FOOD NEOPHOBIA, FEEDING AND SORTING BEHAVIOUR IN DAIRY CALVES

by

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Abstract

Standard practice within the dairy industry is to separate calves from the dam immediately after birth and raise calves in individual pens during the milk-feeding period with little or no contact with conspecifics. I reviewed empirical work (Chapter 2) on the social development of calves, the effects of social isolation and the practices associated with group housing of dairy calves. From this review I identified literature gaps that were explored in the following chapters. In Chapter 3, I explored how pairing age affects performance and feeding behaviour development in dairy calves. Early pairing (3 d of age) increased solid feed intake and weight gains in comparison to late-pairing (42 d of age) and individual housing. In Chapter 4, I investigated how individual housing of calves affects food neophobia. The results suggested that calves raised in a complex social environment are less reluctant to ingest new feed types. Chapter 5 investigated whether being grouped with experienced dairy cows would affect the development of grazing behaviours in pregnant dairy heifers first introduced to pasture. The results indicated that grouping heifers with pasture-experienced cows improves grazing behaviour in the first hours following introduction to pasture. Chapter 6 assessed whether weaned calves would sort a total mixed ration (TMR) and if sorting was affected by the availability of a separate grain source. I found that calves can sort a total mixed ration and that the provision of a separate source of concentrate reduces sorting. I conclude that calves raised in more complex social environments early in life experience benefits related to feeding behaviour development, performance, ability to cope with novelty, and that experienced companions can be used to mitigate stress associated with novelty.

Preface

I completed this thesis under the supervision of Dr. Daniel M. Weary. In addition to Dr. Weary, my supervisory committee included Drs. Marina A. G. von Keyserlingk and Jennifer Black, all from the University of British Columbia. The studies described in this thesis were approved by the University of British Columbia's Animal Care Committee (AUP A12-0337). The animals were cared for according to the guidelines outlined by the Canadian Council of Animal Care (2009).

A version of Chapter 2 has been submitted for publication and is awaiting decision: Costa, J. H. C., M. A. G. von Keyserlingk and D. M. Weary. Effects of group housing of dairy calves on behavioural and cognitive development, performance and health. The paper was co-authored with D. M. Weary and M. A. G. von Keyserlingk (University of British Columbia). Co-authors supervised, helped interpret material, and edited drafts. The paper main ideas for the manuscript were developed by JHCC, DMW, MvK and were researched by me.

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João Henrique C. Costa, October 2015

For my family, Tracy and calves around the world…

1 Introduction

In North America there are more than 4 million dairy calves and heifers (<225 kg), 450 thousand in Canada and 3.9 million in the USA (USDA, 2008; Statistics Canada, 2015). Over the last 5 decades the majority of research on dairy cattle health and welfare has focused on the adult dairy cow (i.e. Oldham and Emmans, 1989; DePeters and Cant, 1992), and little research has focused on the optimal conditions in which to raise the future dairy cow. Given that management and housing conditions can impact the health and welfare of the adult cows it follows that the quality of dairy replacement animals' rearing conditions may also impact the growth, health, welfare and perhaps future productivity.

Calf mortality rates are high globally (i.e. Brickel et al., 2009; USDA, 2010; Walker et al., 2012; Hur et al., 2013; Raboisson et al., 2013) and are considered an important welfare issue, and one of the most important indicators of herd health (Ortiz-Pelaez et al., 2008). Moreover, calves are routinely separated from their mothers within the first 24 hours after birth, and raised in single pens until weaning. Individual housing for calves is used on 77 % of farms in USA (USDA, 2008), 87.9 % in Canada (Vasseur et al., 2010), 70% in Brazil (Hötzel et al., 2014) and is common in much of Europe (Pettersson et al., 2001; EFSA, 2009; Staněk et al., 2014).

Given the high morbidity and mortality rates during the milk feeding period (USDA, 2008; Hur et al., 2013) early weaning is a very important step in the success of dairy calf rearing. However, successful weaning requires that dairy calves begin consuming solid feed early in life, as they must be well established on solids at the time of weaning. Calves that do not consume adequate amounts of solid feed before weaning are more likely to experience poor growth and prolonged hunger after weaning (de Paula Vieira et al., 2008; de Passillé et al., 2011). The development of solid feeding is still poorly understood in dairy calves.

There is a need to investigate new rearing systems that facilitate the early development of social and feeding behaviour in these young calves. Research on this topic will provide a scientific basis for recommendations for the dairy industry. This research has the potential to improve the lives of millions of animals.

This thesis will thus identify gaps in knowledge regarding the effects of the social environment on neophobia and feeding behaviour in growing dairy cattle, facilitating the adoption of housing practices that are beneficial for the health and welfare of dairy calves. In this chapter, I will introduce the topics that will be discussed and investigated throughout the thesis, as well as present and discuss the knowledge gaps and research questions presented in this dissertation. In Chapter 2, I review the effects of the social environment early in life, focussing on the effects of social rearing on dairy calves. In Chapters 3 and 4, I describe empirically the effects of early life social environments on the development of solid feeding, performance and reluctance to eat a novel feed. The effects of social rearing for calves on mitigating stress associated with novelty are addressed in Chapter 5. The development of feed sorting in calves is investigated in Chapter 6. Finally, Chapter 7 provides a general discussion of key thesis findings and limitations, and points to future research directions.

1.1 Social Environment in Early Life

Infancy is one of the most sensitive periods of development for mammals, with the environment playing a crucial role in development (see review by Bornstein, 1989). The detrimental effects of maternal separation and social isolation during infancy have been studied in a range of social species, especially rodents (Heim et al., 2004), primates (Harlow et al., 1965) and humans (Troller-Renfree et al., 2014). Numerous negative effects of social deprivation have been identified, including abnormal behaviour and other developmental problems, such as impaired maternal care (e.g. Lovic et al., 2011), increased aggression (e.g. Toth et al., 2011), and impaired social recognition (e.g. Lukas et al., 2011).

Farmed mammals (e.g. sheep, pigs, horses and beef cattle) are typically housed together with their dam during the milk-feeding period. In all of these cases the young normally also have contact with siblings and conspecifics of similar age. Dairy cattle production is the exception. Standard practice within the industry is to separate calves from the dam immediately after birth and raise calves in individual pens during the milk feeding period with little or no visual contact with other calves (USDA, 2008; Vasseur et al., 2010). This limited maternal and social contact is in contrast to what occurs under natural conditions (Reinhardt and Reinhardt, 1981). In Chapter 2 I review the available information regarding the effect of social isolation in animals, especially dairy cattle.

1.2 Social Influences on Feeding Behaviour Development

A complex social environment early in life is thought to result in earlier and increased ingestion of solid feed in dairy calves (Key and MacIver, 1980; Nolte et al., 1990). When young calves are housed individually, they may have little opportunity to learn how and what to eat from other animals, specifically older, experienced foragers. Young ruminants must rapidly learn how to select and eat the appropriate foods (Freeland and Janzen, 1974). Herbivores that feed in large mixed-generation groups are likely to use social learning as a tool to pass on food selecting information from experienced to inexperienced foragers (Boyd and Richerson, 1996). Social learning enables the inexperienced heifer to avoid the inefficiency and risk of testing everything on her own.

Recent research has shown that pair housed calves have reduced behavioural responses to weaning and improved performance when mixed with a larger group after weaning (de Paula Vieira et al., 2012b). Housing young calves with an older, weaned companion further stimulates feeding behaviour and growth before and after weaning (de Paula Vieira et al., 2012a). Rearing with a social partner also improves exploratory behaviour (Jensen et al., 1997). Contact with an adult animal within the first few weeks of life may stimulate calves to start sampling solid feed at a younger age (Key and MacIver, 1980; Nolte et al., 1990). Age of contact with other conspecifics is one of the main factors that influences feeding behaviour development. Until the work described in Chapter 3, no research had investigated the effect of age at which social contact is provided on the development of solid feeding behaviour.

1.3 Social Influences on Responses to Novelty

Farm animals are exposed to a number of stressful events throughout their lives, including diet changes, movement to a new pen, and regrouping with different animals. Dairy cows are exposed to the challenges of adapting to novel food and novel environments several times throughout the production cycle. Exposure to novelty can cause fear (Forkman et al., 2007), and novelty is generally considered a powerful stressor for cattle (Moberg and Wood, 1982).

1.3.1 Food Neophobia

Food neophobia is the avoidance of and reluctance to taste unfamiliar foods (Cooke et al., 2006), and is well known in ruminants (Chapple and Lynch, 1986). Neophobia is adaptive in that this helps animals avoid toxic foods and those too rich in certain nutrients (Provenza et al., 1995). Ruminants offered novel diets often sample these cautiously, resulting in decreased food intake and productivity (Launchbaugh et al., 1997). Food neophobia has been documented in several farm animal species (e.g. sheep: Villalba et al., 2009; Villalba et al., 2012; goats: Distel and Provenza, 1991; pigs: Oostindjer et al., 2011a). In dairy cattle, neophobia towards new feed types can be problematic in different stages of life. Some examples include the transition from milk to solid feed, and the transition from indoor housing to pasture. During these transitions more flexible animals would be more ready to accept the novel diets, likely easing the transition. Little is known about neophobia in dairy calves, and how the environment in which the calves are raised affects it. Thus, in in Chapter 4 I investigated neophobia towards new feed types and its relationship with the environment in which dairy calves are raised.

1.3.2 Access to Pasture

Dairy heifers are often reared indoors and provided no access to pasture until at the earliest after weaning, and sometimes much later, such as when already pregnant, depending upon season and management on that farm. These animals do not have the opportunity to graze when they are young, and often first-season grazing dairy heifers are placed on pasture without any companions. These first-time grazers are thus faced with several challenges, including learning how to eat a novel feed type (Hessle, 2009), habituating to a novel environment (de Paula Vieira et al., 2012b), and often coping with new conspecifics. There has been little research on the challenges that naïve dairy heifers face during the introduction to pasture, and acute effects have not been investigated. One possible solution to the challenges faced by first-time grazers is to provide experienced animals that can act as social models. Thus, in Chapter 5 I tested whether the presence of cows with previous experience on pasture affects the development of grazing behaviour of naïve pregnant dairy heifers when first introduced to pasture.

1.4 Sorting Behaviour

The most common feeding method on dairy farms in North America is the total mixed ration (TMR; USDA, 2008), which is a blend of different feed components, normally forages, minerals and concentrates in ratios designed to meet the needs of the modern dairy cow. However, cattle sort out the different components of the mixed rations, and therefore may consume an unbalanced diet.

According to optimal foraging theory, ruminants are expected to forage in a way that maximizes energy obtained while minimizing efforts expended (Provenza and Balph, 1987; Hughes, 1993). Dairy cattle tend to sort in favour of fine high-energy grain particles and against the long particles (Leonardi and Armentano, 2003; Miller-Cushon and DeVries, 2009). This means that the high-energy and rapidly digestible particles are selectively consumed and the caloric value of TMR is reduced during the day, leaving more large particles (DeVries et al., 2005). Excessive consumption of these quickly digestible particles and reducing the fibre content of the diet consumed reduces the ruminal pH, leading to an increased risk of subacute ruminal acidosis (SARA) (Krause and Oetzel, 2005; 2006). This condition is known to decrease milk productivity, increase veterinary costs (Krause and Oetzel, 2006), and is a concern for animal welfare (DeVries et al., 2008). While sorting is recognized as a widespread concern among dairy cattle, little is known about how early life experiences affect sorting behaviour in cattle (Leonardi and Armentano, 2003).

