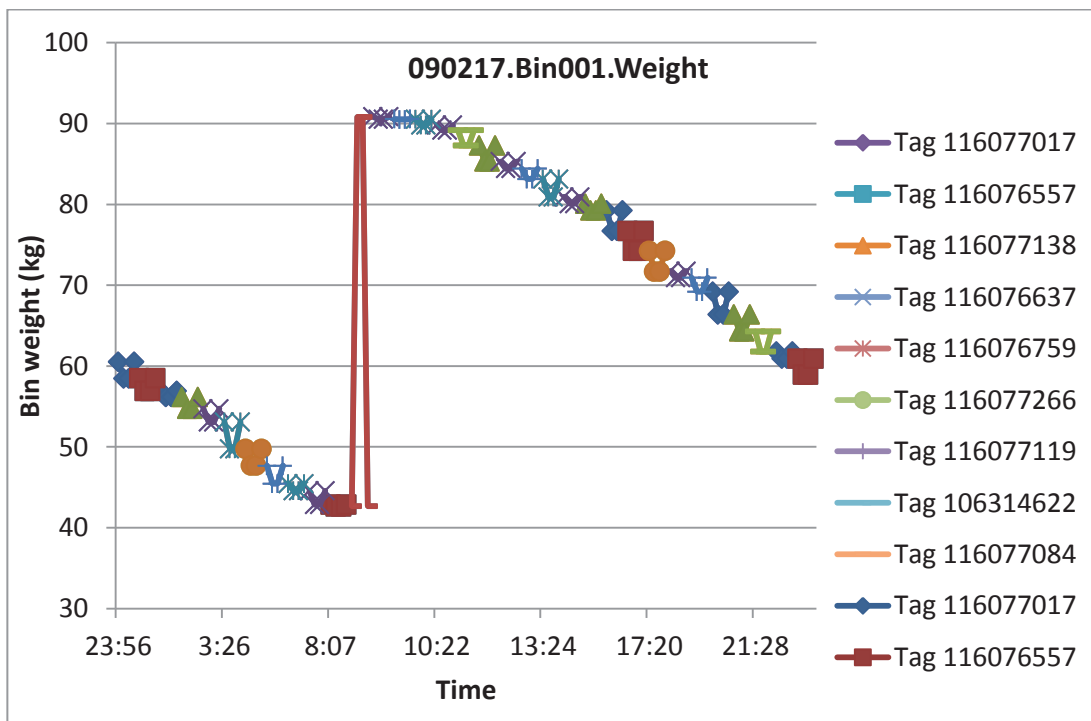


Figure 7.9: Example of changes in bin weights over time, including a filling event.

7.2 Appendix II

This appendix provides additional data used in the analyses; section 7.2.1 depicts data from Cohort 2 that were used in development of regression relationships between RFI and feeding parameters, that were then applied to all cohorts. Details are also provided for most and least efficient groups from all cohorts (section 7.2.2) and the analysis of temporal feeding patterns in all cohorts (section 7.2.3). Pen activity profiles are presented as histograms for each pen in section 7.2.4.

7.2.1 Correlations between feeding behaviour and RFI in Cohort 2

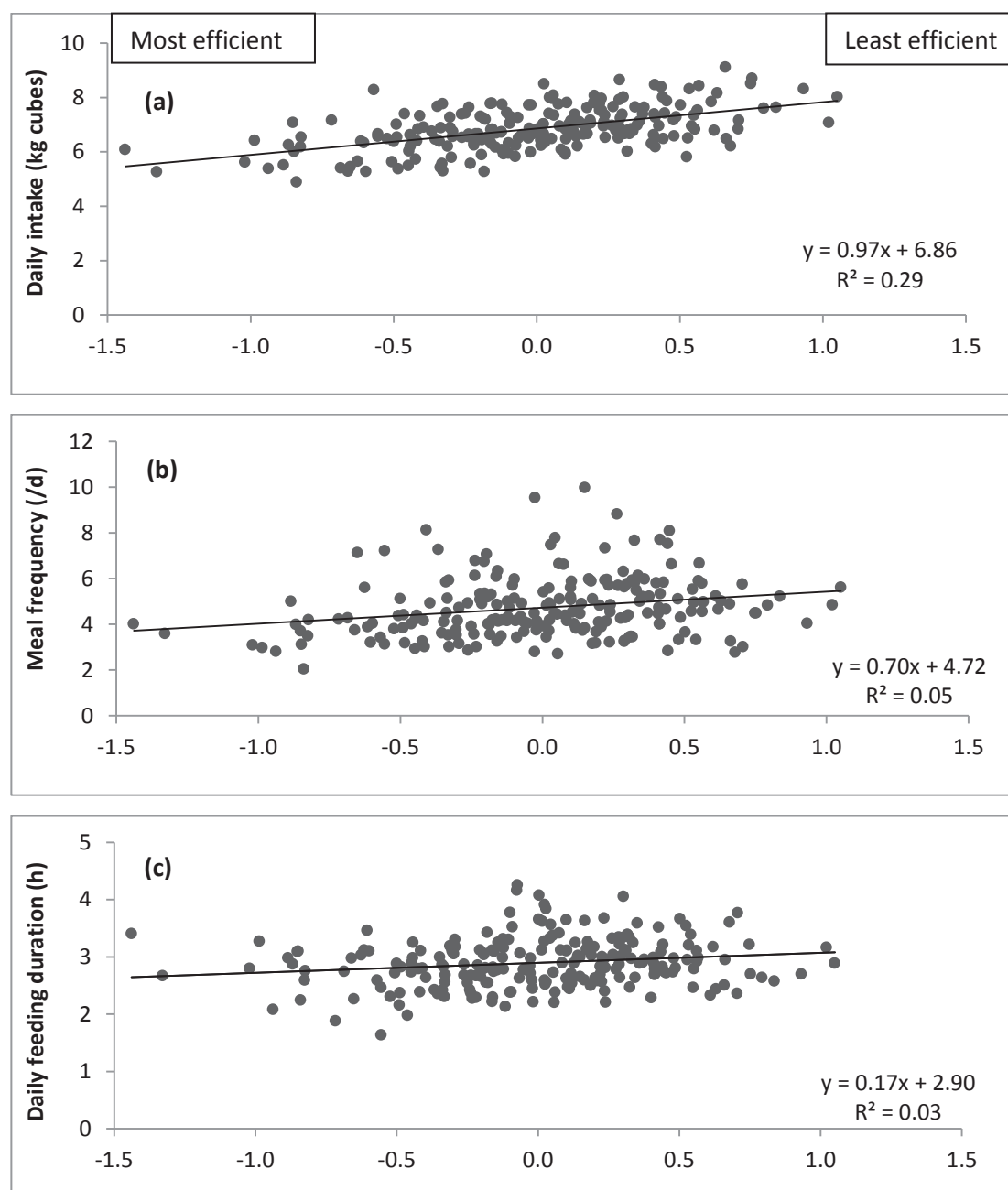


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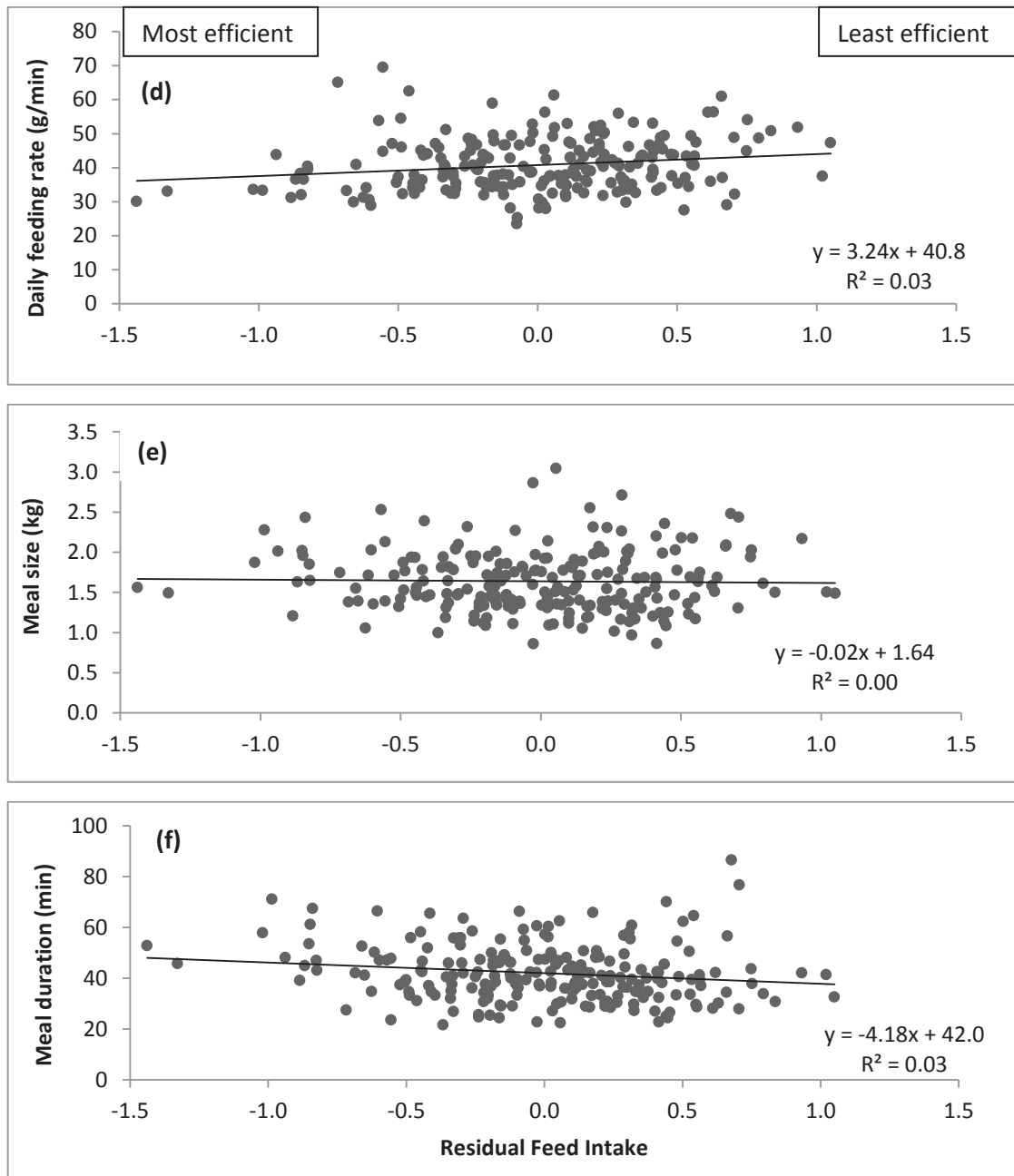


Figure 7.10: Examples from Cohort 2 of correlations between residual feed intake (RFI) and feeding behaviour characteristics: (a) intake, (b) meal frequency, (c) feeding duration, (d) feeding rate, (e) meal size, (f) meal duration.

7.2.2 Comparison of the 10% most efficient and 10% least efficient from each cohort

Table 7.1: Mean values of the 10% most (n = 16) and 10% least (n = 16) efficient animals in **Cohort 1** for residual feed intake (RFI), average daily liveweight gain (ADG), liveweight (mid-point of the regression over the trial period), and feeding behaviour.

Cohort 1	10% most efficient	10% least efficient	SED	p value
RFI (kg cubes)	-0.94	0.87	0.13	<0.0001
ADG (kg/d)	0.94	0.88	0.04	0.120
Liveweight (kg)	243	237	5.27	0.286
Daily intake (kg cubes)	8.40	10.27	0.32	<0.0001
Meal frequency (/d)	10.8	17.1	2.80	0.031
Feeding duration (h/d)	2.46	2.44	0.16	0.914
Feeding rate (g cubes/min)	59.8	71.6	4.06	0.006
Meal size (kg cubes/meal)	0.94	0.84	0.13	0.453
Meal duration (min/meal)	16.7	12.4	2.46	0.088

Table 7.2: Mean values of the 10% most (n = 22) and 10% least (n = 22) efficient animals in **Cohort 2** for residual feed intake (RFI), average daily liveweight gain (ADG), liveweight (mid-point of the regression over the trial period), and feeding behaviour.

Cohort 2	10% most efficient	10% least efficient	SED	p value
RFI (kg cubes)	-0.82	0.69	0.06	<0.0001
ADG (kg/d)	0.77	0.77	0.04	0.889
Liveweight (kg)	173	176	5.98	0.525
Daily intake (kg cubes)	6.04	7.61	0.24	<0.0001
Meal frequency (/d)	3.9	4.8	0.31	0.006
Feeding duration (h/d)	2.80	2.90	0.12	0.384
Feeding rate (g cubes/min)	37.3	45.0	2.58	0.004
Meal size (kg cubes/meal)	1.77	1.77	0.11	0.962
Meal duration (min/meal)	49.4	42.0	4.04	0.072

Table 7.3: Mean values of the 10% most (n = 22) and 10% least (n = 22) efficient animals in **Cohort 3** for residual feed intake (RFI), average daily liveweight gain (ADG), liveweight (mid-point of the regression over the trial period), and feeding behaviour.

Cohort 3	10% most efficient	10% least efficient	SED	p value
RFI (kg cubes)	-0.95	0.88	0.11	<0.0001
ADG (kg/d)	0.89	0.90	0.04	0.677
Liveweight (kg)	193	197	5.40	0.478
Daily intake (kg cubes)	7.33	9.19	0.24	<0.0001
Meal frequency (/d)	8.2	6.8	1.05	0.212
Feeding duration (h/d)	2.81	2.88	0.16	0.683
Feeding rate (g cubes/min)	46.8	54.4	3.28	0.024
Meal size (kg cubes/meal)	1.22	1.51	0.10	0.006
Meal duration (min/meal)	29.1	28.5	2.47	0.816

Table 7.4: Mean values of the 10% most (n = 22) and 10% least (n = 22) efficient animals in **Cohort 4** for residual feed intake (RFI), average daily liveweight gain (ADG), liveweight (mid-point of the regression over the trial period), and feeding behaviour.

Cohort 4	10% most efficient	10% least efficient	SED	p value
RFI (kg cubes)	-0.86	0.73	0.10	<0.0001
ADG (kg/d)	0.92	0.93	0.04	0.816
Liveweight (kg)	181	181	4.22	0.959
Daily intake (kg cubes)	6.67	8.29	0.21	<0.0001
Meal frequency (/d)	4.9	7.3	1.24	0.065
Feeding duration (h/d)	2.69	2.89	0.16	0.212
Feeding rate (g cubes/min)	44.4	49.4	3.37	0.142
Meal size (kg cubes/meal)	1.59	1.54	0.14	0.714
Meal duration (min/meal)	39.8	32.1	4.05	0.064

Table 7.5: Mean values of the 10% most (n = 22) and 10% least (n = 22) efficient animals in **Cohort 5** for residual feed intake (RFI), average daily liveweight gain (ADG), liveweight (mid-point of the regression over the trial period), and feeding behaviour.

Cohort 5	10% most efficient	10% least efficient	SED	p value
RFI (kg cubes)	-1.04	0.95	0.09	<0.0001
ADG (kg/d)	0.87	0.89	0.03	0.510
Liveweight (kg)	191	191	3.84	0.943
Daily intake (kg cubes)	6.78	8.80	0.17	<0.0001
Meal frequency (/d)	5.1	7.3	0.94	0.021
Feeding duration (h/d)	2.71	3.04	0.12	0.010
Feeding rate (g cubes/min)	43.0	49.6	1.97	0.002
Meal size (kg cubes/meal)	1.55	1.57	0.13	0.894
Meal duration (min/meal)	37.6	32.9	3.33	0.170

7.2.3 Temporal feeding patterns

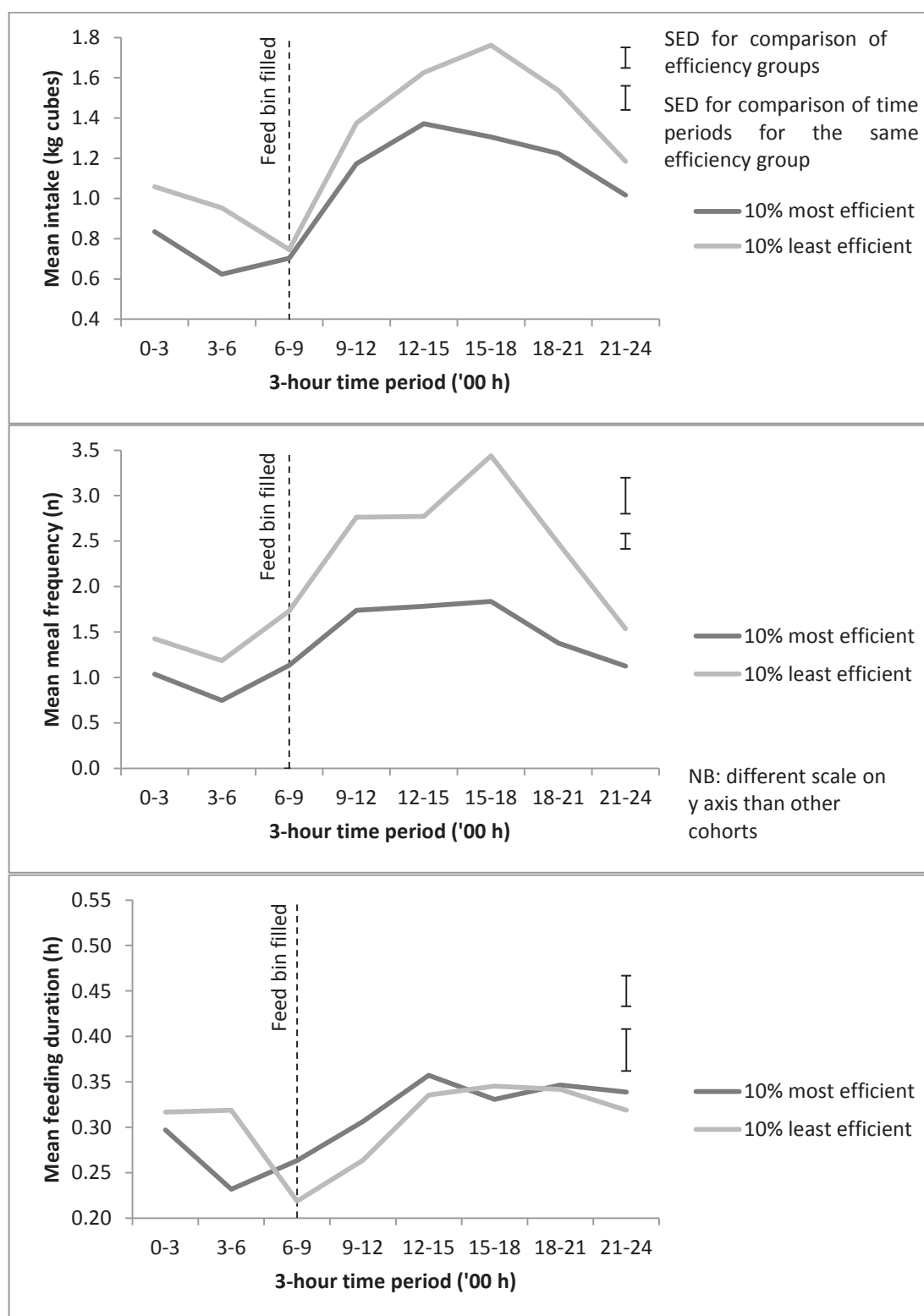


Figure 7.11: Temporal feeding patterns per 3-hour time period (commencing midnight) of the 10% most efficient and 10% least efficient animals in **Cohort 1**. Error bars indicate the standard error of the difference (SED).

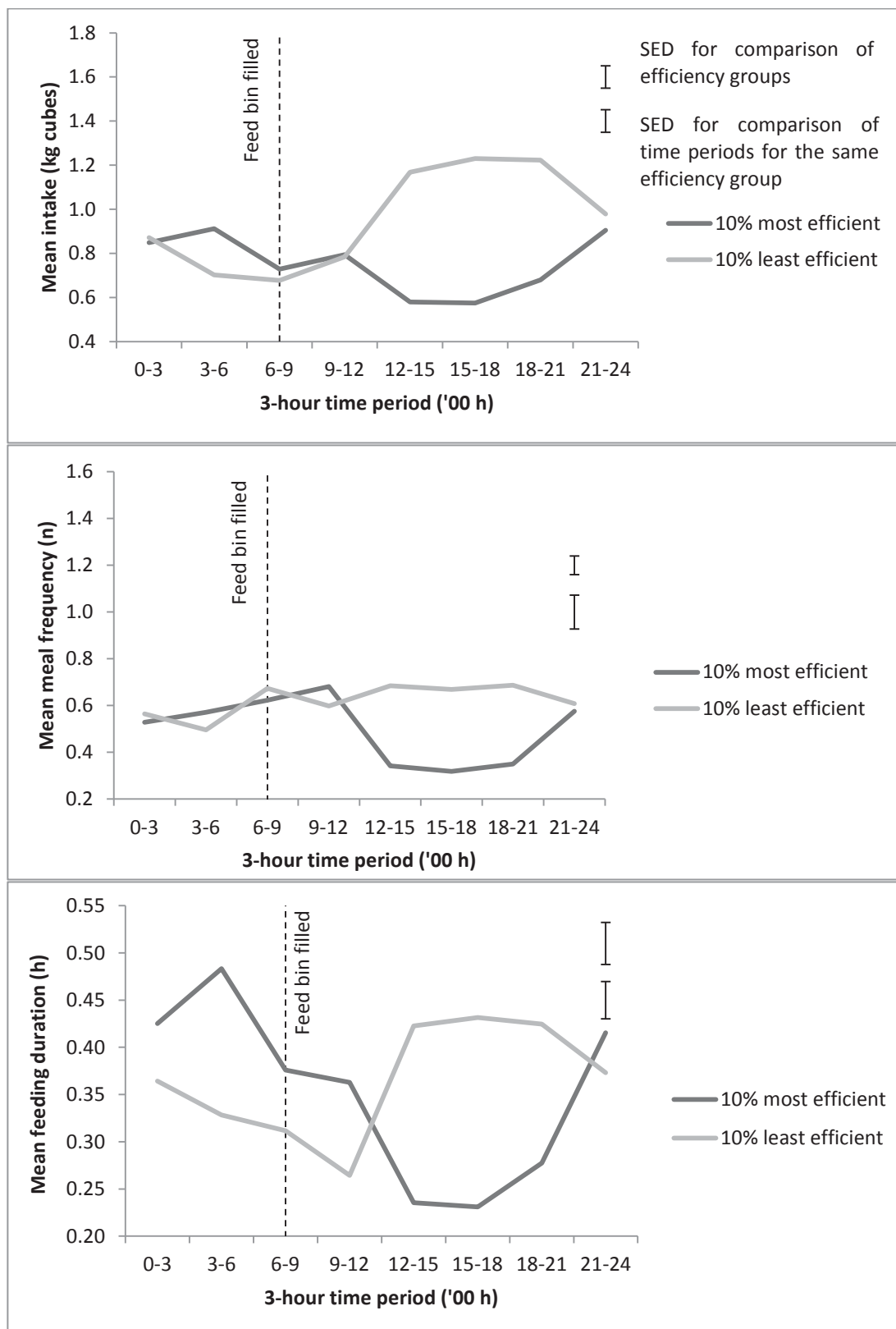


Figure 7.12: Temporal feeding patterns per 3-hour time period (commencing midnight) of the 10% most efficient and 10% least efficient animals in **Cohort 2**. Error bars indicate the standard error of the difference (SED).

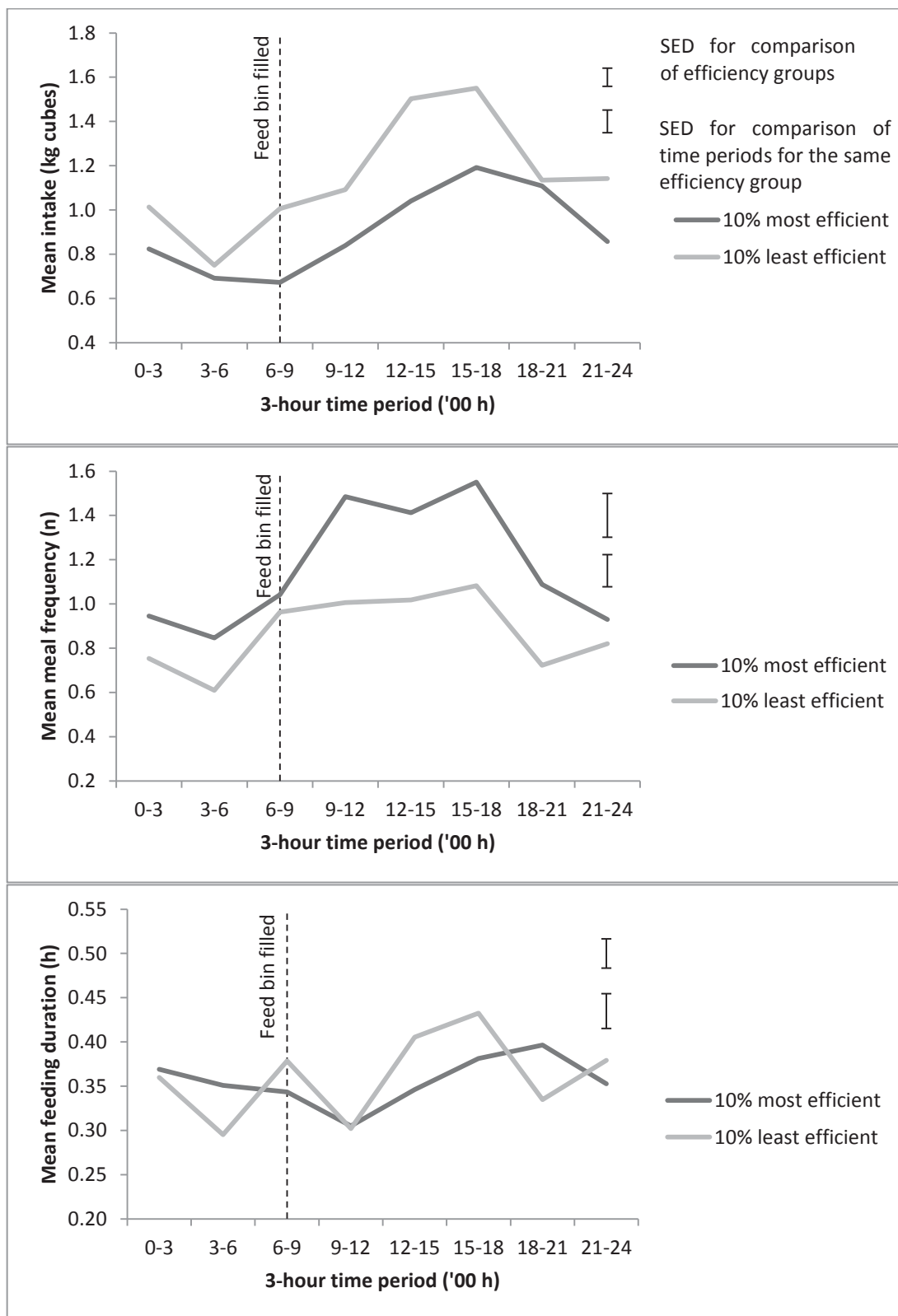


Figure 7.13: Temporal feeding patterns per 3-hour time period (commencing midnight) of the 10% most efficient and 10% least efficient animals in **Cohort 3**. Error bars indicate the standard error of the difference (SED).