It seems that calves prefer feed components higher in protein and carbohydrate, such as concentrate over forage (Miller-Cushon et al., 2014). However, diet selection is not simple. There are many examples of ruminants showing foraging behaviour other than maximizing energy intake. For example, sheep will consume a large amount of forage when offered a choice between forage and concentrate, even though forage is less nutrient and energy dense and requires more energy to chew and digest (Forbes and Kyriazakis, 1995). Thus, acquisition of energy is not the only motivation behind sorting behaviour of ruminants. Little is known about how sorting behaviour develops over calfhood, and how availability of different feed types affects sorting. In Chapter 6 I measured sorting in young dairy calves, and determined if varying the provision of supplementary concentrate would affect the expression of this behaviour.

1.5 Thesis Objectives

The overall goals of this thesis were to: 1) contribute to the understanding of the development of feeding behaviour of young dairy calves raised in intensive dairy systems, with a specific focus on the effects of early life social contact on feed preferences, food neophobia and nutrition during the milk feeding and weaning period of dairy calves, and 2) further understand and contribute to the development of strategies to minimize the negative impact of diet changes on pre-weaned and weaned dairy calves and heifers.

My overall hypothesis was that social housing and early social experience positively affect how dairy calves and heifers perceive novelty, cope with challenges, and develop their solid feeding behaviours. Also, I hypothesized that young dairy cattle are able to sort solid feed and consume particle sizes in relation to feed provided in their environment.

2 Effects of Group Housing of Dairy Calves on Behavioural and Cognitive Development, Performance and Health [1]

2.1 Introduction

Despite the near ubiquity of these practices on modern dairies (i.e. Vasseur et al., 2010), there is relatively little information on how social isolation affects calves, and to my knowledge no attempt has been made to summarize the available scientific information on the effects of social isolation on calves. This review describes the research to date assessing the role of isolation and social housing on calf development. I begin with a brief account of social development in natural settings when cows rear their young. I then review the literature on cattle and other species describing the effects on neonates of maternal and other types of social deprivation, and where applicable, draw from theories based on the human and laboratory animal literature. Lastly I discuss the group housing literature, describing challenges and successful practices associated with social housing of dairy calves. Where possible I include recommendations for future research and considerations for application on farms.

2.2 Social Development in Calves

Shortly before parturition cows tend to separate themselves from the herd and give birth in a secluded area (Lidfors et al., 1994). Once the calf is born, a series of maternal behaviours are observed, including licking of the calf and specific vocalizations (reviewed by von Keyserlingk and Weary, 2007). The dam normally keeps the young hidden in bushes or tall grass for the first few days while she forages nearby (Langbein and Raasch, 2000). The newborn calf is fully dependent on the milk provided by the dam and will suckle approximately 8 to 12 times daily during the first week of life, with each suckling bout lasting approximately 10 min (e.g. Reinhardt and Reinhardt, 1981; Day et al., 1987; Lidfors, 1996).

[1]A version of Chapter 2 has submitted for publication: Costa, J. H. C., M. A. G. von Keyserlingk and D. M. Weary. Invited Review: Effects of group housing of dairy calves on behavioural and cognitive development, performance and health.

After several days, the calf and mother re-integrate into the herd (Bouissou et al., 2001). During the second week of life, the calf starts to increase the distance from the dam and begins interacting with peers and may form small groups with other calves (Vitale et al., 1986; Sato et al., 1987). These calf groups also interact with older animals, and it has been reported that adolescents and adults without newborn calves will graze near to calf groups (e.g. Sato et al., 1987; Murphey and Moura Duarte, 1990). This suite of characteristics and behaviours are also observed in other ungulates such as caribou (*Rangifer tarandus*; Rettie and Messier, 2001) and moose (*Alces alces*; Bowyer et al., 1999).

Under natural or semi-natural conditions grazing ruminants select their diets from a wide variety of plants differing in nutritional composition and availability (Provenza and Balph, 1987; Baumont, 2000). Calves that are reared with their dam and other conspecifics start grazing and ruminating at approximately 3 wks of age and graze regularly with the herd at 3 to 6 mo of age (Reinhardt and Reinhardt, 1981; Vitale et al., 1986). The social interactions of young ungulates are associated with learning to recognize suitable diet and habitat, where selection happens through the mimicking of social companions (i.e. Key and MacIver, 1980; Mirza and Provenza, 1992, 1994). The progression from maternal care to independence is an important period for learning for young foragers (Provenza and Balph, 1987), making social partners important influences on diet selection for young ruminants (Nolte et al., 1990; Provenza et al., 2003).

Social learning allows individuals to learn from the positive or negative effects on another individual (Bandura, 1977; Conte and Paolucci, 2001); this type of learning is thought to be important in the development of feeding behaviour in many farmed species (Keeling and Hurnik, 1996; Launchbaugh and Howery, 2005). Social learning theory suggests that the most effective social models are the dam and dominant peers (Bandura, 1977). Herbivores that feed in large mixed-generation groups, like cattle, are able to use social learning to transmit information about suitable food items from experienced to inexperienced foragers (Boyd and Richerson, 1996).

Food neophobia is well known in ruminants (Chapple and Lynch, 1986) and is defined as avoidance and reluctance to taste unfamiliar foods (Cooke et al., 2006). Food neophobia is known to decrease in the presence of companions in lambs (Nolte et al., 1990). In nature, young ruminants must learn how to select and eat appropriate foods (Freeland and Janzen, 1974); social learning enables an inexperienced animal to avoid the inefficiency and risk of testing each novel feed type, since the strategy of ‘trial and error’ can lead to the ingestion of toxic feed (Galef and Laland, 2005; Nicol, 2006).

In summary, young ruminants naturally form social relationships starting with the dam and then with other individuals even in the first weeks of life. During the milk-feeding period, the calf relies on social cues from the dam and other conspecifics that influence behavioural development. Given that most dairy calves are separated from their mothers at birth and reared individually, [e.g. 77% in USA (USDA, 2008); 88% in Canada (Vasseur et al., 2010); 70% in Brazil (Hötzel et al., 2014)] numerous questions arise regarding potential negative effects of social isolation on social and feeding behaviours and other aspects of development. In addition to the effects outlined above, the results from a number of species suggest that social isolation maybe have important effects on cognitive development, as described below.

2.3 Effects of Social Isolation: Evidence from Other Species

There is considerable variation within the literature in what is called ‘social isolation’, ranging from complete isolation for extended periods (e.g. Sackett et al., 1981) to 2 h daily during the second week of age (Tuchscherer et al., 2006). Social isolation was defined by Gottman (1977) as an absence or low frequency of peer interaction during an extended period of time. This definition applies to most dairy calves during the milk-feeding period.

Bowlby (1969) famously described how events during childhood have profound influences on behaviour, even as adults. Social isolation influences how human infants perceive stressors (Gunnar and Donzella, 2002), and individuals who experience social isolation or social deprivation during childhood tend to have psychological and behavioural disorders later in life, such as a greater tendency to develop schizophrenia (Rutter, 1979) and to express violent behaviour and abnormal emotional responses (Bowlby, 1969). Some of these effects are also found when social isolation occurs in adulthood (as reviewed by Cacioppo et al., 2011). There is also evidence for long-term neurological (Heim and Nemeroff, 2001; Shanks and Lightman, 2001), neuroendocrine, and immune alterations from negative events during childhood (as reviewed by Neigh et al., 2009). Social isolation can also be an important risk factor for morbidity and mortality; as reviewed by House et al. (1988) social isolation increases the likelihood of smoking, obesity, sedentary lifestyle, and high blood pressure.

A variety of studies have shown how maternal separation or social deprivation from conspecifics early in life adversely affects brain and behaviour development in non-human animals [e.g. primates (Harlow et al., 1965); rats (Heim et al., 2004, Haller et al., 2014); mice (Kercmar et al., 2014); pigs (Worobec et al., 1999); voles (Shapiro and Insel, 1990)]. Social isolation in rodents is often associated with increased anxiety-like behaviour (as reviewed by Hall, 1998; Fone and

Porkees, 2008), and enhanced hypothalamic–pituitary–adrenal axis (HPA) responsiveness to stressors (Serra et al., 2007).

Early social deprivation has been associated with long-term alterations in social behaviour of non-human animals, such as when adults express impaired maternal care (Lovic et al., 2011), increased aggression (Veenema et al., 2006, 2007; Toth et al., 2011), and impaired social recognition (Lukas et al., 2011). Together these are labelled as the 'isolation-induced stress syndrome' in rodents (Valzelli, 1973; Holson et al., 1991). Maternal separation, total or partial, has been associated with long-term alteration in behaviours in non-humans animals, and with changes in emotionality (Kraemer et al., 1991), cognitive functions, physiological and stress coping mechanisms (Fahlke et al., 2000), excessive alcohol consumption (Higley et al., 1991; Fahlke et al., 2000), and associated neuroendocrine and neuronal adaptations (Poletto et al., 2006a,b). Nursery rearing, an example of maternal deprivation, had a strong detrimental impact on the development of rhesus macaques and has been shown to cause disruptions in social behaviour, hyperactivity, and increased sensitivity to stressors (Harlow et al., 1965; Suomi et al., 1971; Suomi, 1991). Infants reared in this manner had increased cortisol responses to social situations during adulthood (Fahlke et al., 2000) and showed signs of depression (Kraemer et al., 1991). The conclusion from this body of work is that social experience with the mother and conspecifics is required for normal development in social species (reviewed by Parker and Maestripieri, 2011).

Relatively little work on social isolation has focused on farm animals, but the limited studies available align with the rodent and primate studies cited above. For example, piglets weaned at younger ages were slower to habituate to their new environment, exhibited more escape behaviour, less interaction with neighbouring pigs, and less time feeding than pigs weaned at an older age (Worobec et al., 1999; Davis et al., 2006). Social isolation also increases cortisol responses to stress in pigs (Kanitz et al., 2009). Premature separation from mothers has detrimental effects, even in precocial species such as sheep. For instance, artificial rearing of lambs, where animals are fed milk by humans instead of conspecifics, has been associated with negative effects on behaviour as well as endocrine and immune levels (i.e. Napolitano et al., 1995; Napolitano et al., 2002). Lambs separated from the dam showed reduced frequency of vocalization, were slower to initiate movements, and displayed an increased cortisol response during an open-field test compared with animals raised in a complex social environment (Moberg and Wood, 1982; Napolitano et al., 2002; also see review by Napolitano et al., 2008). In summary, research on a number of different species has shown that social isolation is associated with abnormal behaviour and developmental problems. It would thus seem reasonable to predict similar effects in dairy calves.

2.4 Effects of Social Isolation on the Dairy Calf

Dairy calves that have been separated from the dam will begin interacting with other calves, when given the opportunity, as early as 2 d after birth (Duve and Jensen, 2012). Socially housed dairy calves spend, on average, only about 2% of their time engaged in social contact during the first 8 weeks of life (Chua et al., 2002), but calves appear to be highly motivated to initiate this contact. For example, calves work to gain access to full social contact with a known calf even when already provided limited social contact across a barrier (Holm et al., 2002; Estevez et al., 2007). Young dairy calves housed in groups showed a preference for a known peer in contrast to an unfamiliar calf during a choice test (Færevik et al., 2006; Duve and Jensen, 2011), providing evidence that they form social connections from a young age. Other work has shown that social relationships that were formed early in life were long lasting (Raussi et al., 2010).

Given that calves are typically provided little or no social contact on dairy farms, and the wealth of information on other species showing detrimental impacts of isolation, exploring the effects of social isolation in dairy calves would seem to be important. The following section reviews research examining the effects of early social deprivation on behavioural problems, coping with novelty, and cognitive development. We also discuss evidence that social support and social buffering may mitigate some of the negative effects of stressful management practices on calves.

2.4.1 Behaviour Problems

A growing body of work has examined the relationship between the social environment and behaviour in calves (summarized in Table 1). This evidence suggests that socially reared calves are less fearful (Bøe and Færevik, 2003) and are more dominant when mixed in groups later in life (Broom and Leaver, 1978; Veissier et al., 1994), compared to calves that have been reared in isolation. A number of factors play a role in social behaviour development, such as age of first contact with conspecifics and level of contact. For instance, calves allowed full social contact with another calf, either from birth or from 3 wks of age, established a stronger bond compared to calves raised with only visual or auditory contact with other calves (Duve and Jensen, 2011). Calves housed individually or with only limited contact were more fearful than pair-housed calves (Jensen and Larsen, 2014). Collectively this evidence suggests that full social contact with peers from an early age is important.

2.4.2 Social Support

Social support is defined as the beneficial effects of the presence of a conspecific, irrespective of whether the individual is being challenged or not (Cohen and Wills, 1985). Social support is known to have beneficial effects on humans (for reviews see Kikusui et al., 2006 and Hennessy et al., 2009). Social buffering is the ability of social partners to decrease the impact of stressors during a challenge (Cohen and Wills, 1985), and is the aspect of social support that has been studied in animals. Social buffering has been demonstrated in humans (Thorsteinsson et al., 1998), rats (Kiyokawa et al., 2014a), guinea pigs (Hennessy et al., 2000), pigs (Reimert et al., 2014) and other farm animals (Rault, 2012). For example, the work on rats has shown a decreased response to stressors in the presence of other rodents (Hennessy et al., 2000; Kiyokawa et al., 2014a), especially when housed with familiar conspecifics (Kiyokawa et al., 2014b).

In cattle, the presence of conspecifics is known to reduce behavioural reactions to social separation (Boissy and Le Neindre, 1997; Piller et al., 1999). For example, calves vocalize less when regrouped with familiar calves compared to when regrouped with unfamiliar calves (Færevik et al., 2006). There is also some evidence of social buffering in calves in response to a non-social stressor; individually housed calves show a stronger vocal responseto weaning from milk in comparison with paired calves (de Paula Vieira et al., 2010). Further work is needed to assess the effects of social support on responses to other husbandry procedures like castration and dehorning. Also, future research should investigate the effects of different individuals (with different social relationship) on social supporter.

2.4.3 Coping with Novelty

Farm animals, including dairy cattle, are often exposed to novel events, such as changes in diet, changes in pen location, regrouping with new social partners, and new milking procedures. Individually reared calves show greater reactivity to environmental novelty compared to socially reared animals. Veissier et al. (1997) showed that isolation of calves promoted reactiveness to startling stimuli and development of self-directed oral behaviours. Calves housed individually for the first 3 mo of life were more reactive to environmental and social novelty than group housed animals when tested at 90 d of age (Jensen et al., 1997).

In contrast, early social contact reduced behavioural and physiological reactivity to environmental novelty. Calves provided social contact showed decreased responses to restraint and increased play and competitive success after weaning (Duve et al., 2012) and showed lower adrenocortical reactivity to stress (Creel and Albright, 1988). Calves raised in pairs or in small groups of calves showed lower heart rates when placed in a pen with an unfamiliar calf (Jensen et al., 1997) and were less fearful and more willing to approach unfamiliar calves when mixed after weaning (de Paula Vieira et al., 2012a).

2.4.4 Cognition

Social isolation early in life can impair cognition in rodents and other species (Jones et al., 1991; Fone and Porkess, 2008). Socially isolated rodents showed deficits in reversal learning (Jones et al., 1991), a method often used to assess behavioural flexibility in animals (Fone and Porkess, 2008). A recent study examined reversal-learning in pair and individually housed calves and found that individually housed calves made more mistakes during the reversal-learning phase and was linked to impaired behavioural flexibility (Gaillard et al., 2014). A follow up study, using a colour discrimination training task, showed that calves housed with either social companions from an early age in a complex social environment (with the presence of their dam and other cows and calves), or simply pair-housed, performed better in reversal-learning than individually raised calves (Meagher et al., 2015). In the latter study, the majority of individually housed calves did not learn the reversal task even when provided twice as many sessions as required by the average socially housed calf. Similar results have been reported in rodents, and these studies indicate that the cognitive deficit is associated with decreased brain development and plasticity (e.g. Schrijver and Wurbel et al., 2001; Fowler et al., 2002; Schrijver et al. 2002; Lipkind et al., 2002). In rodents, it is well established that the prefrontal cortex is responsible for behavioural control, decision-making, and inhibition of behaviour (Dalley et al., 2004). These controls are essential for success in reversal learning.

We conclude that calves raised in isolation exhibit deficient social skills, difficulties in coping with novel situations and poor learning abilities, all of which may reduce the animal’s ability to adjust to variable environments on the dairy farm. Behavioural flexibility is widely believed to depend on exposure to a variable environment in early life (Sackett, 1970). Future studies should investigate if there is a critical life stage during which calves must be socialized to reverse the deleterious effects on cognition and behavioural inflexibility described above, for example, testing the effects of companions at different ages during the milk-feeding period. Further work is also required to test the effects of providing more complex environments (e.g. more naturalistic environments such as access to the outdoors, increased human contact or access to interactive toys), with and without access to social conspecifics. Work is also required to better understand the longer-term effects of social deprivation on cognitive impairment, and whether these can be reversed.

2.4.5 Longer-term Effects

Most of work to date in dairy calves has focused on the effects of social isolation during the milk feeding period, the weaning period and the days immediately following weaning. The lack of work on longer-term effects is likely due to the time required and the challenges associated with maintaining adequate controls. Work to date suggests that negative effects can persist. For example, studies by Le Neindre (1989 a, b) found that calves reared with a foster cow showed more pronounced maternal behaviour and more locomotion and exploration during isolation tests years later. Another study reported that dam-reared calves better transitioned into the lactating herd, suggesting that social housing of calves may enhance social skills useful later in life (Wagner et al., 2012). In a complementary study, long-term effects of dam rearing were tested using an isolation challenge when cows were 2.5 y old. Cows that had experienced 12 wks of contact with the dam showed greater behavioural activity during the isolation test in comparison with cows that have been individually raised (Wagner et al., 2014). However these studies should be considered preliminary due to the lack of controls during the growing phase and the small sample sizes (as few as 5 animals per treatment). Further work should assess the longer-term effects of social versus individual rearing on behavioural flexibility as adults, and whether the detrimental effects of social isolation can be reversed through enriched environments during or other means.

We conclude that rearing dairy calves individually has negative effects on calf development. Housing systems for newborn and milk-fed dairy calves should meet their thermal, physical, psychological, and behavioural needs (Stull and Reynolds, 2008); the common practice of individual rearing violates at least two of these criteria (i.e. psychological and behavioural). However, if dairy farms are to rear milk-fed calves in groups, understanding the practical benefits and constraints of social housing is essential. We turn to these more practical issues in the following section.

Table 1. Summary of research on effects of social housing on behaviour of calves. For each study I indicate the class of animal considered, the types of social housing treatment imposed, and the parameter(s) studied. I also indicate the direction (- negative; + positive; = no difference) of the reported effect for socially housed versus individually housed calves.

Treatments	Animals	Parameters	Effects of socialization	Reference
Individual; Group (3 calves)	Heifers	Social Rank	+	Broom and Leaver, 1978
Individual; Pairs	Heifers	Vocalization after teat removal	+	De Paula Vieira et al., 2010
Individual; Pairs	Heifers	Latency to feed in a novel environment	+	De Paula Vieira et al., 2010
Individual; Pairs	Heifers	Intake of feed after being moved to a new environment	+	De Paula Vieira et al., 2010
Individual; pairs; kept with dam[2]	Heifers & bulls	Response to restraint during blood sampling	–	Duve et al., 2012
Individual; pairs; kept with dam[2]	Heifers & bulls	Play behaviour	+	Duve et al., 2012
Individual; pairs; kept with dam[2]	Heifers & bulls	Competitive success	+	Duve et al., 2012

Treatments	Animals	Parameters	Effects of socialization	Reference
Individual[1]; Pair	Heifers & bulls	Latency to touch an unfamiliar calf	+	Jensen and Larsen, 2014
Individual; Group[3]	Heifers	Avoidance of unfamiliar calf	_	Jensen et al., 1997
Individual; Group[3]	Heifers	Fear in open field test	_	Jensen et al., 1997
Individual; Pair[2]	Heifers & bulls	Playing behaviour	=	Jensen et al., 2015
Individual; Group (4 calves)	Bulls	Aggression at mixing	_	Veissier et al., 1994
Individual; Group (4 calves)	Bulls	Social rank	+	Veissier et al., 1994

1. Individually reared calves were raised with different levels of contact with other calves (auditory, auditory +visual and auditory + visual + tactile).

2. Milk allowance was also investigated in this study, where individual and pair housed calves were raised in an enhanced or standard milk feeding plan.

3. Space allowance was also investigated in this study, where individual and group housed calves were raised in small or large pens.

2.5 Group Housing of Dairy Calves: Challenges and Solutions

There are also well-established benefits of housing calves in groups including reduced labour requirements per head (Broom and Leaver, 1978). One recent study reported that ‘‘reducing labour’’ and ‘‘saving time’’ were among the main reasons that farmers provided for group housing dairy calves (Hötzel et al., 2014). The development of automated feeding systems for calves has accelerated adoption of group housing of dairy calves particularly for larger dairy farms (Kung et al., 1997). There is also increased awareness of animal welfare by both dairy producers and the general public, and one important welfare concern is the social isolation of calves (Boogaard et al., 2010; Ventura et al., 2013). Furthermore, group housing has been associated with increased average daily gain (ADG) in dairy calves (Bernal-Rigoli et al., 2012; Jensen et al., 2015). A growing body of work has also examined the relationship between social environment and performance in dairy calves. Collectively these results support the idea that social housing positively influences performance of dairy calves.

2.5.1 Improved Feed Intakes and Weight Gains in Socially Reared Calves

Group housing of calves is associated with increased weight gains compared with individually housing, likely due to increased dry matter intake (DMI) as summarized in Table 2. Contact with the dam or other older animals within the first few weeks of life is known to stimulate young ungulates to start sampling solid feed at a younger age (Key and MacIver, 1980; Nolte et al., 1990) and eat more, especially in the pre-weaning phase. Calves housed individually have little opportunity to interact with conspecifics, and the onset of solid feed consumption might be delayed as a result. Warnick et al. (1977) reported that social housing increased concentrate intake during the pre-weaning period, resulting in higher weight gains after weaning. These authors speculated that these benefits were due to social learning by group-housed calves. Also, the stimulus of another animal eating, approaching and manipulating the feed, may increase attention toward the feed without any learning per se (Galef, 1981). This process of ‘social facilitation’ was defined by Galef (1988) as "the initiation of a particular response while observing others engaged in that behaviour" and several authors have suggested that social facilitation may be important in cattle (e.g. Ralphs et al., 1994; de Paula Vieira et al., 2012b). Regardless of the mechanism, both social facilitation and social learning may result in socially housed calves showing higher intakes of solid feed and improved weight gains compared to individually housed calves.

Further work is required to understand the mechanism of social influence on the feeding behaviour of dairy calves. We suggest the use of a two-action and control experimental design where social learning is tested by exposing naïve animals to different demonstrators trained on one of two feeding patterns and a control with no demonstrator (Whiten and Mesoudi, 2008). This design would help to disentangle social facilitation from social learning. Also, Calves housed with the dam or other older animals may have different influences compared to those only provided contact with conspecifics of the same age. Little is known about how the mother and others function as social models on early preferences for solid feed.