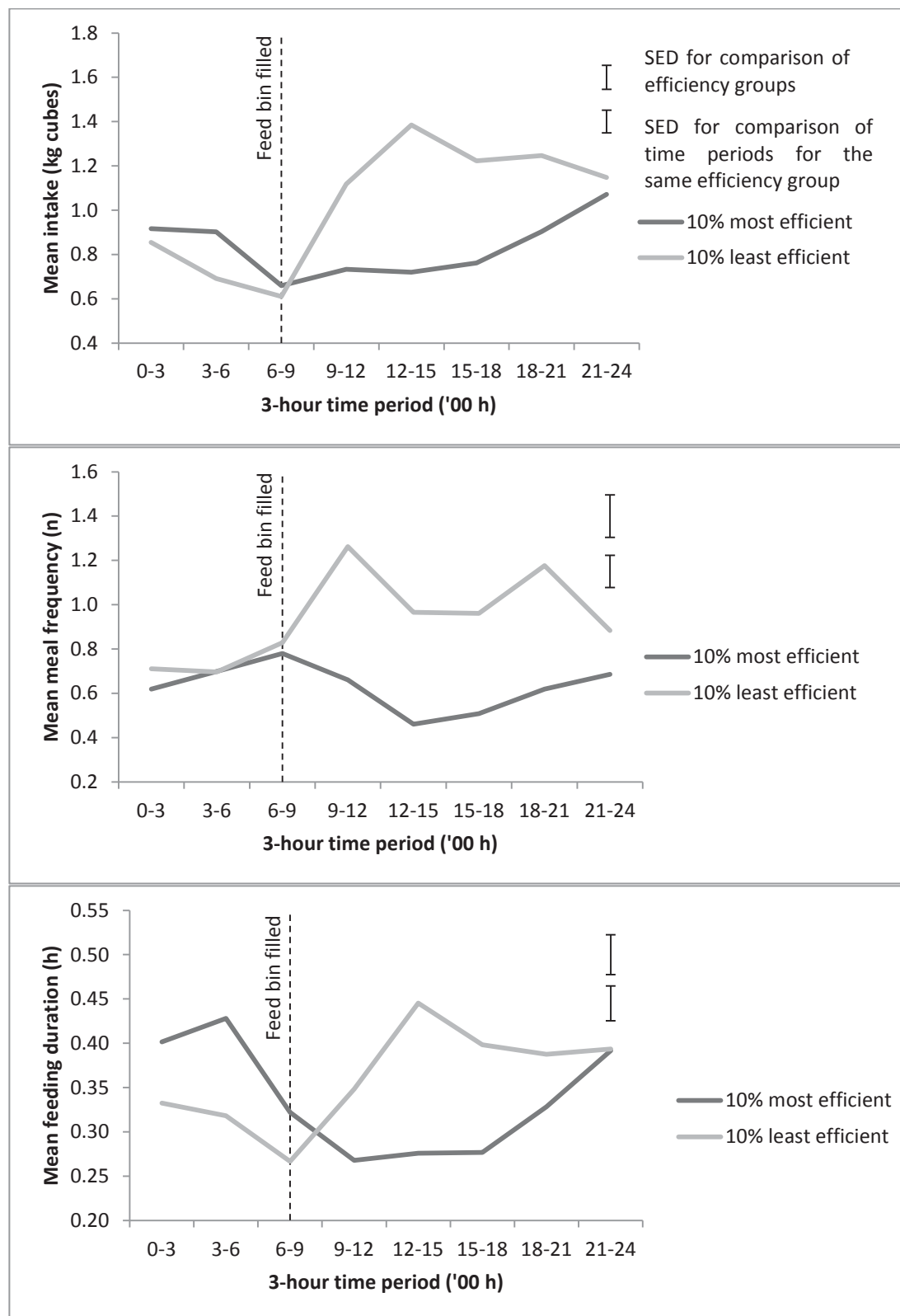


Figure 7.14: Temporal feeding patterns per 3-hour time period (commencing midnight) of the 10% most efficient and 10% least efficient animals in **Cohort 4**. Error bars indicate the standard error of the difference (SED).

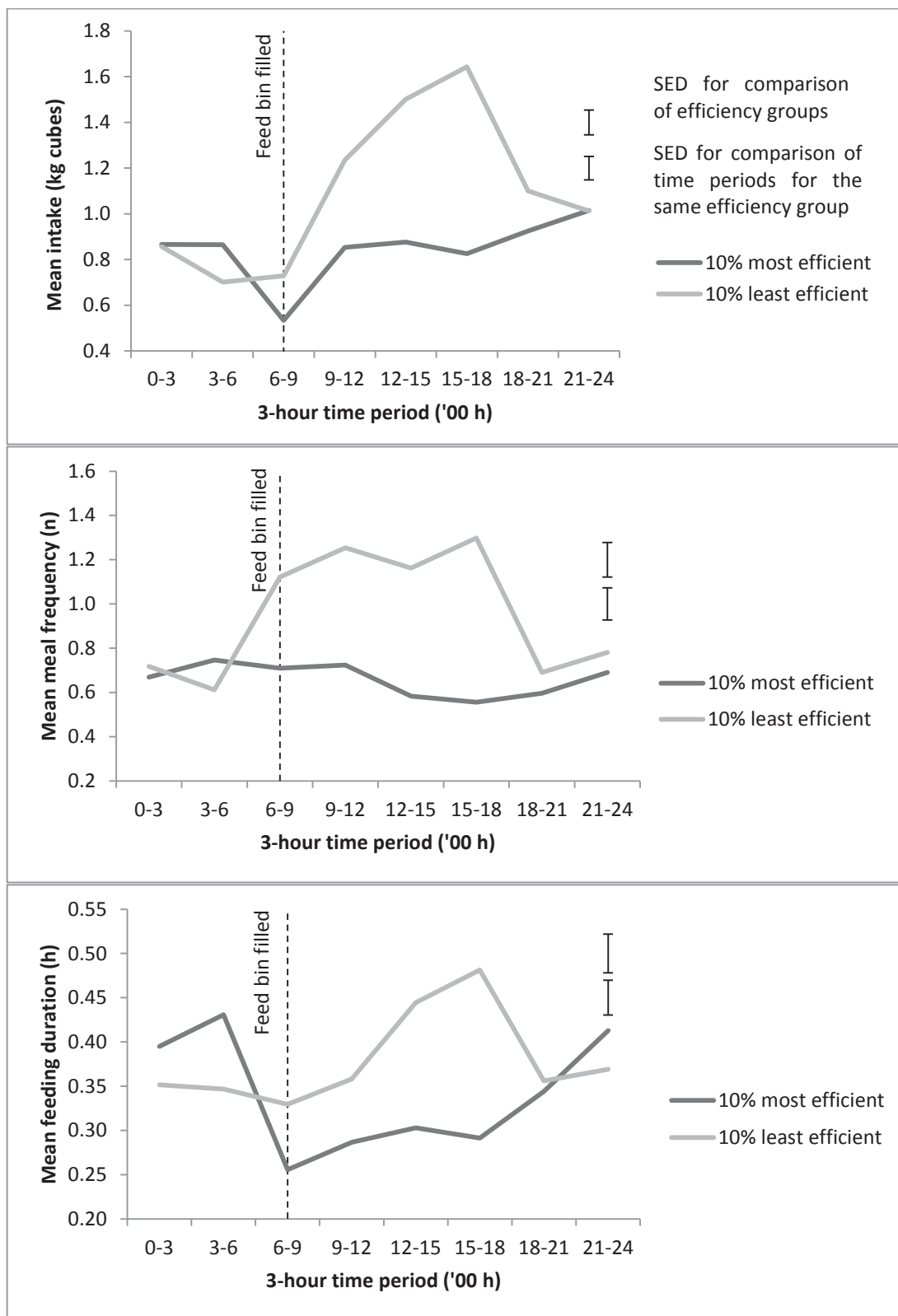


Figure 7.15: Temporal feeding patterns per 3-hour time period (commencing midnight) of the 10% most efficient and 10% least efficient animals in **Cohort 5**. Error bars indicate the standard error of the difference (SED).

7.2.4 Pen activity profiles

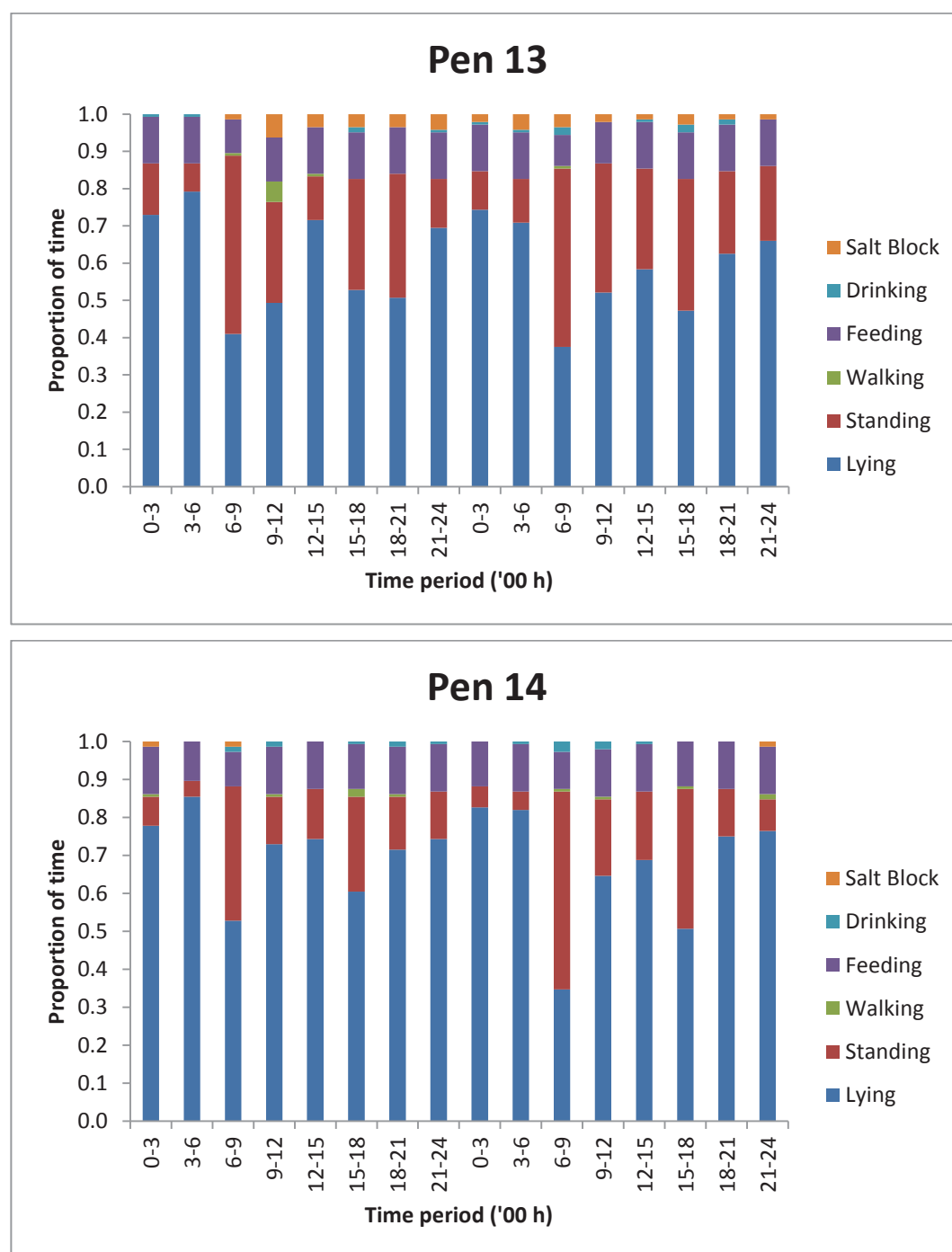


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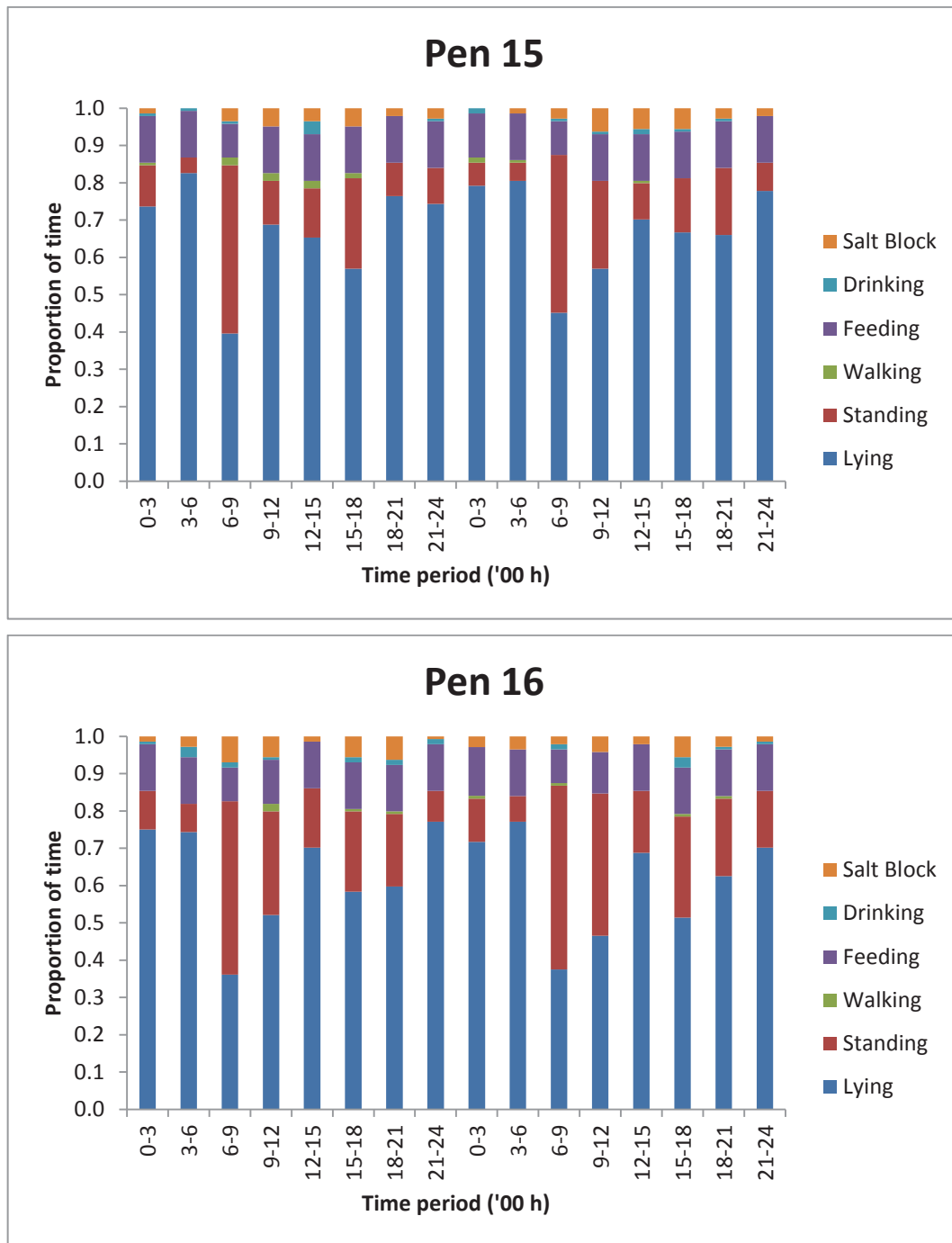


Figure 7.16: Average percentage of time spent in each activity in 3-hour time periods (commencing midnight) by animals in four pens (13-16) over 48 hours.

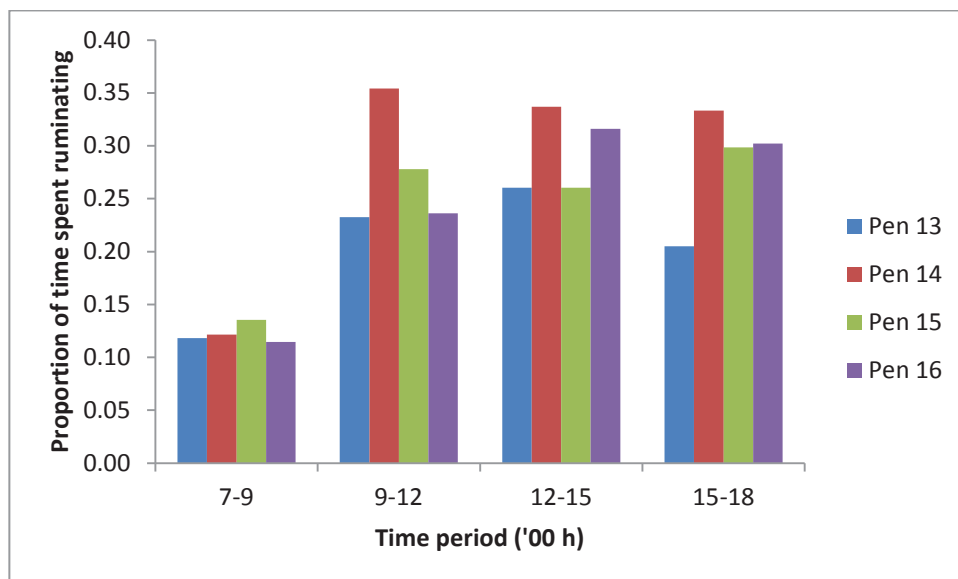


Figure 7.17: Proportion of time spent ruminating by animals in each pen during recording from 0700 - 1800 h. NB: rumination was not recorded from 0600 to 0700 h.

7.3 Appendix III

The topic of this thesis was not primarily concerned with animal welfare, but as a prelude to this research, I undertook Masters level university coursework. One of the papers that I studied was Animal Welfare Science. As a result of the ideas explored and discussed, my thinking on this subject area was further developed, resulting in a joint review publication with myself as the first author. This publication was awarded first prize for Most Commended Paper published in the New Zealand Veterinary Journal in 2011 by the Australian and New Zealand College of Veterinary Scientists (ANZCVS). The award letter and post-peer-reviewed version of the paper (to meet copyright regulations) are presented here (section 7.3.1).

The initial results of this study were also presented at the New Zealand Society of Animal Production conference in 2011. This publication is included in section 7.3.2 and is reproduced with the permission of the New Zealand Society of Animal Production.

7.3.1 Green, T. C., & Mellor, D. J. (2011). Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. New Zealand Veterinary Journal 59(6): 263-271, winner of the ANZCVS prize for Most Commended Paper published in the New Zealand Veterinary Journal in 2011.

May 14, 2012

Talia Green
DairyNZ Ltd
PO Box 10002
WELLINGTON 6143

Dear Talia

I am delighted to inform you that the review you co-authored with Professor David Mellor entitled, "Extending ideas about animal welfare assessment to include 'quality of life' and related concepts" has been judged the Most Commended Paper published in the *New Zealand Veterinary Journal* in 2011.

The award for Most Commended Paper is made by the Australian and New Zealand College of Veterinary Scientists (ANZCVS), a professional postgraduate certifying college that seeks to serve the veterinary profession and reward excellence.

The citation of the winning paper is:

Green TC, Mellor DJ. Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. *New Zealand Veterinary Journal* 59 (6), 263–71, 2011.

This is a distinction awarded by peers and colleagues in the veterinary profession throughout Australia and New Zealand that recognises the quality of scientific and/or observational content, style and presentation, applicability of findings to veterinary clinical practice, and the stage of the senior author's career when the work was undertaken.

On behalf of the Editors and Editorial Board of the *New Zealand Veterinary Journal* I congratulate you and David on your achievement. The College will notify you of arrangements for the award in due course.

Yours sincerely



Peter D Jolly BVSc BPhil PhD
Managing Editor

Extending ideas about animal welfare assessment to include ‘quality of life’ and related concepts

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Abstract

Ideas within the animal welfare science arena have evolved continuously throughout the last 30 years, and will continue to do so. This paper outlines some of these developments. These included reformulation of the five freedoms concept into the five domains of potential welfare compromise. This accommodated weaknesses in the former by distinguishing between the physical/functional and the mental factors that contribute to an animal’s welfare state. This development reflected a rising scientific acceptance that the mental experiences of animals were legitimate foci for study and highlighted that what the animal itself experiences represents its welfare status. Initially, most concepts of animal welfare emphasised predominantly negative subjective experiences, such as thirst, hunger and pain, and negative affective states or feelings including anxiety, fear and boredom, but today positive experiences or emotions such as satiety, vitality, reward, contentment, curiosity and playfulness are also considered to be important. During the same period, the focus shifted from evaluating the impacts of individual mental subjective experiences or emotions towards seeking a more comprehensive, multifactorial understanding. The five domains concept was specifically designed to achieve this. Subsequent notions about quality of life (QoL) had the same objective, and emphasised the importance of positive experiences. However, some approaches to QoL assessment relied heavily on empathetic speculation about what animals may experience subjectively and this raised concerns about inappropriate anthropomorphic projections. Such pitfalls may be minimised when informed personnel rigorously apply objectively based methodologies to QoL assessments limited to a short time frame. It is clear that both formal and somewhat less formal QoL assessments of this type are already used to guide decision-making about the ongoing care and therapeutic management of animals on a daily basis. However, application of the recently introduced concepts of ‘a life not worth living’, ‘a life worth avoiding’, ‘a life worth living’ and ‘a good life’ is problematical, because extending the assessment time scale to the whole of life is attended by a number of as yet

unresolved difficulties. Accordingly, their value in the practical management of animals is limited so that, at present, reliance on the minimum standards and recommendations for best practice outlined in codes of practice or welfare will continue to be necessary and worthwhile. Nevertheless, these concepts have value in providing a contextual theme that strongly focuses attention on the promotion of a lifelong QoL with an overall balance that is positive.

KEY WORDS: *Animal welfare, assessment criteria, quality of life, lifelong perspectives, a life worth living*

FAWC	Farm Animal Welfare Council of the United Kingdom
QoL	Quality of life

Introduction

The literature on animal welfare is diverse and expanding and reveals that ideas about animal welfare have evolved since it became established as a field of scientific investigations about 25-30 years ago (Nordenfelt 2006; Fraser 2008b; Mellor *et al.* 2009). Its scientific roots are multi-disciplinary (Sandøe and Simonsen 1992) and include fields such as ethology, physiology, pathology, biochemistry, genetics, immunology, nutrition, cognitive-neural science and veterinary epidemiology (Lassen *et al.* 2006; Fraser 2008b; Mellor *et al.* 2009). In addition, scientific thinking about animal welfare has been influenced by societal views on what constitutes acceptable and unacceptable ways of treating animals, views which reflected prevailing and evolving ethical, social, cultural, religious, economic and other values (Fisher and Mellor 2008; Fraser 2008b). One outcome is that novice readers and others, such as veterinarians and animal-based scientists who may simply wish to update their understanding for professional reasons, are confronted with a potentially bewildering complexity of intermeshed and sometimes contradictory ideas about animal welfare and how it can be assessed. Accordingly, this review is an attempt to bring some clarity to this area by outlining some key developments in past animal welfare science thinking and how they have given rise to current ideas.

It is important to note at the outset that no universally endorsed definition of animal welfare has emerged despite considerable effort to derive one (Nordenfelt 2006; Fisher 2009; Mellor *et al.* 2009). This occurred for several related reasons (Mellor and Bayvel 2011). First, being a fledgling scientific discipline 30 years ago, it is not surprising that early attempted definitions were modified or alternatives proposed as more investigators gave thought to the subject. Second, at each point in time changes in thinking were driven by interactions between what

was then new knowledge about animal functionality and the then current ideas regarding animal welfare, and these in turn gave rise to fresh thinking about both animal welfare and related functionality. Such refinement and replacement of ideas is anticipated to continue into the future. Third, as already noted, at each stage this scientific thinking was conducted in the context of dominant and changing societal views on what constitutes acceptable and unacceptable ways of treating animals (Fisher and Mellor 2008; Fraser 2008b). Despite the complexity, it is possible to discern several key orientations towards animal welfare, such that, in general, attempts to define it have emphasised coping with environmental challenges, meeting biological needs and wants, and recognition of the significance of subjective sensory or emotional experiences, feelings or affective states (Nordenfelt 2006; Broom 2008; Fisher 2009).