The increased solid feed intake in socially reared calves may occur due to increased attention to the feed given that other animals are also in contact with the feed. Thus, exploring alternative methods that draw attention to the feed may be effective at increasing intakes. For example, mechanically shaking or simply changing the feed more frequently may increase attention and ultimately increase intakes. In piglets, it has been shown that a 'play feeder' (an open trough with 3 protrusions to stimulate exploration) can increase creep feed intake (Kuller et al., 2010). To our knowledge this approach has not been applied to calves.

One study found that grass intake and time spent grazing were greater for grouped calves than for individual calves (Phillips, 2004) and another found that raising calves in groups increased concentrate consumption and the early onset of rumination compared to individual rearing (Babu et al., 2004). Bernal-Rigoli et al. (2012) found that dry matter intake (DMI) was greater for group housed vs. individually housed calves after 41 d of age, resulting in greater body weight (BW) gains for group-housed calves. Similarly, pair housing of dairy calves has been associated with increased solid feed intake (Jensen et al., 2015). One study found that calves paired at birth or at 3 wks of age consumed more solids than did individually housed calves (Tapki, 2007). Calves that were group housed early in life, in addition to having increased solid feed intakes, also show reduced behavioural responses to mixing and weaning (Chua et al., 2002; de Paula Vieira et al., 2012 a,b).

Table 2. Summary of research on effects of social housing on feeding behaviour and performance of calves. For each study I indicate the class of animal considered, the types of social housing treatment imposed, and the parameter(s) studied. I also indicate the direction (- negative; + positive; = no difference) of the reported effect for socially housed versus individually housed calves.

Treatments	Animals	Parameters	Effects of socialization	Reference
Individual; Group (3 calves)	Bulls	BW	+	Andrighetto et al., 1999
Individual; Group (6 calves)	Heifers & bulls	Solid feed intake	+	Babu et al., 2004
Individual; Group (6 calves)	Heifers & bulls	ADG	+	Babu et al., 2009
Individual; Group (6 calves)	Heifers & bulls	Solid feed intake	=	Babu et al., 2009
Individual; Group (3 or 4 calves)[1]	Bulls	DMI	+	Bernal-Rigoli et al., 2012
Individual; Group (3 or 4 calves)[1]	Bulls	BW	+	Bernal-Rigoli et al., 2012
Individual; Group (3 or 4 calves)[1]	Bulls	ADG	=	Bernal-Rigoli et al., 2012
Individual; Pairs	Heifers & bulls	Solid Feed Intake	=	Chua et al., 2002
Individual; Pairs	Heifers & bulls	ADG	=	Chua et al., 2002

Treatments	Animals	Parameters	Effects of socialization	Reference
Individual; Pairs	Heifers	Concentrate Intake	+	De Paula Vierira et al., 2010
Individual; Pairs	Heifers	ADG	=	De Paula Vierira et al., 2010
Individual; Pairs[4]	Bulls	ADG	=	Hänninen et al., 2005
Individual; Group (4 calves)[3]	Bulls	Solid feed intake	+	Hepola et al., 2006
Individual; Group (4 calves)[3]	Bulls	ADG	+	Hepola et al., 2006
Individual; Pairs[2]	Heifers & bulls	Concentrate Intake	+	Jensen et al., 2015
Individual; Pairs[2]	Heifers & bulls	BW	+	Jensen et al., 2015
Individual; Pairs[1]	Heifers	Solid feed intake	=	Pempek et al., 2013
Individual; Pairs[1]	Heifers	ADG	=	Pempek et al., 2013

Treatments	Animals	Parameters	Effects of socialization	Reference
Individual; Group (3 calves)	Heifers	Grass Intake	+	Phillips, 2004
Individual; Group (3 calves)	Heifers	BW gain	=	Phillips, 2004
Individual; Group (3 calves)	Heifers & bulls	Final BW	+	Richard et al., 1998
Individual; Group (3 calves)	Heifers & bulls	Concentrate intake	=	Richard et al., 1998
Individual; Group (3 calves)	Heifers & bulls	Solid feed intake	+	Tapki, 2007
Individual; Group (3 calves)	Heifers & bulls	ADG	+	Tapki, 2007
Individual; Group (5 calves)	Bulls	Solid feed	=	Terré et al., 2006
Individual; Group (5 calves)	Bulls	BW	=	Terré et al., 2006
Individual; Group (6 calves)	Heifers & bulls	Solid Feed Intake	=	Warnick et al., 1977
Individual; Group (6 calves)	Heifers & bulls	ADG	+	Warnick et al., 1977
Individual; Group (4 calves)	Bulls	BW	+	Xiccato et al., 2002
Individual; Group (4 calves)	Bulls	ADG	+	Xiccato et al., 2002

1. Milk feeding method was also investigated in this study, where individual and pair housed calves were bottle or bucket-fed.

2. Milk allowance was also investigated in this study, where individual and pair housed calves were raised in an enhanced or standard milk feeding plan.

3. Environmental temperature (warm or cold buildings) was also investigated in this study

4. Flooring type (concrete vs. rubber mat) was also investigated in this study

Calves reared in groups continue to benefit from higher concentrate intakes than calves previously reared individually, even after all calves are mixed in group pens (de Paula Vieira et al., 2010). These effects that persist beyond the period of individual housing might be due to the better learning abilities of socially housed calves described above, allowing them to more rapidly learn where and how to use new feeders. The findings of Duve et al. (2012), that group housed calves were faster at locating feed and spent more time eating concentrates in competitive situations than calves that had been individually housed, are consistent with the interpretation that intake differences persisting beyond the period of individual rearing are due in part to cognitive deficits. In addition, pre-weaning intake of solid feed helps to improve the transition from milk to solid feed at weaning (reviewed by Weary et al., 2009), such that calves that do not achieve adequate solid feed intakes before weaning experience poor growth and increased distress during weaning (de Paula Vieira et al., 2008; de Passillé et al., 2011).

Bull calves that were reared in groups also gained weight more rapidly than individually housed calves (Andrighetto et al., 1999; Xiccato et al., 2002). Other work has shown that the advantages of early gains on the onset of puberty and milk production in the first and later lactations (Moallem et al., 2010; Soberon et al., 2012). A similar line of research has shown that Holstein bull calves reach puberty earlier and have larger testicular mass when offered a high level of nutrition early in life (Dance et al., 2015). Thus, early growth achieved in the first weeks of life can have profound effects on production and reproduction later in life.

The social environment can have profound influences on total food intake, diet and persistence of solid feed intake of calves. Provision of social companions facilitates increased intakes of solids during the milk-feeding phase and weaning, which results in performance differences in the majority of trials. As illustrated in Table 2, some studies failed to find a difference between individually housed and group-housed calves, but no study has reported decreased performance in group-housing. Despite these benefits, a number of concerns hinder the adoption of group housing on dairy farms including cross-sucking, aggression and transmission of disease (Quigley, 1997; Pempek et al., 2013; Hötzel et al., 2014). These concerns and possible solutions are reviewed below.

2.5.2 Cross-sucking

Cross-sucking is defined as the suckling of one calf directed to the body of another (Jensen, 2003); it is considered a management problem and potentially associated with udder deformations, mastitis and milk loss (Lidfors and Isberg, 2003). Some studies have reported high levels of cross-sucking in group housed calves (e.g. Lidfors and Isberg, 2003), but other studies have reported little or none (e.g. Chua et al., 2002; Mattiello et al., 2002), suggesting that the problem can be managed.

One important aspect is the ability to engage in natural suckling behaviour. When calves are raised naturally with the dam (Margerison et al., 2003), or with a nurse cow (Krohn et al., 1999), cross-sucking is rare. Several experiments (see review by Jensen, 2003) have demonstrated that feeding milk through a teat instead of a bucket, allowing calves to access milk for many hours of the day instead of just one or two feedings, and even providing a dry teat for calves to suck upon can reduce cross-sucking (Veissier et al., 2002; Lidfors and Isberg, 2003). Calves are highly motivated to suck, but motivation for this behaviour is closely associated with motivation to drink milk (de Passillé, 2001). Teat feeders and enhanced milk-feeding programs minimize the incidence of cross-sucking by allowing calves to express their natural suckling behaviour (de Passillé et al., 2010). Recent studies on calves fed milk via automatic feeders have reported some cross suckling, especially around weaning (e.g. Nielsen et al., 2008; de Passillé et al., 2011). More gradual weaning procedures appeared to reduce cross suckling in calves (Nielsen et al., 2008), but cross-suckling was not strongly affected by milk allowance (6L vs 12 L) or weaning age (47 vs 89 d) (de Passillé et al., 2011); however all calves studied stopped cross-sucking with age (de Passillé et al., 2011).

Although individual housing prevents cross-sucking, individually housed calves engage in other forms of abnormal oral behaviours including excessive licking of their own bodies, walls and fixtures of the environment (Bokkers and Koene, 2001). These authors and others (Veissier et al., 1997; Jensen, 2003) have argued that expression of abnormal oral behaviours is likely caused by poor milk feeding practices (i.e. low milk allowance, bucket feeding, abrupt weaning). When these practices are corrected abnormal oral behaviours will be rare.

2.5.3 Competition and Aggression

Competition and aggression can also be prevented by social isolation. In early life, competition and aggression are normally associated with feeding (Herrmann and Knierim, 1999). For calves reared in groups fed from a single automatic milk feeder, 89% of aggression events happened around the feeder (Herrmann and Knierim, 1999). Not surprisingly, aggression was intensified when calves were fed restricted milk allowances; higher competition at the milk teat can also reduce feeding time and milk intake (von Keyserlingk et al., 2004).

Some management strategies to mitigate competition during milk feeding have been studied. Providing more teats (ideally at least 1 / calf) reduces the competition (von Keyserlingk et al., 2004). Automated feeders often use much higher ratios of calves to teats, but reducing the ratio helps to reduce competition. For example, one study found that calves in groups of 24 animals with one teat had increased levels of disturbance when feeding (and had a higher feeding rate) compared to groups of 12 calves (Jensen, 2004). Providing also well-separated teats reduces teat switching (Nielsen et al., 2008). The placement of barriers between the teats also reduces competition, especially when long barriers separate calves' heads and shoulders (Jensen et al., 2008). Offering milk in fewer and larger portions can lower competition for access to teats (Jensen, 2004), likely because the larger meals are more effective at satiating the calves and thus reduce non-nutritive sucking at the teat (de Paula Vieira et al., 2008).

Aggressive behaviour also can be reduced by maintaining stable groups. Calves kept in stable groups have fewer aggressive interactions during feeding than regrouped animals (Mounier et al., 2006). Given that it can be difficult to maintain stable groups after weaning, limiting regrouping to the mixing of two previously stable groups results in fewer aggressive and more positive social interactions of weaned dairy calves in comparison to other mixing options (Færevik et al., 2007). In summary, these results suggest that problems with competition among calves can be mitigated by providing enough milk, enough feeding stations, designing and placing these stations effectively, and by maintaining stable social grouping where possible.

2.5.4 Health

Calf morbidity and mortality are most important indicators of herd health status (Ortiz-Pelaez et al., 2008). Calf mortality rates are often high: a study of large farms in Korea reported a mortality rate of 10.7% during the first year of life (Hur et al., 2013), a UK survey reported a mortality rate of 14.5% from birth to first calving (Brickell et al., 2009), and in France mortality rates averaged 4.4% and 3.2% for 3 d to 1 mo old and 1- to 6-mo old, respectively (Raboisson et al., 2013). Yearly mortality of heifers in the United States has been reported to be 6.9% and 7.8% on calf ranches and dairy farms, respectively (Walker et al., 2012: USDA, 2008).