More specifically, there have been several key developments in thinking. The seminal idea of the five freedoms, which was formulated in 1979 (Webster 1994; Anonymous 2009), was reformulated into the concept of the five domains of potential welfare compromise (Mellor and Reid 1994), which were themselves then refined further (Mellor and Stafford 2001; Mellor 2004b; Mellor *et al.* 2009). In addition, three major orientations towards animal welfare thinking were shown to have emerged, namely, biological function, affective state and natural living (Fraser 2003), and relationships between them were explored (Mellor and Bayvel 2011). Within the affective state orientation, thinking moved from welfare status assessments being restricted mainly to individual negative experiences (Duncan 2005) to attempted assessments of multifactorial negative impacts representing a more integrated consideration of welfare state, for instance via the five domains approach (Mellor *et al.* 2009). Recently, increasing attention has been given to concepts of quality of life (QoL) that include positive experiences (Bono and De Mori 2005; Kirkwood 2007; Yeates and Main 2008). Now, the possibility of extending QoL concepts to include related notions of ‘a life not worth living’, ‘a life worth living’ and ‘a good life’ is being explored (Anonymous 2009; Wathes 2010; Yeates 2011). In the rest of this paper, these more recent ideas about animal welfare are presented and discussed, as is the direction of thinking that has given rise to the notion of quality of life and its further refinements. It is acknowledged that the development of these ideas was influenced by and influenced parallel developments in ethical thinking about animal welfare. As these have been documented in detail elsewhere (Nordenfelt 2006; Fraser 2008), apart from very brief reference to contextual ethical thinking, the emphasis here is on the scientific content of ideas about animal welfare.

Three orientations to animal welfare

As already noted, current animal welfare thinking recognises three major orientations: biological function, affective state and natural living (Fraser 2003). As these orientations have developed from different roots, the predominant one adopted by each person will reflect their particular worldview and convictions, i.e. their values. Moreover, each orientation has been and is informed by scientific knowledge. Hence, there is interplay of values and science, and different conclusions about animal welfare status may be reached because of the different values frameworks adopted (Fraser 2003). As expected, these three orientations to some extent reflect the historical development of related scientific thinking and together contribute to a more comprehensive understanding of animal welfare.

Biological function

According to the biological function orientation an animal has good welfare when, among other attributes, it grows well, is in good health, reproduces successfully, and is relatively stress free (Barnett and Hemsworth 2003; Fraser 2003; Mellor *et al.* 2009). This orientation arose during the early 1980s when physiological and behavioural indices of these forms of biological performance were well established and at a time when scientists were still strongly discouraged from inferring that animals could experience mental subjective states or feelings (Wemelsfelder 1997; Duncan 2005; Fraser 2008b). At this time, reference to biological function, which represents the physical wellbeing of animals, appeared to have been a sound starting point, and still has a place today (see below), but by excluding or down playing relationships to associated mental states it provided a limited perspective. Thus, in the early 1990s other animal welfare scientists began to give more attention to the mental experiences animals may have, including both negative and positive affective states (Duncan and Petherick 1991; Fraser and Duncan 1998; Duncan 2005).

Affective state

Although the idea that welfare includes both the mental and physical wellbeing of an animal was articulated at least 55 years ago (Kirkden and Pajor 2006; Anonymous 2009), it took until the mid-1990s for this notion to begin to be accepted scientifically. By the early 2000s the concept of affective state or feelings had become well accepted (Gregory 2004; Duncan 2005) and today is the basis of much animal welfare science thinking (Wemelsfelder 2007; Broom 2010; Mellor 2011). Clearly, mental (welfare) states whether good or bad can only be experienced by an animal when it is both sentient and conscious (Mellor and Diesch 2006; Mellor *et al.* 2009; Webster 2011). Thus, most scientists now accept that the sophisticated central nervous systems of mammals can support conscious mental experiences (Kirkden and Pajor 2006; Denton *et al.* 2009) and few would question whether such animals could have

subjective experiences or feelings (Duncan 2005) such as thirst, hunger, pain, breathlessness and nausea (Mellor *et al.* 2009; Webster 2011). Mammals are also considered to experience emotional or affective states (Duncan 2005; Kirkden and Pajor 2006; Mendl *et al.* 2010). For instance, they are often observed to engage in actions or behaviours with purpose, energy and intention (Wemelsfelder 1997; Panksepp 2005; Kirkden and Pajor 2006). They appear motivated to achieve a certain goal; they persist with it, and if they do not succeed, they may show what appears to be frustration or anger (Panksepp 2005; Kirkden and Pajor 2006; Boissy *et al.* 2011). As in humans, it seems likely that apparently strong urges of this type would be accompanied by negative or positive feelings (Wemelsfelder 1997; Panksepp 2005; Mendl *et al.* 2010). Examples of such negative feelings are likely to include anxiety, fear, boredom, helplessness and loneliness (Mellor *et al.* 2009; Mendl *et al.* 2010). Positive feelings, including satiety, vitality, reward, contentment, curiosity and playfulness, are likely to accompany good health, companionship, exploration, foraging and play (Panksepp 2005; Mendl *et al.* 2010; Mellor 2011). According to the affective state orientation, therefore, an animal's welfare will be good when it adapts with positive emotional experiences and/or without negative experiences during its interactions with other animals, people and the environment (Fraser 2003).

Natural living

The natural living orientation, which developed in parallel with the other two orientations, incorporates the view that the closer an animal is to its natural, wild state, especially with regard to its ability to express natural behaviours, the better its welfare may be (Fraser 2003). While this view can provide a useful perspective when, for example, farming systems restrict behavioural expression in barren environments, it must also be noted that the welfare of the wild ancestors of current domesticated species was not necessarily good in other respects. Thus, although animals in the wild live naturally, without human intervention they may be in poor physical condition as a result of nutritional inadequacies, climatic challenge, disease states and predation, to give only a few examples of factors that would have negative impacts on their welfare (Mellor *et al.* 2009). Hence, when evaluating animal welfare status, reference to natural living alone is probably not adequate when viewed in terms of its full welfare implications. However, in highlighting negative behavioural consequences of restrictive housing conditions, for example, it is useful to consider natural living together with the biological function and affective state orientations (Mellor and Bayvel 2011).

The five domains

The five domains of potential welfare compromise, originally formulated in 1994 (Mellor and Reid 1994), have been refined subsequently (Mellor and Stafford 2001; Mellor 2004b; Mellor

et al. 2009). They were derived from the five freedoms (Table 1), which were developed by the United Kingdom Farm Animal Welfare Council (FAWC) in 1979 (Webster 1994; Anonymous 2009) when biological function dominated early animal welfare science thinking.

The five freedoms represented a good initial way to characterise various dimensions of animal welfare in terms that were current during the 1980s, and the freedoms are still widely referenced today (Bayvel 2004; Anonymous 2009). However, they have limitations. Being expressed in terms of freedoms, i.e. a complete absence of the named features, they represent idealised goals, which in fact are not attainable during the life of any animal. Also, they conflated the named freedom and its remedy, and thereby did not specifically identify the physical/functional source of the associated welfare compromise. However, one benefit was that the freedoms directed attention towards thirst, hunger, discomfort, pain, fear and distress, and thereby anticipated the later acceptance of subjective experiences, including affective or emotional states, as an important component of animal welfare science thinking.

The concept of the five domains of potential welfare compromise and its refinements (Mellor *et al.* 2009) were formulated to remedy these difficulties (Table 2). Expressed in terms of compromise, and not freedoms, they address more directly the practical reality of what can go wrong with an animal's welfare. The five domains are: nutrition, environment, health, behaviour, and mental state. The first four domains are predominantly physical/functional, and the last, mental state, represents the overall experience of the animal, i.e. its welfare status. In this way the five domains integrate the biological function and affective state orientations as identifiable entities.

Conditions in the first four domains give rise to sensory inputs that may lead to perceived subjective experiences in the mental domain (Mellor *et al.* 2009). For example: in the nutrition domain, water or food deprivation may lead to the subjective experience of thirst or hunger, respectively; in the environment domain, extremes of cold or heat may lead to chilling-related debilitation or hyperthermic distress, respectively; disease or injury in the health domain may lead to a number of experiences including breathlessness, nausea, sickness, pain, distress, fear or anxiety; and limitations on behavioural expression due to space restrictions, isolation or barren environments may lead to feelings such as boredom, frustration, loneliness or helplessness. In the mental domain, internally-derived sensory inputs arising from compromise in the other four domains, plus cognitive inputs and related mental activity arising from external environmental challenges that elicit 'fight-flight-fright' or other responses, may give rise to sensations of thirst, hunger, weakness, debility, breathlessness, nausea, sickness, pain, distress, fear, anxiety, helplessness, boredom, and so on (Table 2). It is noteworthy that this

list of potential negative experiences significantly extends that incorporated originally in the five freedoms (Table 1).

As well as such negative subjective states, animals are likely to have positive experiences (Duncan 2005; Yeates and Main 2008; Mendl *et al.* 2010). Indeed, good animal welfare is now considered to result not only from an absence of negative experiences, but also from the presence of positive experiences or sensations (Kendrick 2007; Yeates and Main 2008; Mellor 2011). Examples of positive experiences, as noted above, may include feelings of satiety, vitality, reward, contentment, curiosity and playfulness (Mellor *et al.* 2009; Mellor 2011). It follows that some forms of welfare compromise may result from an absence of such feelings so that the presence of some positive feelings might be considered to represent a ‘need’ in the mental domain.

Considered in these terms, therefore, an animal’s welfare may be said to be good when its nutritional, environmental, health, behavioural and mental needs are met, and meeting these needs can be accomplished by managing animals in ways that both avoid negative mental states and promote positive mental states (Mellor *et al.* 2009).

Quality of life

Paralleling these later developments was the introduction of the notion of ‘quality of life’ (QoL). This initially provided a different perspective on animal welfare via a conceptual shift in focus from preventing mistreatment to improving the life conditions of animals (Bono and De Mori 2005). Now, attempts are being made to further refine QoL thinking to include consideration of whether or not animals have a life worth living or a good life (Anonymous 2009; Wathes 2010). However, there is currently no accepted definition of QoL in animals (Taylor and Mills 2007).

The origin of QoL thinking in animal welfare science was the idea of human QoL (Taylor and Mills 2007). The World Health Organisation Quality of Life Research Group concept is frequently referenced, defining QoL as: “individuals’ perception of their position in life in the context of the culture and value systems in which they live and in relation to their goals, expectations, standards and concerns. It is a broad ranging concept, incorporating in a complex way individuals’ physical health, psychological state, level of independence, social relationships, personal beliefs, and their relationships to salient features of the environment” (Anonymous 1995, P 1405). This definition presents some difficulties when applied to animals, because QoL is the perception of individuals about themselves and human observers can have no direct knowledge of how animals perceive their own life (Scott *et al.* 2007). Hence, QoL in animals must be inferred from a number of outward signs. Empathy is needed

in determining what animals may be experiencing, but caution is also required to avoid becoming inappropriately anthropomorphic (Bradshaw and Casey 2007).

Some attempts at defining the QoL of animals have included the following: “Quality of life is the affective and cognitive (to the degree that the animal can form such a cognitive construct) assessment that an animal makes of its life overall, of how its life is faring, experienced on a continuum of good to bad. This assessment is derived from the balance between the various pleasant and unpleasant affects experienced by the animal at and recently preceding the QoL assessment. In general, the further the affect balance tips towards the pleasant side, the higher the QoL. The contributory weights of the specific affects vary between individuals and are determined by the psychological impact of the affects on that individual” (McMillan 2005, P 193). “An animal’s quality of life requires that both positive and negative experiences are assessed throughout its life up to the moment of death. Assessment must take into account the extent, nature and duration of both types of experience...” (Anonymous 2009, P 41).

Also, Bono and De Mori (2005) considered QoL to be the degree to which the individual animal’s needs and desires are satisfied, leading it to experience good health, happiness and longevity. Rollin (2007) emphasised the extent to which the animal’s ‘telos’, i.e. its essence and purpose, is fulfilled. Broom (2007) took the view that QoL is to do with coping – i.e. whether the animal is coping well, badly, or not at all – and that QoL is a subset of welfare, or very similar to welfare, because QoL relates to an animal’s state as it attempts to cope with its environment. Kendrick (2007) added that an animal with a good QoL will experience ‘good’ feelings and a few ‘bad’ ones, but recognised that brain science is not yet sufficiently advanced to be able to answer questions about what exactly an animal can think or feel (Kendrick 2007). Hence, he argued that, at present, behavioural assessments probably provide the most useful information about an animal’s wellbeing. Wemelsfelder (2007) agreed and showed how aspects of this might be achieved (see below). However, Hewson *et al.* (2007) suggested that there would be benefit in including physiological parameters along with behaviour, but use of such parameters as an indicator for QoL as experienced subjectively needed further investigation. Finally, Webster (2011) recently proposed that animals may have expectations of the future modulated by their past experience and that this may affect their QoL by influencing how well they feel they can cope both with their present experiences and their anticipated future experiences.

Overall, therefore, QoL concepts give greater emphasis to the individual animal and to positive mental experiences expressed in terms of satisfied needs and expectations. Also emphasised is the balance of positive and negative mental experiences over extended periods of time (McMillan 2007; Yeates 2011). If the positive experiences of an animal outweigh its

negative experiences, then that animal is said to have an acceptable QoL, and vice versa (McMillan 2007; Wathes 2010). However, the extended periods of QoL assessment increase the likelihood that the wide range of factors that contribute to QoL would interact in complicated ways. For example: early experiences may influence how animals would respond to stimuli later in life (Mellor 2004a; McCracken *et al.* 2010); scoring the relative noxiousness of experiences such as thirst, hunger, breathlessness, nausea and pain (Mellor *et al.* 2009), and the many different types of pain (Gregory 2004), is problematic; and, the absence of particular negative states may permit positive states to be experienced, whereas the presence of positive experiences may make negative ones more tolerable (Yeates and Main 2008; Mellor *et al.* 2009). Finally, as the emphasis of QoL is on the animal's own perspective, i.e. its mental state, its QoL will be affected by its accumulated experience to that point (Webster, 2011), and that experience would probably vary greatly between individuals. Salient experiences would include those arising from good and poor health and pleasant or unpleasant interactions with other animals, people and the environment. Thus, QoL will vary as these and other factors change over an animal's lifetime (McMillan 2007).

It is evident that QoL ideas may be accommodated within the five domains concept, because QoL focuses on an animal's mental state, i.e. on experiences resulting from conditions in the four physical/functional domains (nutrition, environment, health, behaviour) in addition to inputs from the external environment that have more direct mental effects. QoL ideas may also be seen to accord with all three animal welfare orientations mentioned above (biological function, affective state, natural living), but QoL concepts are firmly rooted within the affective state orientation and give greater emphasis to positive feelings (Taylor and Mills 2007; Mellor and Stafford 2009). However, QoL is problematic to grade, rank, assess or measure due to its focus on the mental state of individual animals, the subjectivity of those states and the complex interactions between the numerous factors involved (Scott *et al.* 2007; Mellor *et al.* 2009).

Scaling quality of life

In a recent development, the possibility of extending the general notion of QoL to include categories of 'a life not worth living', 'a life worth living' and 'a good life' is being explored. If successful, this would offer the opportunity to assess QoL where these categories would represent different segments on a scale that ranges from the worst imaginable life, to a life that is neither good nor bad, through to the best life imaginable (Anonymous 2009; Wathes 2010). Animals would be assigned to particular categories according to the criteria that characterise each of them (Table 3).

‘A life not worth living’ and related concepts

An animal’s life would not be worth living when the balance of its negative experiences outweighs its positive experiences. FAWC suggested that an animal in such a state would be better off dead, but qualified this position by asserting that the QoL of such an animal should be improved rapidly by veterinary treatment or a change in husbandry practices, and failing that the animal’s life should be ended humanely (Anonymous 2009). Clearly, an animal may not be better off dead if its QoL could be improved sufficiently by expeditious veterinary treatment or husbandry change. Thus, the qualified, although indirectly stated, FAWC position appears to have been that ‘in the absence of successful human intervention’ an animal in such a negative state would be better off dead. Even so, with the emphasis still on death being the preferable alternative to such a life, the category of ‘a life not worth living’ evidently occupies much of the extreme negative end of the QoL scale.

However, less extreme, more easily remedied negative states would also be included in the category of ‘a life not worth living’ as characterised by FAWC (Anonymous 2009). This category would therefore include states where, overall, the negative experiences override positive ones on a wide range from a very strong imbalance towards the negative extreme to a marginally negative imbalance just below the neutral point of negative-positive balance on the QoL scale. As a predominance of negative experiences over this complete range would usually be worth avoiding, the descriptor ‘a life worth avoiding’ proposed by Yeates (2011) may be an appropriate substitute for FAWC’s ‘a life not worth living’. Alternatively, the term ‘a life not worth living’ could be reserved for extreme states where the only humane course of action would be for the animal to be subject to euthanasia because its suffering could not be otherwise reduced while it is both alive and conscious. In like manner, the term ‘a life worth avoiding’ could be reserved for those states where remedial action would achieve an upward shift in the animal’s state to at least reach a neutral balance, but preferably a positive balance on the QoL scale (Table 3). There appears to be merit in making this distinction.

The term ‘a life worth nothing’ has been suggested to represent the point of balance on the scale where, overall, negative and positive experiences equal each other (Yeates 2011). This term may lack appeal because assessors may be unable or unwilling to ignore other values, such as a value of life independent of the animal’s experiences. However, what is envisaged is not the notion that such an animal’s life per se is worthless; rather it is that an animal’s life as it experiences it lacks value because, overall, nothing positive about it stands out. In addition, practically, it would be virtually impossible to determine if an exact negative-positive balance existed in any animal. Thus, it is suggested here that the term ‘point of balance’ would be more appropriate than ‘a life worth nothing’ to designate theoretically where, on the QoL

scale, an animal's overall life experience changes from negative to positive, or vice versa (Table 3).

The term 'a life without experience' has also been introduced (Yeates 2011). It represents the condition of non-sentient animals. It also refers to mammalian and avian young before the onset of conscious perception, which, it has been argued, usually does not occur until after birth or hatching (Mellor and Diesch 2006, 2007; Mellor *et al.* 2010). It is therefore a useful term for indicating those species or developmental stages where animal welfare compromise cannot occur, and it might also have utility as a theoretical benchmark or zero point by which concepts concerned with conscious experience of QoL may be given definition.

'A life worth living'

The next category on the QoL scale is 'a life worth living' (Table 3). It denotes a better QoL than 'a life not worth living' or 'a life worth avoiding' (Anonymous 2009; Yeates 2011). Overall, positive experiences outweigh negative ones (Anonymous 2009) and, presumably, are valued by the animal as worth having, thereby supporting the notion that such a life would be worth living (Anonymous 2009; Yeates 2011). Practically, achieving 'a life worth living' would involve, at least, good husbandry, handling, transport and veterinary care, and good stockmanship (Anonymous 2009). It also requires that the manner of the animal's death be humane (Anonymous 2009). 'A life worth living' should result when all minimum standards in codes of practice or welfare are met (Wathes 2010), a view that accords with the value of such codes as instruments to maintain acceptable levels of animal welfare. However, 'a life worth living' does not exclude negative experiences, provided that, overall, the balance is positive. Thus, for example, brief periods of pain following precautionary tail docking or therapeutic surgical interventions may be justified by subsequent authentic improvements in the animal's QoL (Anonymous 2009; Yeates 2011).

'A good life'

'A good life', the highest category on the scale, represents a much better QoL (welfare status) than 'a life worth living' (Anonymous 2009). The practical requirements to achieve 'a good life' go well beyond those for 'a life worth living' (Anonymous 2009; Wathes 2010). Not only must there be full compliance with all legally mandated minimum standards in codes of practice or welfare, but also with all related best practice guidelines in those codes (Table 3). Therefore, FAWC argued that good welfare should be a main aim of husbandry whereby: disease is controlled by the strictest measures and with minimal prevalence; the expression of normal behaviour is encouraged; environmental choices are available and harmless wants are met; most, if not all, mutilations are banned; certain husbandry practices, including the manner of death, are prescribed or forbidden; opportunities are provided for the animal's comfort,

pleasure, interest and confidence; the highest standards of veterinary care are applied; and, above all else, the highest standards of stockmanship are provided (Anonymous 2009).

The key QoL objectives of these practical measures include the following (expanded from Anonymous 2009): consuming the food provided should be a pleasurable experience; the animals' environments should be engaging and should foster satisfaction and enjoyment; the pain produced by necessary surgical interventions should be minimised or eliminated by adequate analgesia; negative experiences caused by necessary therapeutic procedures should be mitigated; and no imposed circumstances should lead to a prolonged state of fear, distress or other unpleasant affects. Under such circumstances an animal's basic functional needs would be met, its fitness would be high, and it would be likely to exhibit positive behaviours such as play or social grooming (Anonymous 2009). Such positive behaviours indicate the presence of good welfare and are encouraged by good stock handlers, but an absence of them cannot necessarily be taken to indicate poor welfare (Anonymous 2009).

A four-tier scale

The original QoL scale envisaged by FAWC (Anonymous 2009) had three categories, one below the neutral point of balance, and two above it. As noted, however, there may be merit in considering a four-tier scale where 'a life not worth living' and 'a life worth avoiding' are below and 'a life worth living' and 'a good life' are above the 'point of balance' (Table 3). This has the benefit that both below and above this point, one category represents states that approach the extreme and the other category includes states that are closer to the 'point of balance'. This scaling advantage outweighs the purely conceptual view that below the 'point of balance' all lives would in fact be 'worth avoiding', including those at the lower extreme that would be 'not worth living', and all those above the 'point of balance' would be 'worth living', including those towards the upper extreme that would be 'good'.

Potential utility of these concepts

The contribution that these suggested extensions to QoL concepts make to animal welfare thinking will depend, at least partly, on their utility in guiding the practical management of animals, and that in turn will depend on their strengths and weaknesses. However, as these new concepts have been expressed in general terms and the extent of scientific support for them has yet to be tested, the following analysis focuses on key issues which merit further consideration, and is not intended to provide definitive answers.

Strengths

A major benefit of the notions of 'a life worth living' and 'a good life' is that they strongly refocus attention towards the promotion and, when present, the celebration of positive welfare

states and away from the avoidance of negative states, although negative states obviously still need to be managed (Wathes 2010). Also, as all categories on the four-tier QoL scale (Table 3) reflect subjective experiences and affective states, they clearly represent animal-based welfare outcomes and refer to the status of individuals (Taylor and Mills 2007; Yeates 2011). Accordingly, another benefit is that this orientation highlights potential limitations of group assessments of welfare status where emphasis may be placed on worst or best cases or group averages, and may thereby not include some individuals that exhibit negative or positive states within a group (Whay *et al.* 2003; Veissier *et al.* 2011). Recognising that a group is made up of individuals whose own QoL matters to them helps to minimise this problem by encouraging assessment of each one (Morton 2007).

QoL concepts refer to an animal's own interpretation of its welfare status, and that would include aspects of its past experience (Mellor *et al.* 2009; Webster 2011). Accordingly, all such concepts relate to an extended time scale. This point is emphasised when an animal's whole life up to the point of the evaluation is to be considered in terms of whether or not it may have been worth living, avoiding or good, including its anticipated or actual mode of death. It follows that sustained as opposed to transient factors may have greater impact on an animal's QoL (Broom 2007; Hewson *et al.* 2007). Thus, for example, chronic underfeeding as opposed to brief periods of starvation and chronic as opposed to acute pain would likely have more negative impact, and sustained good health or participation in rewarding behavioural activity compared to short bouts of illness or behavioural restriction would probably have greater positive impact. Implied here is acceptance that no life can be completely free of negative experiences, so that in terms of QoL, it is an overall positive balance that counts (Anonymous 2009). Important procedures with transiently negative effects, including for example those applied to farm animals such as vaccination, tail docking, castration, transport and slaughter, expertly and humanely executed, could therefore be regarded as acceptable when considered in these terms (Anonymous 2009).

To this point the benefits of these new concepts have been reviewed in terms of QoL outcomes for individual animals. However, another potential benefit has a more global character. It is the possibility of using these concepts to benchmark or grade the QoL standards that may be achievable within whole systems or groups of animals (Anonymous 2009; Wathes 2010). A lifelong QoL perspective would be required for prospective assessments of whether or not target standards could be achieved or maintained in light of prescribed management inputs including the available facilities, all animal care and husbandry procedures in use, and the skill levels of the personnel (Anonymous 2009). Such assessments could be applied to gauging the acceptability of existing, modified or proposed new systems for keeping animals, and whether the QoL of new animal types, such as might be derived from the wild or by genetic

modification, could be managed appropriately throughout their lives. Although using these QoL concepts in this way may have intuitive appeal, perhaps especially for members of the public (Yeates 2011), a number of difficulties remain to be resolved.

Weaknesses

A major limitation of some QoL assessment methodologies applied to individual animals is that heavy reliance is placed on empathetic speculation about what animals may experience subjectively and this may lead to inappropriate anthropomorphic projections (Bradshaw and Casey 2007). An example, which highlights several pitfalls of such approaches, involves a proposed four-step process (McMillan 2005): first, list all feelings in the animal's life which are pleasant or unpleasant and are emotional or physical in origin; second, weight each one according to its level of biological or survival value or urgency; third, individualise the weighting attributed to these feelings for each animal; and fourth, construct a scale to assign weights to the adjusted important feelings. Such a process may be of value for those attempting to gain a more comprehensive understanding of the wider dimensions of an animal's subjective experiences, but as some, perhaps many, of the conclusions arrived at with each step in this process appear to lack an objective foundation they would be open to challenge (Mellor and Stafford 2009). A 'best guess' is the probable outcome (McMillan 2005). Although this process might allow positive or negative changes in estimated QoL to be inferred for particular animals, it would preclude the derivation of any overall QoL ranking for comparison between animals in the same system or in different systems (Mellor and Stafford 2009). Moreover, when the methodology permits only a 'best guess' outcome (McMillan 2005), any implied precision conferred by numerical scoring of QoL attributes based on such impressions would be questionable. The potential for inter-observer inconsistency would also be high (Yeates 2011).