Enteric and respiratory diseases can be spread through horizontal calf-calf transmission, especially fecal-oral and direct nose-nose contact, behaviours that can be minimized by individual housing (Steenkamer, 1982; Maatje et al., 1993; McGuirk, 2008). Individual pens may also facilitate monitoring, and thus result in better treatment of disease (Kung et al., 1997). Despite these mechanisms, there is little evidence of a consistent relationship between individual housing and calf health. Some studies (e.g. Webster et al., 1985; Gulliksen et al., 2009) have indeed reported more health problems in group-reared calves, but other empirical studies have found no advantage of individual housing when compared with small groups (e.g. Waltner-Toews et al., 1986 a, b; Perez et al., 1990, Johnson et al., 2011). As reviewed below, different factors including the amount of milk fed, bedding management and group size can affect disease risk and should be considered in any comparison between systems.

Early work (Warnick et al., 1977) found that raising calves in groups resulted in higher treatment rates compared to individually housed calves. Another early study reported that chronic and acute respiratory diseases and diarrhea occurred more frequently in group-housed veal calves (Maatje et al., 1993) but this comparison was confounded by differences in milk feeding methods between grouped (computer-controlled) and individual (bucket feeding twice per day) calves.

Group size can play a role in the health of group-housed calves. One study on commercial farms in Sweden reported that calves housed in pens of 8 to 12 calves had a higher incidence of respiratory illness than calves housed in groups of 6 to 9 calves, but there was no differences in diarrhea between these treatments (Svensson and Liberg, 2006). Another study found that severe cases of diarrhea were more common in large groups (Svensson et al., 2003). A U.S. study (Losinger and Heinrichs, 1997) found that raising calves in groups with more than 7 calves was associated with a higher mortality, but found no differences between farms with individually housed calves or groups of six or fewer. Another study found no difference in disease incidence when comparing groups of 2, 4 and 8 calves (Abdelfattah et al., 2013). Higher morbidity and mortality in large groups of calves may be due to difficulty in detecting, examining and treating sick calves, resulting in delayed treatments (Steenkamer, 1982; van Putten, 1982).

Another factor that influences disease risk in group-housed dairy calves is the method of grouping. Pedersen et al. (2009) reported that groups in which new calves were continuously introduced and removed (i.e., dynamic groups) had lower daily gains and a higher incidence of disease than did stable groups (e.g., using all in–all out management). The aim of all-in–all-out systems is to prevent the spread of infections between groups of animals raised in the same unit, allowing for cleaning and disinfection between groups of animals. In fattening pigs and broilers, all-in–all-out systems reduce the occurrence of infectious disease (i.e. Wierup, 2000).

Some studies found no difference in the incidence of respiratory disorders (Hanekamp, 1994) and other health issues between individually reared calves and calves reared in groups (Hänninen et al., 2003). Work on veal calves has shown that contagious diseases including *E. coli* O157 (Rugbjerg et al., 2003), *Salmonella ssp*. (Losinger et al., 1995) and *Cryptosporidium parvum* (Mohammed et al., 1999) were not associated with group housing.

Some work has also reported improved health in grouped calves. For example, Hänninen et al. (2003) found that the incidence of diarrhea was lower in group-housed calves compared to individually housed calves. Babu et al. (2009) also found that diarrhea and respiratory disease were less common in socially housed calves compared to those individually raised.

In summary, diarrhea and respiratory illness, the most common diseases in young calves, are not consistently associated with group housing. Disease transmission is complex and many other management practices influence the risk of these diseases, including methods of milk feeding, hygiene, ventilation, colostrum practices, diet and health monitoring. We suggest that controlling these variables is a more effective method of minimizing health problems in dairy calves. The results above indicate that calves can be grouped in good health if housing is properly managed, but more research is required on factors that improve the health of grouped calves. In particular we urge long-term studies that focus on factors including ventilation, age of contact, feeding program and preventive measures. Additionally, the effect of group housing on the future health status of the adults is worthy of investigation.

2.6 Conclusions

The detrimental effects of social isolation are now recognized in a range of species. Similarly, dairy calves reared in isolation show deficient social skills, difficulties in coping with novel situations and poor learning abilities. Social housing improves solid feed intakes pre-weaning, and helps improve calf weight gains before and after calves are weaned from milk to solid feed. We encourage future work on the persistence of the negative effects of social isolation on cognition and behavioural flexibility, and on the critical periods during which these effects can be reversed. We also urge new studies on the longer-term effects of social rearing on heifer and cow behaviour, health and production. Together, this will lead to a better understanding of housing and management conditions required for group housing to succeed.

3 Early Pair Housing Increases Solid Feed Intake and Weight Gains in Dairy Calves [2]

3.1 Introduction

Dairy farms often separate calves from their dams within 24 h after birth and then house calves individually (USDA, 2008; Vasseur et al., 2010; Hötzel et al., 2014). Housing milk-fed calves in pairs or groups is increasing in popularity, in part due to the potential of reducing labour requirements per head. Social housing can also provide animal welfare benefits as it allows calves to perform social behaviours and can provide calves more useable space (Jensen et al., 1997; Færevik et al., 2006).

Calves that consume little solid feed before weaning are more likely to experience poor growth and prolonged hunger after weaning, until intake of solid feed meets their requirements for maintenance and growth (Jasper and Weary, 2002; de Passillé et al., 2011). Encouraging solid intakes early in life can help smooth the transition from milk to solid feed at weaning. Social housing of dairy calves has been shown to reduce behavioural responses to weaning and improve performance when mixed with a larger group after weaning (de Paula Vieira et al., 2012b). Group-housed calves have increased weaning weights compared with individually housed calves, likely due to increased DMI during the pre-weaning period (Chua et al., 2002; Xicatto et al., 2002; de Paula Vieira et al., 2010, Bernal-Rigoli et al., 2012). Increased DMI is often attributed to social learning and social facilitation during feeding (Launchbaugh and Howery, 2005).

On some farms calves are housed individually for the first weeks of life and then paired or moved to a group around the time of weaning (Staněk et al., 2014), but it is unknown when contact with peers is necessary to achieve the benefit of increased early intake of solids. The aim of this study was to assess the effects of early and late pairing on feeding intake and weight gain before and after weaning. I predicted that calves paired early in life (at 6 d) would begin eating solids at a younger age, consume more solids throughout the pre-weaning period, and gain more BW in comparison with calves housed individually or calves paired later in life (6 weeks of age).

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[2] Costa, J. H. C., R. K. Meagher M. A. G. von Keyserlingk and D. M. Weary. 2015. Early pair housing increases solid feed intake and weight gains in dairy calves. J. Dairy Sci. 98:6381-6386.

3.2 Materials and Methods

This experiment was carried out between April and December of 2013 at The University of British Columbia's (UBC) Dairy Education and Research Centre, located in Agassiz, British Colombia, Canada (49°N, 121°W). All procedures carried out in this study were approved by the UBC Animal Ethics Committee (AUP A12-0337). The animals were cared for according to the guidelines outlined by the Canadian Council of Animal Care (2009).

3.2.1 General Methodology and Treatments

Forty Holstein bull calves were enrolled at birth. Calves were separated from their dam and fed at least 4L of colostrum (with > 50 g/L of IgG) by bottle within 6 h of birth. Blood samples were collected from the jugular vein 24 h after the first feeding of colostrum and serum was analyzed using a Reichert AR 200 Digital Handheld Refractometer (Reichert, Depew, USA). Only calves with serum protein >5.5 g/dL were kept in the trial. After birth, calves were weighed (mean 43.5 ± 5.1 kg BW) and moved to individual pens with no visual contact with any other calf and were bottle-fed up to 8 L of whole milk daily.

At 6 ± 3 d of age calves were assigned to one of three treatments: individual (n=8), early pair (n=8 pairs) or late pair (n=8 pair). Assignment was random within blocks of 5 calves, within the constraint that calves closest in age were assigned to pair treatments. Individually-reared calves were kept in individual pens (1.2 m × 2 m) on sawdust bedding, with no visual contact with any other calf for the entire length of the experiment (70 d). For early-paired calves, 2 calves were paired at 6 ± 3 days of age by having the barrier to the neighbouring pen removed to create a double pen. For late-paired calves, the individual housing continued until the age of 43 ± 3 d, 14 d before weaning. In both pair housing treatments, calves were provided twice the area (2.4 m × 2.0 m), milk bottle holders, water and solid feed buckets in the same pen system as the individually raised calves.

3.2.2 Milk Delivery, Solid Feeding and Weaning

All calves were bottle-fed pasteurized whole milk twice per day. From 0 d to 28 d of age calves in all treatments received 8 L/d of pasteurized whole milk, divided in 2 feedings, delivered at 0800h and 1630h. From d 29 to d 49 calves were fed 6 L/d, fed as described above. From d 50 to d 54 milk was reduced by 20%/d for 5 days until calves were completely weaned at d 55. Calves were enrolled in the experiment until d 70. All calves had ad libitum access to water, total mixed ration

(TMR) (shown as % of DM, consisting of 26.1 % corn silage, 14.8 % grass silage, 10 % alfalfa hay and 49 % concentrated mix; which was on average 49.1 ± 1.5 % DM; chemical composition shown as % of dry matter (DM), crude protein (CP) 17 %, neutral detergent fibre (NDF) 32 %, acid detergent fibre (ADF) 20 %) and calf starter (Hi-Pro Medicated Calf Starter, Chilliwack, BC, Canada with an overall DM of 89.5%; chemical composition shown as % of DM, 90% DM; CP 21%, NDF 19%, ADF 11%; medicated with a coccidiostat [50 mg/kg of Lasalocid Sodium]) during the experimental period. Samples of the feed were taken prior to feeding once every other week and frozen, at the end of the experiment the samples were sent to A&L Canada Laboratories Inc. (London, ON). Samples for nutrient and DM analysis were oven dried at 55°C for 48 h. Dried samples were ground to pass though a 1-mm screen and for analysis of ADF (AOAC International, 2000: method 973.18), NDF with heat-stable α-amylase and sodium sulphite (Van Soest et al., 1991), and CP (N x 6.25; AOAC International 2000: method 990.03; Leco FP-528 Nitrogen Analyzer, Leco, St. Joseph, MI). Fresh feed and water were delivered daily at approximately 0830h, and feed refusals were removed before the new feed was delivered. Daily (24 h) calf starter and TMR intakes were determined each morning by disappearance.

3.2.3 Performance and Health

Calves were weighed and health scored weekly. Individual BW of each calf was recorded and average daily gain (ADG) was calculated for the pre-weaning period (3 to 6 wk.), the weaning period (6 to 10 wk.) and over the whole experimental period (3 to 10 wk.). Health checks were performed following de Paula Vieira et al. (2010), which consisted of diarrhoea scoring, where 1 = normal feces; 2 = plaques but not watery; 3 = watery and body temperature < 39.5°C; 4 = watery and body temperature ≥ 39.5°C. Calves with a score = 4 were treated with electrolytic solutions (Hydrafeed, EXL Laboratories, Minneapolis, MN, USA), and calves failing to respond to treatment within 2-d were administered a nonsteroidal anti-inflammatory drug (NSAID) (Metacam 20 mg/mL, Boehringer Ingelheim, Burlington, Ont., Canada), according to UBC research farm standard procedure. During the experimental period 3 calves from the early-paired, 3 calves from the late-paired and 1 calf from the individually-reared treatment were treated with NSAID. Clinical examination of respiratory health was also performed. Calves showing nasal discharge and pathological sounds of pulmonary infection during auscultation were classified as ill, and treated with antibiotic drugs (Resflor GOLD®, Intervet Inc. Roseland, NJ, USA) according to the farm's standard operating procedure. During the experimental period 2 calves from each treatment were treated with antibiotic drugs.