An alternative, more rigorous approach has been described by Wemelsfelder who developed and evaluated a methodology that is based on qualitative interpretation of animal behaviour judged by skilled human observers (Wemelsfelder 1997; Wemelsfelder *et al.* 2001; Wemelsfelder 2007). The conceptual foundation of this methodology is that such qualitative judgments constitute an integrated whole animal perspective, and that this perspective recognises behaviour as being a dynamically expressive body language that provides a consistent basis for assessing the quality of an animal's experience (Wemelsfelder 2007). The required skills depend on knowledge of species-specific behaviour, experience of observing and interacting with animals in different contexts, and a willingness to engage with animals as sentient beings. For this methodology to be credible, however, such judgements about an animal's likely experience would need to correspond to its actual state. It is encouraging, therefore, that when such judgements were ranked for degrees of positive or negative affect

they were correlated with quantitative, salient measures of behaviour and physiological state, and were repeatable both within and between observers (Wemelsfelder *et al.* 2001; Wemelsfelder 2007). Carefully evaluated behavioural responses to preference, motivation and aversion tests (Kirkden and Pajor 2006) will help to clarify the level of confidence that can be placed in the objective bases of approaches such as this.

A further example is the assessment of welfare status (QoL) using the five domains system (Mellor and Reid 1994; Mellor 2004b). These assessments are based on well established linkages between functional states and subjective experiences or affective states, where the functional states are clearly defined physiologically, pathophysiologically and behaviourally (see above; Mellor and Bayvel 2008; Mellor *et al.* 2009). Assessments of this character have been required in New Zealand since 1997 to rank the anticipated and observed negative impacts of every scientific procedure conducted on living animals (Williams *et al.* 2006).

Taken together, these observations support the view that, although such QoL assessments are largely qualitative in character, some methodologies do have objective foundations which enable consistent judgements to be made by experienced individuals. Such individuals include veterinarians, animal-based scientists, stock handlers, informed pet owners and others who have daily engagement with animals in clinical, production, scientific, domestic and other contexts. Also, training inexperienced individuals in such QoL assessments would be expected to improve their performance (Wemelsfelder 2007). The view expressed by Wathes (2010) that knowledgeable observers should be able to assess key factors that contribute to an animal's QoL at a particular time is therefore realistic. However, this may not be straightforward for the assessment of overall, lifelong QoL as anticipated by FAWC (Anonymous 2009) in the context of gauging whether or not animals have lives worth living or avoiding, or lives that are good.

Lifelong QoL assessments focused on individual animals would be hindered in several major ways. First, as noted above, the longer the period to which an assessment applies the greater is the likelihood that the wide range of factors that contribute to QoL will interact in complex and unknown ways. Second, as QoL is dynamic and changes throughout the life of an animal (McMillan 2007) information about the animal's whole life is required, but this may not be available, for example, for the times before its arrival on a farm or in a home, or after its departure from it. Moreover, an attempt to conduct a lifelong assessment of an animal while it is still alive would require speculation about its subsequent QoL until its death and this may be variably affected by assessor bias, priorities and values which may change with time (McMillan 2007; Yeates 2011). Third, the word 'worth' relates to what the animal would value (Anonymous 2009), and although this might be accessible through preference,

motivation and aversion testing (Kirkden and Pajor 2006), what an animal may prioritise as important to itself would probably also change over time, as it does with human beings. In addition, between-animal variations in temperament affecting behavioural responsiveness to pleasant or unpleasant stimuli or situations (Wemelsfelder *et al.* 2001; Morton 2007) could add to these complications.

It appears, therefore, that although consistent and informative QoL assessments appear to be possible by employing skilled interpretation of behaviour expressed at the whole animal level, each such assessment may be most reliable when applied to a short timeframe. Thus, in order to undertake lifelong QoL assessments repeated short timeframe assessments would probably be required. Even then, the hindrances to long-term QoL assessments noted above would question the level of objective support for, and therefore the credibility of, many of the conclusions that may be drawn on a lifelong basis. A further impediment is that, except at the extremes, there is lack of precision in the criteria that are currently used to distinguish the categories on the QoL scale to which an animal could be assigned (Anonymous 2009). It follows that until these problems have been overcome, they would hinder the utility of the lifelong QoL concepts as proposed by FAWC (Anonymous 2009) when applied to animal welfare codes, regulations and laws, and to labels designed to guide consumer purchases of animal-based products. At present, therefore, their value in the practical management of animals would be limited so that reliance on the minimum standards and recommendations for best practice outlined in codes of practice or welfare will continue to be necessary and worthwhile.

Concluding remarks

Ideas within the animal welfare science arena have evolved continuously throughout the last 30 years, and will continue to do so (Fraser 2008b; Mellor *et al.* 2009). During that period the significance attributed to animals' subjective experiences and affective states has increased so that today they are firmly established as an essential part of the scientific understanding of what animal welfare represents (Wemelsfelder 2007; Broom 2008, 2010). Thus, related key ideas progressed from an initial predominant focus on evaluating individual subjective experiences and affective states towards emphasising multifactorial approaches that combined individual experiences in attempts to achieve a more comprehensive understanding of overall welfare status (Mellor *et al.* 2009). QoL assessment falls into this latter category. The pitfalls of unsubstantiated subjective speculation in QoL assessment may be minimised provided that objectively based methodologies are rigorously applied by informed personnel, and that the scope of the assessment is limited to a short time frame. It is clear that both formal and somewhat less formal QoL assessments are already used to guide decision-making about the

ongoing care and therapeutic management of animals or, at the negative extreme, euthanasia. Indeed, numerous knowledgeable, experienced and skilled individuals, including veterinarians, scientists, stock handlers and other animal care staff competently undertake such assessments on a daily basis (Mellor *et al.* 2009; Wathes 2010). However, extending the time scale to the whole of life, as recommended by FAWC (Anonymous 2009), would be attended by a number of difficulties (also see Yeates 2011) which, until resolved, will hinder the practical, regulatory and/or commercial applications of the concepts of ‘a life not worth living’, ‘a life worth avoiding’, ‘a life worth living’ and ‘a good life’. Accordingly, their value in the practical management of animals is limited so that, at present, reliance on the minimum standards and recommendations for best practice outlined in codes of practice or welfare will continue to be necessary and worthwhile. Nevertheless, these concepts have value in providing a contextual theme that strongly focuses attention on the promotion of a lifelong QoL with an overall balance that is positive.

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Table 1. The five freedoms and actions taken to promote them, as formulated in 1979 by the Farm Animal Welfare Council in the United Kingdom.

Freedom	Action
From thirst, hunger and malnutrition	By providing ready access to fresh water and a diet to maintain full health and vigour
From discomfort	By providing an appropriate environment including shelter and a comfortable resting area
From pain, injury, and disease	By prevention or rapid diagnosis and treatment
To express normal behaviour	By providing sufficient space, proper facilities and company of the animal's own kind
From fear and distress	By ensuring conditions and treatment which avoid mental suffering

Table 2. The five domains of potential animal welfare compromise (Mellor and Reid 1997; Mellor et al. 2009): effects in the four physical/functional domains give rise to subjective or emotional experiences in the mental domain, and the mental domain also manifests such experiences via the animal's cognitive perception of its external circumstances.

Physical/functional domains	Examples of compromising factors	Examples of physical/functional effects	Subjective or emotional experiences manifested in the mental domain
Nutrition	Water deprivation Food deprivation	Dehydration Negative energy balance	Thirst Hunger
Environment	Marked cold exposure Heat overload	Hypothermia Hyperthermia	Chilling-related debility Heat load debility, malaise
Health	Disease Physical injury	Lung damage, gut inflammation, fever Tissue damage, inflammatory reactions, impaired mobility or escape capacity	Breathlessness, nausea, sickness Pain, distress, fear and/or anxiety
Behaviour	Space restriction, isolation, barren environments	Muscle atrophy/reduced muscle strength; stereotypical, self-harming or externally directed destructive behaviour; withdrawal	Weakness, boredom, frustration, loneliness, helplessness, depression, also pain from injuries
Mental	Cognitive awareness of external challenges	Brain activation of fight-flight-fright physiological and behavioural activities	Anger, assertiveness, anxiety, fear, nervousness

Table 3. A quality of life (QoL) scale where the different categories are defined in terms of the relative balance of positive and negative experiences animals may have (derived from Anonymous (2009) and Yeates (2011)).

Category	General description
A good life	The balance of salient positive and negative experiences is strongly positive. Achieved by full compliance with best practice advice well above the minimum requirements of codes of practice or welfare
A life worth living	The balance of salient positive and negative experiences is favourable but less so. Achieved by full compliance with the minimum requirements of code of practice or welfare
Point of balance	The neutral point where salient positive and negative experiences are equally balanced
A life worth avoiding	The balance of salient positive and negative experiences is unfavourable, but can be remedied rapidly by veterinary treatment or a change in husbandry practices
A life not worth living	The balance of salient positive and negative experiences is strongly negative and cannot be remedied rapidly so that euthanasia is the only humane alternative

**7.3.2 Green, T. C., Waghorn, G. C., Beausoleil, N. J., & Macdonald, K. A. (2011).
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**Feeding behaviour differs between dairy calves selected for divergent feed conversion
efficiency**

Short title: Feeding behaviour and efficiency

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ABSTRACT

Feeding behaviour and efficiency of feed utilisation (measured as residual feed intake, RFI, defined as actual feed intake minus predicted feed required) were measured in dairy calves aged 6-7 months, and associations between the two variables were determined. The intake, feeding behaviour, and liveweight of 219 female Holstein-Friesian calves were recorded for 46 days. Animals were housed in an outdoor facility comprising 28 pens, each with a single-access feeder containing dried, cubed lucerne. Efficient animals were associated with lower intakes ($r^2 = 0.29$), fewer meals/day ($r^2 = 0.05$), less time spent eating/day ($r^2 = 0.03$), and slower eating rates ($r^2 = 0.03$). The 30 most efficient animals consumed less (mean $\pm$ SED; 6.15 vs 7.46 $\pm$ 0.20 kg cubes/day), had fewer meals (4.03 vs 4.85 $\pm$ 0.29 meals/day), and spent less time feeding (2.68 vs 2.93 $\pm$ 0.11 h/day) compared to the 30 least efficient animals (all $P < 0.05$). But rate of liveweight gain, eating rate, amount eaten per meal, and meal duration did not differ between the 30 most efficient and 30 least inefficient animals ($P > 0.05$). In conclusion, differences in feeding behaviour were found between dairy calves selected for divergence in efficiency, and these may have implications for their management.

Keywords: feed conversion efficiency; residual feed intake; feeding behaviour; dairy cattle.

INTRODUCTION

Cattle differ in the efficiency with which they use feed for liveweight gain. This is sometimes referred to as residual feed intake (RFI) or net feed intake, defined here as the actual intake minus the predicted feed requirement of an animal (Herd & Arthur, 2009). Predicted feed requirements are calculated based on animal liveweight and level of performance. Individual measurement of feed intake in conjunction with liveweight gain, usually over a period of several weeks, enables animals that use their feed efficiently or inefficiently to be identified.

The biological mechanisms controlling RFI are not fully understood, but include digestion, physiological demands for nutrients and biochemical efficiencies of feed utilisation (Herd & Arthur, 2009). Feeding behaviour may contribute to variation in efficiency through the energetic costs associated with feeding activity, such as time spent feeding, rate of eating, and nutrient supply (Richardson & Herd, 2004; Lancaster *et al.*, 2009; Kelly *et al.*, 2010). Feeding behaviour also affects intake, which will influence both production and RFI.

Published studies with beef cattle showed that animals of divergent RFI differed significantly in their feeding behaviour (Nkrumah *et al.*, 2007; Lancaster *et al.*, 2009). The measured behaviours included feeding frequency, daily feeding duration, eating rate, meal amount, and meal duration. However, these studies have given highly variable results, with each feeding characteristic explaining between 2 and 24% of the variation in RFI (Robinson & Oddy, 2004; Nkrumah *et al.*, 2007; Lancaster *et al.*, 2009; Kelly *et al.*, 2010; Montanholi *et al.*, 2010). No studies have been undertaken with dairy cattle fed forage diets.

An understanding of factors associated with RFI, such as feeding behaviour, will provide a better understanding of the mechanisms regulating efficiency and could help predict RFI if relationships are sufficiently high (Nkrumah *et al.*, 2007; Montanholi *et al.*, 2010). An improved understanding of feeding behaviour could improve animal management, lessen stress and improve production.

This study was undertaken to measure differences in feeding behaviour of young (6-7 mo) dairy heifers during a screening procedure to identify individuals with negative RFI (efficient) and positive RFI (inefficient). We hypothesised that there would be differences in behavioural characteristics of efficient and inefficient individuals and that these characteristics would be associated with RFI.

MATERIALS AND METHODS

Animals and facility

This study used data collected from 219 female Holstein-Friesian calves of approximately 6-7 months of age (167 ± 16.5 kg liveweight) in 2009. The animals were kept in an outdoor feeding facility at the Westpac Taranaki Agricultural Research Station, Hawera, New Zealand. Calves were randomly allocated to 28 pens (eight animals in most pens) at the commencement of the trial; they were held in these pens for an 11-day adaptation period followed by a 46-day trial period. Each pen was 42 m² (6 x 7 m), had bedding of post peelings and a single feeding station, enabling only one animal to have access to the feed at a time. Calves were fed dried lucerne cubes (Kapt-al, Vancouver, Canada), and both water and salt blocks were freely available. The cubes averaged 84.5% dry matter (DM) and contained 18.7 % crude protein and 45.8% neutral detergent fibre in the DM with a predicted organic matter digestibility of 65.0% (FeedTECH, AgResearch, Palmerston North, New Zealand). Allocation of eight animals/pen was based on preliminary evaluations that showed that sufficient time was available for eight animals to eat *ad libitum* from a single feeding station. This trial was one group of a larger evaluation using 1050 dairy calves to identify those with divergent efficiencies of feed utilisation (Carnie *et al.*, 2010).

Data recording and analyses

Data used for this analysis comprised feed intakes, animal electronic identification (EID: SmartReader R600 panel reader, Gallagher Ltd., Hamilton, New Zealand), the time that individuals ate from the feed bin, and individual liveweights measured three times per week. Intake, calculated from changes in feed bin weight at each individual feeding event by each individual calf, and feeding behaviour were recorded each second for the duration of the trial by an automatic recording system developed by Gallagher Ltd., Hamilton, New Zealand. Feed bin weight was measured by two load bars (SmartScale 300 weigh scale, Gallagher Ltd., Hamilton, New Zealand) located beneath each bin, and animals were identified upon entry to the bin by an EID reader positioned over the feed bin. Data were processed so that information from all 28 feed bins was received and logged onto two computers at one-second intervals, and these data were formatted and checked for accuracy prior to analysis.

The data used for analysis of feeding behaviour included average daily intake, number of meals per day, time spent feeding per day (h/day), daily eating rate (g/min), meal amount (kg cubes/meal), and meal duration (min/meal). A 'meal' was defined as being a feeding event in which ≥ 0.01 kg was consumed. The meal began when the animal put its head into the feed bin and ended when the animal left the feed bin for more than 15 minutes, or when another animal entered the feed bin.

Residual feed intake

Determination of RFI in this study was calculated as the difference between actual intake and the predicted feed requirements of individual animals. Predicted feed requirements were calculated for the 219 animals by regressing actual daily feed intake (kg cubes/day) against liveweight gain (kg/day) and mean metabolic liveweight ($\text{kg}^{0.75}$). Average liveweight gain was calculated by regression analysis of liveweights versus time, over the 46-day measurement period. The resulting equation was:

Predicted feed requirements (kg cubes/day) = $1.44 \text{ kg/day liveweight gain} + 0.19 \text{ kg liveweight}^{0.75} - 3.4$ ($r^2 = 0.61$).

Hence, residual feed intake (RFI), the measure of efficiency used in this paper, is determined as the amount actually consumed by a calf (kg cubes/day) minus the predicted feed requirement calculated for that calf from the above equation. More efficient animals have negative values for RFI, as the amount that they actually eat is less than their predicted feed requirements; whereas less efficient animals have positive values for RFI.

Statistics

Associations between RFI and each feeding behaviour characteristic of all 219 animals were calculated by regression using GenStat (VSN International, 2010). Comparisons of each feeding behaviour characteristic between the 30 most and 30 least efficient animals (divergent RFI) used ANOVA.

RESULTS

Results from all the animals

The animals accepted the cube diet and appeared to adapt to the feeding facility with ease during the adaptation period. Intakes averaged 6.86 ± 0.78 kg cubes/day (5.82 ± 0.66 kg DM/day) for all 219 animals over the 46-day measurement period. The average daily liveweight gain was 0.80 ± 0.12 kg/day over the 46-day measurement period, with lowest and highest values of 0.47 and 1.09 kg/day, respectively. Average daily intakes increased from 5.80 to 7.57 kg cubes/day (SED = 0.07) from the commencement to the end of the experimental period. The time spent eating within a 24 h period averaged 2.90 ± 0.43 h, with 4.7 ± 1.3 meals and an average eating rate of 40.8 ± 7.9 g cubes/minute, increasing from 34.9 to 45.4 g/min (SED = 0.48) from the commencement (days 1-5) to the conclusion (day 41-46) of the trial.

All the feeding behaviour characteristics measured had statistically significant associations with RFI (Table 1; $P < 0.05$), with the exception of meal amount. Efficient animals had lower

daily feed intakes, spent less time feeding per day, ate more slowly, and had fewer meals of longer duration than inefficient animals (Table 1). An example of the distribution of data is given in Figure 1, where the average number of meals per day over the duration of the trial is plotted against RFI. Although the relationship was highly significant ($P < 0.001$), this variable accounted for only 5% of the variation in RFI.

Comparison of 30 most and 30 least efficient animals

The 30 most and 30 least efficient animals had similar average liveweight and daily liveweight gain (Table 2). The most efficient animals (negative RFI) consumed less feed, had fewer meals, and spent less time eating than did the least efficient animals (positive RFI) (Table 2; $P < 0.05$). There were no differences in eating rate, meal duration, or meal amount between efficient and inefficient animals (Table 2).

DISCUSSION

The feeding facility and diet enabled good rates of gain, similar to about 0.77 kg/day reported for Holstein-Friesian animals of a similar age fed *ad libitum* on high quality pasture and silage (Macdonald *et al.*, 2005). Analysis of feeding behaviour identified significant differences between efficient and inefficient calves. In addition to differences in feed intake, which is a component of RFI, both analyses (of all 219 animals, and comparisons between the 30 most efficient animals and the 30 least efficient animals) showed that efficient animals ate fewer meals and spent less time feeding per day. Meal amount was not different between efficient and inefficient animals in either analysis, and the slower eating rate and longer meal durations associated with efficiency ($n=219$) were not evident in comparison of the 30 most and least efficient. Daily feed intake was moderately associated with RFI, and this has also been found in studies on beef cattle (Robinson & Oddy, 2004; Lancaster *et al.*, 2009). The r^2 values for the associations between RFI and each of the other feeding behaviour characteristics (Table 1) were low, suggesting their contributions to RFI were small, despite being statistically significant. Significance was due in part to the large number of animals used, but the associations with feeding characteristics were too small to be used as predictors of RFI in these animals.

The associations reported in the present paper between each of five feeding behaviour traits and RFI were at the lower end of the range of those obtained in beef studies. For example, number of meals/24 h explained 0.05 of the variance in RFI in the present study, but values for beef cattle explained 0.03-0.20 of variance (Robinson & Oddy, 2004; Nkrumah *et al.*, 2007; Lancaster *et al.*, 2009; Kelly *et al.*, 2010). There were also large ranges in the amount of variance in RFI accounted for by other traits in beef cattle: time spent eating/day, 0.03-0.24;

eating rate, 0.02-0.19 (Robinson & Oddy, 2004; Nkrumah *et al.*, 2007; Lancaster *et al.*, 2009; Kelly *et al.*, 2010; Montanholi *et al.*, 2010). Meal duration was negatively associated with RFI in this study ($r^2 = 0.03$), and in one beef study (Montanholi *et al.*, 2010), but Lancaster *et al.* (2009) reported a positive association with RFI ($r^2 = 0.17$). The association between meal amount and RFI was not statistically significant in the present study, but Montanholi *et al.* (2010) reported a significant association with RFI ($r^2 = 0.17$). The varying associations between studies suggest other factors are having a large effect on behaviour (and perhaps RFI), for example animal age, breed, diet, feeding facilities and analytical interpretation. Nevertheless, the weak associations reported in the present paper between feeding behaviour characteristics and RFI suggest that feeding behaviour accounts for a small portion of the difference between animals, with digestion and metabolic factors such as protein synthesis and cellular ion fluxes probably explaining a larger portion of differences in efficiency (Herd & Arthur, 2009).

When the extremes in RFI were compared in this study, efficient animals had lower daily consumption, spent less time eating/day, and had fewer meals/day than inefficient animals, but meal amount, meal duration, and eating rate did not differ, suggesting these traits were less important. These findings correspond with measurements from beef animals, where most studies showed efficient animals had fewer meals (Nkrumah *et al.*, 2006; Bingham *et al.*, 2009; Kelly *et al.*, 2010), although Dobos & Herd (2008) reported no differences. Most studies reported no difference between efficient and inefficient animals in time spent eating (Dobos & Herd, 2008; Bingham *et al.*, 2009; Kelly *et al.*, 2010; Montanholi *et al.*, 2010) in contrast to findings reported here and those of Nkrumah *et al.* (2006) where efficient animals ate for less time per day. There is a lack of consensus in the literature relating RFI and eating rate; no differences were found here or by Dobos & Herd (2008) or Golden *et al.* (2008), whereas Bingham *et al.* (2009), Kelly *et al.* (2010) and Montanholi *et al.* (2010) found efficient beef cattle ate faster than inefficient animals.

In summary, there are large differences between the published results of studies investigating associations between feeding behaviour and RFI, and this is likely due to differences in the experimental designs of these studies, suggesting that behaviour is sensitive to circumstances. In particular, differences in the numbers of animals used, the facility or housing set-up, the group size and density of the animals, and the diet fed have a large impact on feeding behaviour (Grant & Albright, 2001; Phillips, 2004; Huzzey *et al.*, 2006; DeVries & von Keyserlingk, 2009). In the work presented here, feeding behaviour explained a small proportion of the differences in RFI between animals, although it was not clear whether differences in feeding behaviour contributed to differences in efficiency or whether efficiency

was driving feeding behaviour. However, differences in feeding behaviour may have implications for management of efficient animals, and results obtained here need further evaluation when the divergent groups are grazing pasture.

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TABLE 1: Relationships between residual feed intake (kg cubes/day) and feeding behaviour characteristics averaged from all the experimental animals (219 calves) fed lucerne cubes for 46 days.

	slope	SE slope	P value	r ²
Daily feed intake (kg cubes/day)	0.97	0.10	0.000	0.29
Number of meals per day	0.70	0.20	0.001	0.05
Time spent feeding per day (h/day)	0.17	0.07	0.010	0.03
Daily eating rate (g/min)	3.24	1.22	0.008	0.03
Meal duration (min/meal)	-4.18	1.75	0.018	0.03
Meal amount (kg cubes/meal)	-0.02	0.06	0.737	0.00

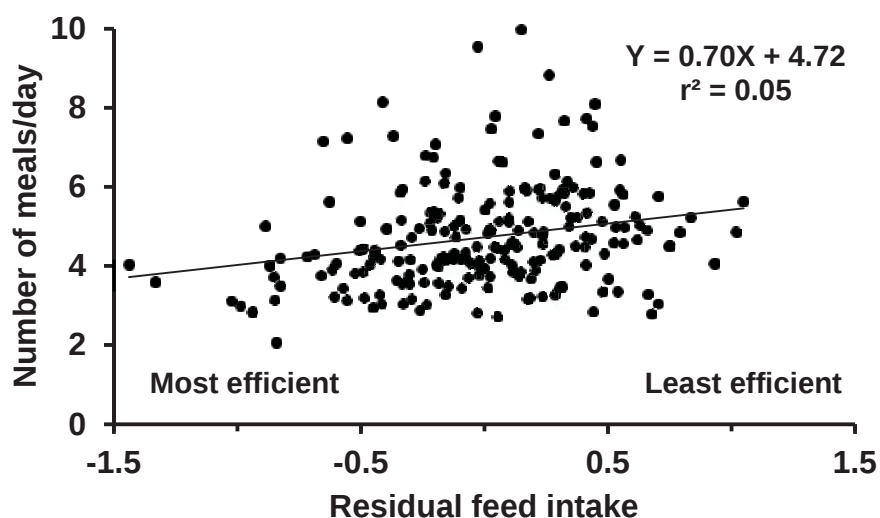


FIGURE 1: The relationship between number of meals per day and residual feed intake of 219 calves fed lucerne cubes for 46 days.

TABLE 2: Mean values for liveweight (midpoint of the regression over the 46-day trial), daily liveweight gain and feeding behaviour characteristics of the 30 most efficient and 30 least efficient calves fed lucerne cubes for 46 days.

	Efficient	Inefficient	SED	P value
Liveweight (kg)	172.9	173.1	4.95	0.960
Daily liveweight gain (kg/day)	0.78	0.76	0.04	0.670
Daily feed intake (kg cubes/day)	6.15	7.46	0.20	0.000
Number of meals per day	4.0	4.9	0.29	0.007
Time spent feeding per day (h/day)	2.68	2.93	0.11	0.024
Daily eating rate (g/min)	40.1	43.7	2.51	0.164
Meal duration (min/meal)	46.0	41.7	3.46	0.209
Meal amount (kg cubes/meal)	1.73	1.71	0.09	0.871

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