3.2.4 Statistical Analysis

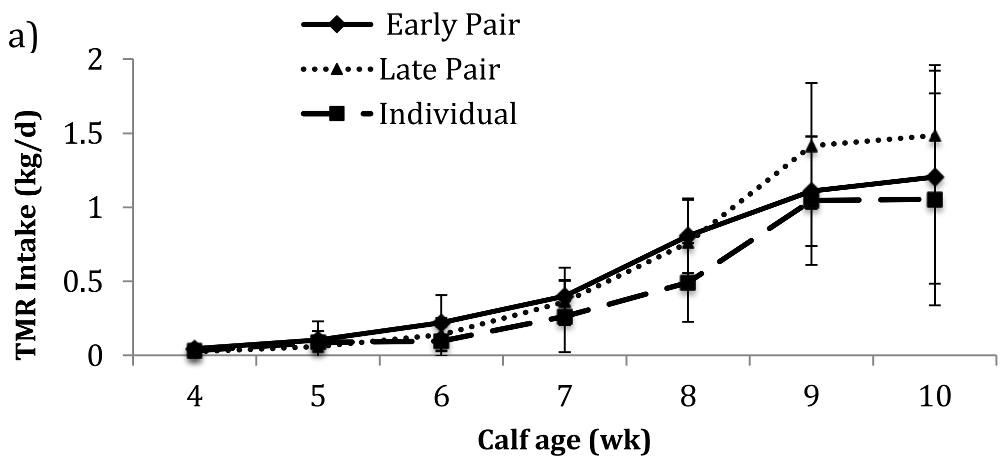
All analyses were performed with SAS (version 9.4; SAS Inst. Inc., Cary, NC) using the pen (i.e. calf or pair) as the experimental unit. Intake of TMR and calf starter were measured daily but averaged to form weekly values for intake per calf per day. Intake of TMR and calf starter are expressed on a DM basis. DMI of TMR and calf starter, total DMI (i.e. TMR + calf starter), ADG and birth BW were considered as dependent variables. Prior to analysis, data were checked for normality using the UNIVARIATE procedure in SAS and probability distribution plots. The effect of treatment on each variable was tested using the MIXED procedure in SAS.

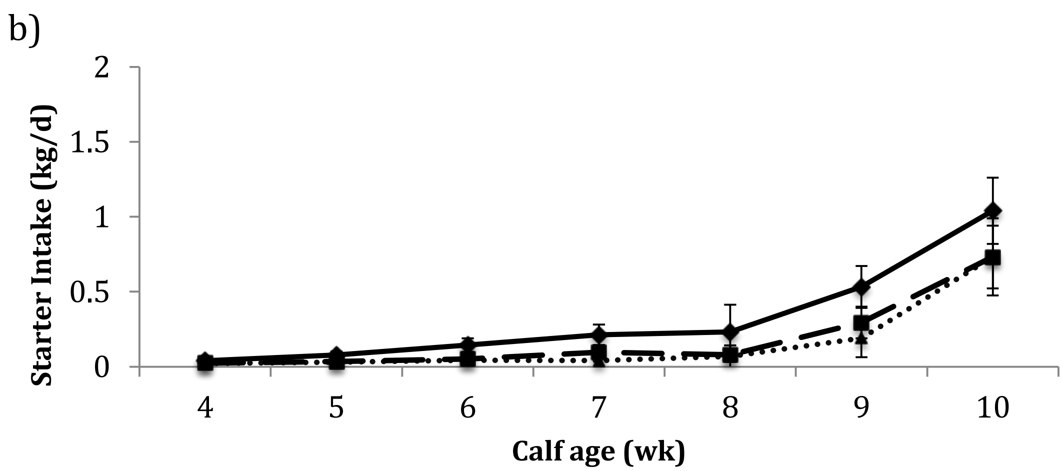
For the variables intake of TMR, calf starter and total DMI the model included treatment, week and the interaction of the week and the treatments. Week was specified as a repeated measure and calf or pair specified as subject, using an autoregressive covariance structure. ADG over each period (pre-weaning, weaning and over the whole experimental period) was calculated and tested in a model that included treatment and calf or pair as a random effect. To determine the differences between specifics treatments, the PDIFF statement was used to compare the least squares means of each combination of treatments, and the p-values were corrected using the Bonferroni correction.

3.3 Results

Intake of TMR was similar across the 3 treatments ($F_{2, 22} = 0.46$; $P = 0.63$; Fig. 1a), but early-paired calves ate more calf starter ($F_{2, 22} = 3.46$; $P = 0.03$; Fig. 1b) and consequently showed higher total DMI ($F_{2, 22} = 10.61$; $P < 0.001$; Fig. 1c) relative to the individual and late pair treatments. Solid feed intake was minimal until calves were 3 wk. old. At 6 wk., intake of TMR was not different between treatments ($F_{2, 22} = 1.40$; $P = 0.27$) and averaged 0.17 ± 0.07 kg/d, 0.31 ± 0.07 kg/d, 0.18 ± 0.06 kg/d, for individually, early pair and late pair housed calves, respectively. Starter intake was similar for the individually-reared and late-paired calves (0.07 ± 0.03 kg/d and 0.05 ± 0.03 kg/d) but higher for the early-paired calves (0.18 ± 0.03 kg/d; $F_{2, 22} = 5.00$; $P = 0.02$). Consumption increased after weaning in all treatments, but this increase was greatest for the early-paired calves. At 10 wk. of age, intake of calf starter was higher than the other two treatments ($F_{2, 22} = 4.11$; $P = 0.03$). Calf starter intake averaged 2.20 ± 0.22 kg/d, 1.09 ± 0.25 kg/d and 1.26 ± 0.33 kg/d for early pair, late pair and individually housed calves, respectively. Intake of TMR did not differ among treatments ($F_{2, 22} = 1.18$; $P = 0.33$), TMR intake averaged 3.27 ± 0.72 kg/d, 3.08 ± 0.46 kg/d, and 2.89 ± 0.54 kg/d for the same three treatments.

Figure 1. Least squares mean (± SE) a) total mixed ration (TMR; kg of DM), b) calf starter (kg of DM) and c) solid feed dry matter intake (DMI; kg of DM) for early-paired (paired at 6 ± 3 d old; n=8 pairs), late-paired calves (paired at 43 ± 3 d old; n=8 pairs) and individually (n=8 calves). Weekly averages are shown in relation to calf age, with age ranging from 4 to 10 wk.





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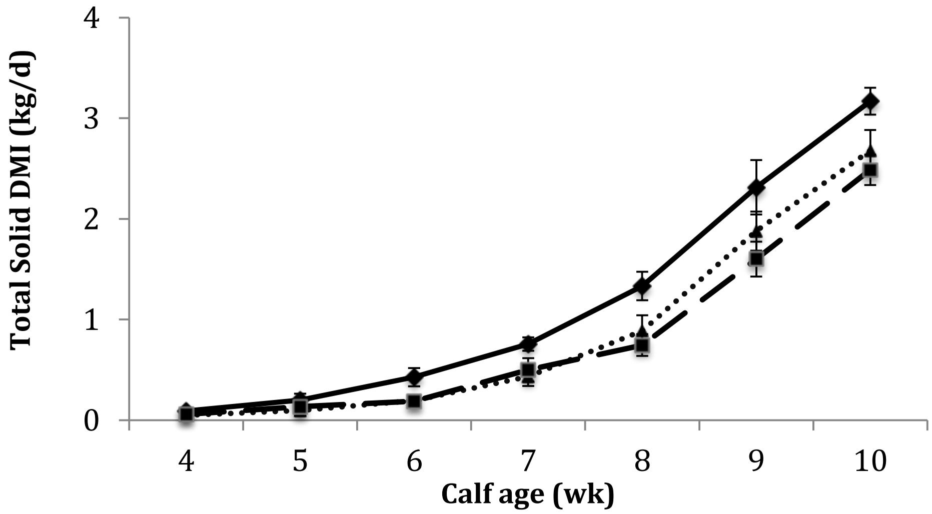
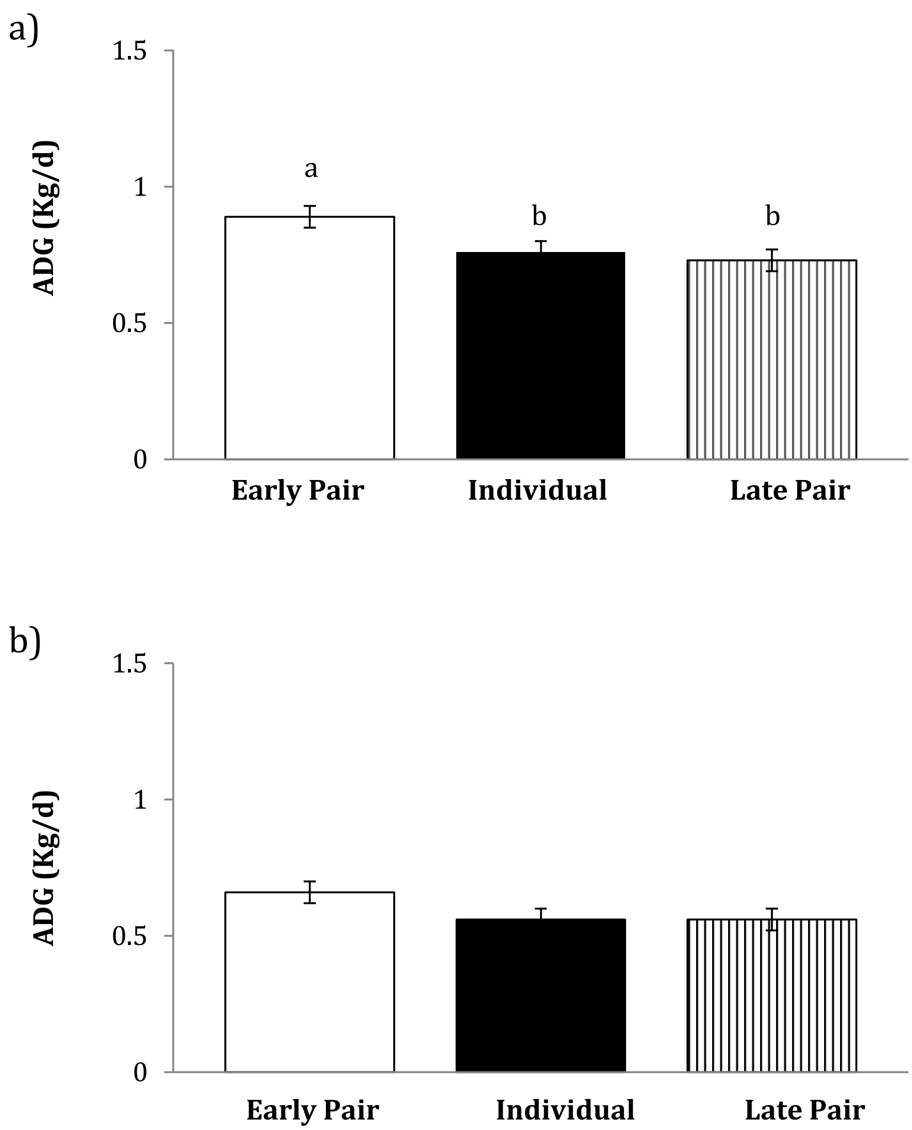


Calves in the early pair treatment gained more weight than did the calves in the other 2 treatments during the entire experimental period (0.89 ± 0.04 kg/d versus 0.76 ± 0.04 kg/d and 0.73 ± 0.04 kg/d for the early-paired, individual and late-paired calves, respectively; $F_{2, 22} = 4.87$; $P < 0.01$). ADG was not different between treatments during the pre-weaning period (3 to 6 wk.) ($F_{2, 22} = 0.98$; $P = 0.39$; Fig 2a) but early-paired calves had higher ADG ($F_{2, 22} = 4.13$; $P = 0.03$; Fig. 2b) during the weaning period (6 to 10 wk.) relative to the individual and late pair treatments.

Figure 2. Least squares mean (± SE) average daily gain (ADG) (kg/d) for early-paired (paired at 6 ± 3 d old; n=8 pairs), late-paired calves (paired at 43 ± 3 d old; n=8 pairs) and individually housed calves (n=8 calves) during a) the entire experimental period (wk. 3 to wk. 10) and separately from b) the pre-weaning period (wk. 3 to wk. 6) and c) the weaning period (wk. 6 to wk. 10).



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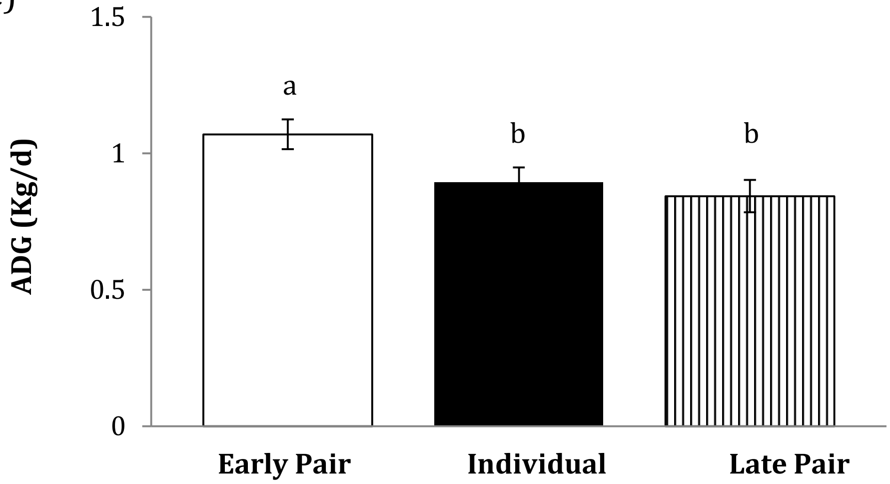

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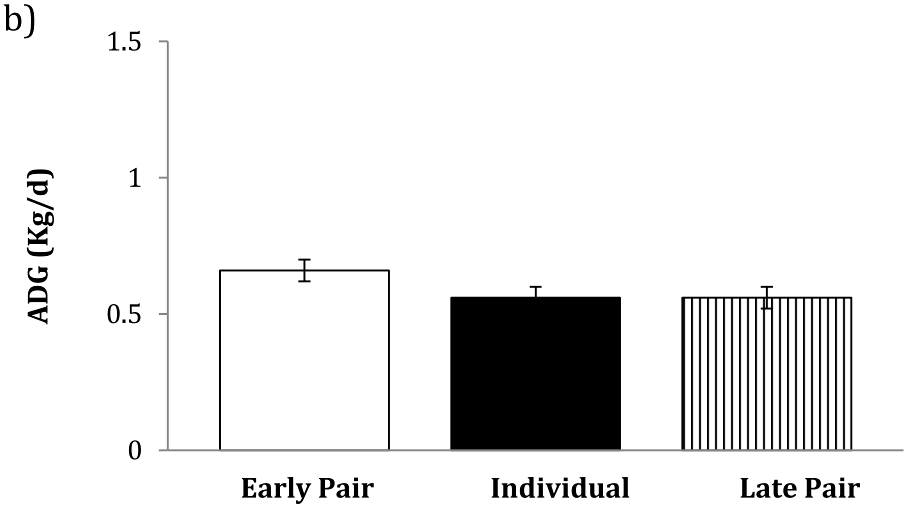


3.4 Discussion

This study is the first to explore the effects on feed intake of late pairing of calves, in comparison to early pair housing and individual housing. Early pair housing increased calf feed intake and BW. Calves paired soon after birth began to consume solid feed earlier than late-paired and individually housed calves likely contributing to the increased weight gains.

The findings of the current study, showing increased intake by socially housed calves, are consistent with earlier work on social versus individual housing (Chua et al., 2002; Xicatto et al., 2002; de Paula Vieira et al., 2010, Bernal-Rigoli et al., 2012). The results of the current study indicate that grouping must occur before 6 wk. to provide this benefit. Tapki (2007) compared calves grouped at birth versus at 3 wk. of age and found no difference in solid feed intake.

The results of the current study are also consistent with previous work showing that early grouping can have an important influence on the development of dairy calves. For example, social housing is associated with cognitive benefits including improved performance in reversal learning and improved object recognition (Gaillard et al., 2014). Duve and Jensen (2012) found that when calves were housed individually for 3 wk. and then paired, they performed more social behaviours than calves housed individually with limited social contact throughout the pre-weaning period. Only minor differences were found between calves housed together from birth compared with those paired at 3 wk. of life. In combination, these results indicate that the critical phase for grouping occurs sometime between 3 and 6 wk. of age, as calves paired at 3wk did not differ from calves paired at birth. Based upon these results my conservative recommendation is to group calves within the first 3 wk. of life.

The early-paired calves in the current study gained weight at a faster rate than did the individually-reared and late-paired calves. This increased ADG can be explained by the greater solid feed intake. Solid feed intakes are likely to be an important determinant of gains, especially when calves are fed limited quantities of milk (see review by Khan et al., 2011b). Solid intakes likely became more important to growth in the current study after 4 wk. of age, when the milk ration was reduced from 8 L to 6 L. An additional benefit of establishing high solid intakes before weaning is that calves should then transition more smoothly to exclusively solid feed when milk is fully withdrawn at weaning. Although all treatment groups exhibited a growth check during weaning at wk. 7, this check was more pronounced in individually raised calves than in late and early paired calves, indicating an advantage to being paired during the weaning phase. A reduced growth check at weaning for group housed calves has also been reported in earlier studies (Chua et al., 2002; de Paula Vieira et al., 2010). In addition to potential animal welfare benefits from the higher gains this early advantage in BW is likely to benefit farm profitability; recent research has shown the advantages of higher weight gains in calves on the onset of puberty and first lactation, as well as overall milk production (Moallem et al., 2010; Soberon et al., 2012).

A recent paper found that social contact was associated with increased solid feed intake when calves were fed a high intake of milk, but not when calves were fed low milk volumes (Jensen et al., 2015). Feeding low volumes of milk increases calf hunger (de Paula Vieira et al., 2008), increasing motivation to eat solid feed. Thus the effects of social housing on solid intakes are expected to be greatest for calves with higher milk intakes, as in the current study.

In the current study TMR intake did not differ among treatments. This result contrasts with that of Phillips (2004) in which calves reared in groups showed increased intakes of grass (but not starter) relative to calves housed individually. The difference between these two studies may be due to differences in motivation to consume solid feed. In the current study, calves were fed 8 L/d and in the study by Phillips (2004) calves received 4L/d. Increased milk allowance is thought to increase motivation to consume forages (as reviewed by Khan et al., 2011b), and all calves in this study consumed high quantities of TMR. Intakes were more variable for calf starter, likely making it easier to detect the beneficial effects of social rearing on calf starter intake. In contrast, Phillips (2004) fed calves just 4 L of milk /d, likely leaving animals highly motivated to eat concentrate. In this context, intakes of concentrates were likely consistently high, such that treatment differences were more likely to be observed for forage intake.

The increased intake of solids may be due to social facilitation, social learning or some combination. Social facilitation can be defined as "the initiation of a particular response while observing others engaged in that behaviour" (Galef, 1988); in this way the stimulus of an animal eating or approaching the feed would increase the likelihood of the other calf in the same pen performing the same behaviours. Social learning can be defined as learning that is influenced by observation of, or interaction with, another individual (Keeling and Hurnik, 1996). In the previous literature on the development of feeding behaviour in farmed species some authors have implicated social facilitation (e.g. Ralphs et al., 1994) and other social learning (e.g. Launchbaugh and Howery, 2005), but in my view distinguishing between these mechanisms is not possible based on the current data and should be explored in future work. Also, if socially reared calves eat more solids simply because their attention is drawn to the feed by their social partner, other methods that draw attention to the feed may also be effective at increasing early intakes. For example, mechanically shaking or changing the feed might also increase attention and ultimately increase intakes. In piglets, it has been shown that a ‘play feeder’ (an open trough with 3 protrusions to stimulate exploration) can increase creep feed intake (Kuller et al., 2010). To my knowledge this approach has never been applied to dairy calves.

In conclusion, dairy calves benefit from early social housing in terms of increased solid intakes and increased gains. To achieve these benefits calves should be grouped within 3 weeks of life.

4 Complex Social Housing Reduces Food Neophobia in Dairy Calves [3]

4.1 Introduction

Dairy cattle are often exposed to new foods. For example, calves are weaned at around 2 mo. of age from milk to a grain-based calf starter, and later to forage-based diets (see review by Khan et al., 2011b). Food neophobia is well known in ruminants (Chapple and Lynch, 1986) and is defined as avoidance of, and reluctance to taste, unfamiliar foods (Cooke et al., 2006). Food neophobia is adaptive in that it helps animals avoid toxic foods and those too rich in undesirable nutrients (Provenza et al., 1995), but food neophobia can be problematic when animals refuse novel feeds provided as part of the farm's management requirements (Villalba et al., 2010). Ruminants offered novel diets often sample these cautiously, resulting in decreased food intake and productivity (Launchbaugh et al., 1997).

Surveys on dairy practices in Canada (Vasseur et al., 2010) and the U.S. (USDA, 2008) indicate that more than 90% of farms routinely separate calves from the dam within 24 h of birth and then typically house calves in individual pens or hutches. In more naturalistic settings, dam and the calf will typically remain in close contact until approximately 6 to 8 months, and co-mingle with other calves and cows (Reinhardt and Reinhardt, 1981).

Early socialization during the milk-feeding phase, generally the first 6 to 8 weeks of life for dairy calves, appears to reduce the problems associated with the transition to new social and feeding environments (De Paula Vieira et al., 2012b). Social contact with the dam and other calves has been shown to decrease responses to restraint and increase play (Duve et al, 2012). Also, calves that are pair housed early in life begin to ingest solid feed sooner and eat more solid feed during the milk

[3] Costa, J. H. C., R. R. Daros; M. A. G. von Keyserlingk, D. M. and Weary. 2014. Complex Social Housing Reduces Food Neophobia in Dairy Calves. J. Dairy Sci. 97:7804–7810.

feeding phase compared to calves housed individually (de Paula Vieira et al., 2010). Calves housed individually show less exploratory behaviour (Jensen et al., 1997; de Paula Vieira et al., 2012a), and are more reactive to environmental and social novelty when compared to socially housed calves (de Paula Vieira et al., 2012b). Collectively, these results suggest that providing access to more complex social environments may improve the calf's ability to cope with novel feeds. I therefore hypothesized that providing a complex social environment for calves would improve their willingness to consume new food items.

An important aspect of modern dairy cow management is the ability to change diets to meet the changing needs of the animal and to match availability of feedstuffs, making it important that the animal be able to transition to new types feed. Thus, the aim of this study was to investigate the effect of complex social housing on neophobic responses to new food items.

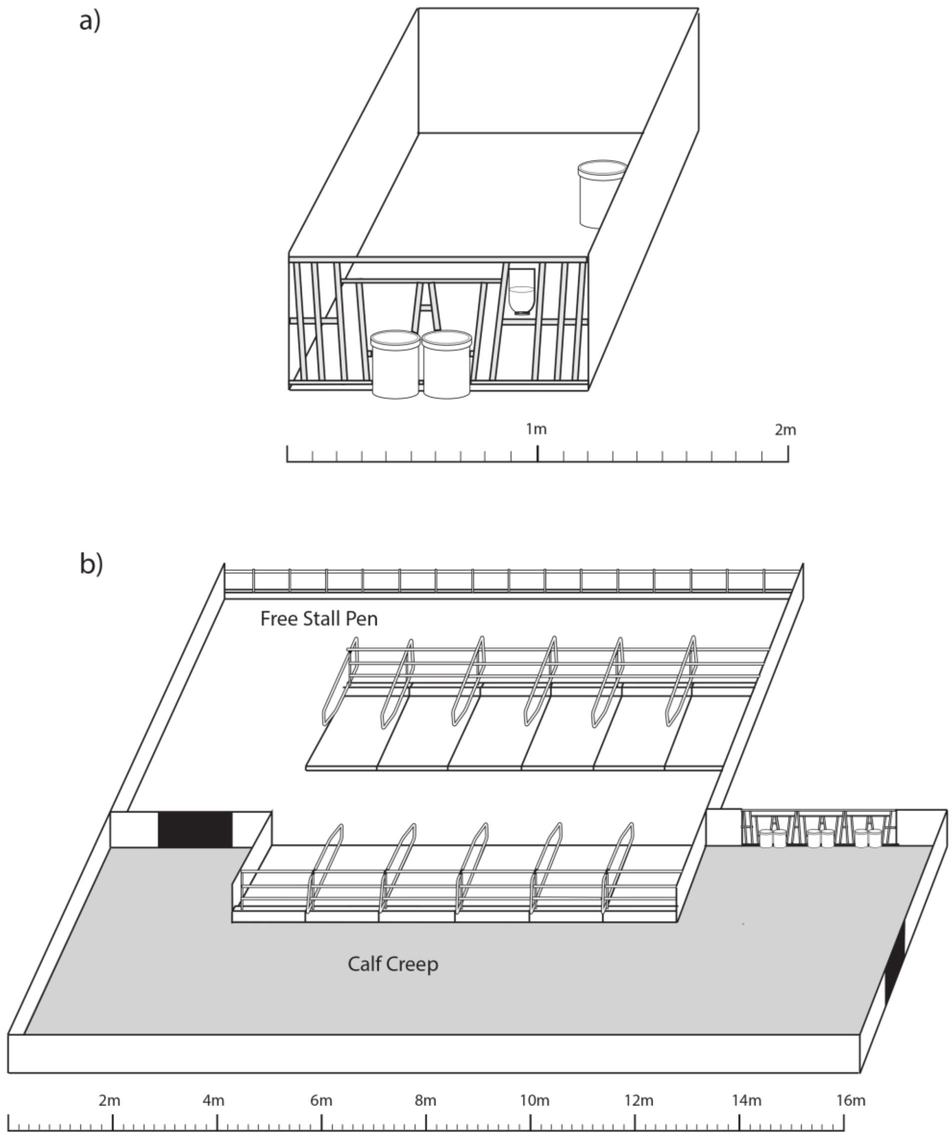
4.2 Materials and Methods

This experiment was carried out between October 2012 and May 2013 at The University of British Columbia's Dairy Education and Research Centre, in Agassiz, British Columbia, Canada (49°N, 121°W). All procedures were approved by the UBC Animal Care Committee according to the guidelines outlined by the Canadian Council of Animal Care (2009).

4.2.1 Animals and Housing

Thirty-six Holstein dairy bull calves were assigned to either individual (n=18) or complex social (n=18) housing. Individually raised calves were separated from their dams immediately after birth and moved to sawdust-bedded pens (1.2 m × 2.0 m) with auditory but no visual contact with other calves (Fig. 3a). Socially housed calves were kept with their dam in the calving pen for 3 d after parturition. Immediately after parturition cows were fitted with udder nets (Large Mesh Udder Support, Franksville Specialty Company, Phillips, WI) to prevent calves accessing the teats. Cow and calf were moved to a dynamic group of cows and calves housed in a single pen containing 12 free-stalls (Fig. 3b). The dynamic group varied in size from 4 to 8 cow-calf pairs over the course of the study; calves were removed from the group at 75 d and calves entered the group at all times until the maximum of 8 calves. Calves were granted access to the cows' pen at night (19:00 to 07:00 h). During the day, calves were restricted to a sawdust-bedded calf creep located immediately adjacent to the cows' pen, and connected by two doors located at either end of the pen. A fence-line system allowed cows and calves to physically interact (e.g. nose touch) during the day. Pens and the calf creep were cleaned and new sawdust replaced once per week. Calves were weighed and received weekly health checks following the standard operating procedures of the farm and the herd veterinarian treated any calves identified as ill. Four calves from the social group and 3 calves from the individual group were treated for diarrhoea, and one calf from the social treatment was treated for respiratory disease during the experimental period.

Figure 3. Experimental pens for a) calves reared individually and for b) for calves reared in a complex social group with their dam and other calves and cows. Individual pens were 2.4 m^2 (1.2 m ×2.0 m) with sawdust bedding and auditory but no visual contact allowed with other calves. Socially housed calves were kept with a group of cows and calves housed in a single pen containing 12 free-stalls; calves were granted access to the free-stall pen at night (1900 to 0700 h) and during the day calves were restricted to a sawdust-bedded calf creep (3.5 m x 12.3 m) located immediately adjacent to the free-stall pen.



Calves in both treatments were fed 4 L of colostrum by bottle within 6 h of birth. From d 0 to d 28 of age, all calves received 8 L/d of whole pasteurized milk, divided in 2 feedings, delivered by bottle at 07:00 h and 16:30 h. From d 29 to d 49, calves were fed 6 L/d, also divided into 2 feedings as described above. From d 50 to d 54, milk was reduced by 20%/d such that calves were completely weaned at d 55. Calves remained in the same pen until d 75. All calves had ad libitum access to water, total mixed ration (TMR) (49% DM; consisting of 26% corn silage, 15% grass silage, 10% alfalfa hay and 49% concentrated mix) and calf starter (90% DM; CP 21%, NDF 19%, ADF 11%; Hi-Pro Medicated Calf Starter, Chilliwack, BC, Canada). Fresh feed and water were delivered daily at approximately 08:30 h and 17:00 h, feed refusals were removed and weighed just before fresh feed was delivered. Eight calves were continuously video observed from 0800 h on the day before neophobia testing until 0800 on the test day, the time spent eating TMR and calf starter were recorded using continuous video observation. Eating was defined as when the calf's muzzle was inside the feed bucket.

4.2.2 Procedures

Neophobia tests were chosen to assess the calves' behavioural responses towards a novel food. The test was repeated for 3 consecutive days to assess habituation to the new food. Testing started when calves were 70 d of age, 2 wk. after weaning and tests were performed starting at 1500 h.

The test arena, measuring 1.2 m x 2m with 1.2 m walls, was located adjacent to the pens where the calves were housed and was bedded with 5 cm of fresh sawdust. Calves received all their milk meals in the test arena from 4 d of age until weaning at 56 d, so calves were fully habituated to the enclosure at the time of testing. Calves were not able to see other calves while in the test arena.

Two white 20 L plastic buckets, identical to those used to provide water in the home pens, were placed in each corner of the wall opposite to the door of the arena. One bucket contained 2 kg of the novel food; the other bucket remained empty.

Firstly, a subset of test calves (20 of the 36) was tested with a more common feed presented to dairy calves, orchard grass hay (83% DM; CP 17%, NDF 49%, ADF 28%) as the novel feed (Trial 1; n=10 per treatment). A second (the remaining 16 test calves) were tested with a very exotic feed, which had bright colour and possibility its more aversive to calves, chopped carrots as the novel feed (Trial 2; carrots were manually chopped into approximately 3 g pieces on the morning of the test day; n=8 per treatment). The position of the bucket containing the novel food was varied at random between the two corners for each test. Calves were placed into the test arena for 30 min. At the end of the test, feed refusals were weighed and total intake (on an as-fed basis) was determined.

Behaviour was video recorded continuously during the neophobia tests (DCRSR100 HDD Handycam Camcorders; Sony Corp., Park Ridge, NJ) using video cameras positioned directly above the test pen. Video recordings were used to measure latency to approach the feed (muzzle less than 5 cm from the bucket), latency to approach the empty bucket (muzzle less than 5 cm from the bucket), latency to eat (collection or chewing of the feed), time spent eating (head in the bucket), and time spent manipulating the empty bucket (licking, sniffing or head in the bucket).

4.2.3 Statistical Analyses

All analyses were performed with SAS (version 9.3; SAS Inst. Inc., Cary, NC) using the calf as the experimental unit. Intake of the novel feed (g), latency to approach the feed and empty buckets, latency to eat, time spent eating (head in the bucket), and time spent with muzzle within 15 cm of the bucket (all measured in s) were considered as dependent variables. Descriptive statistics were performed using the UNIVARIATE procedure and probability distribution plots in SAS. Where necessary, a square-root transformation was used to normalize error distributions; back-transformed results are presented for these data. Results throughout the text are present as least squares means and standard errors of the mean, F-value ($df_{effects}$, df_{error}), and P-value.

Firstly, I tested the influence of time spent eating the day and body weight (kg) before the neophobia tests were analyzed in a model which included the effects of Trial (1 versus 2) and birth weight. The effect of the housing treatment on each variable was analyzed with a linear mixed model, using the MIXED procedure in SAS. The model included the effects of Trial (1 versus 2), experimental day (specified as a repeated measure) and calf (specified as subject), and used an autoregressive covariance structure. Significance was declared at $P< 0.05$.

4.3 Results

Calves housed in the complex social environment consumed more of the novel food than did individually housed calves in both Trial 1 and 2 (Fig. 4a; $F_{1,33}= 18.44$, $P < 0.01$). Calves tended to eat more during trial 1, hay, than during trial 2, chopped carrots ($F_{1,33}= 3.53$, $P = 0.07$), but there was no interaction between treatment and Trial ($F_{1,33}= 2.15$, $P > 0.1$). The amount of novel feed consumed did not change across the 3 test days (Table 3; $F_{2,69}= 0.22$, $P > 0.1$) and there was no day x treatment interaction ($F_{2,69}= 0.71$, $P > 0.1$).

Social rearing decreased the latency to eat novel feed in both trials (Fig. 4b; $F_{1,35}= 12.86$, $P < 0.01$). Calves presented shorter latency to eat novel feed during trial 1, hay, than during trial 2, chopped carrots ($F_{1,35}= 6.90$, $P = 0.01$), but there was no interaction between treatment and Trial ($F_{1,35}= 0.01$, $P > 0.1$). There was no change in latency to eat the novel feeds across testing periods ($F_{2,57}= 0.27$, $P>0.1$) and no interaction between test day and treatment (Table 3; $F_{2,57}= 0.29$, $P > 0.1$).

There was no effect of treatment on the time calves spent eating the novel feeds; calves spent on average ± SD, 4:06 ± 4:03 min:s eating hay and 2:59 ± 4:09 min:s eating carrots. Also, there was no effect of treatment on latency to approach the food bucket or the empty bucket and no effect of treatment on time spent manipulating the empty bucket (Table 4). Body weight at the time of testing averaged ± SD 93.0 ± 11.83 kg and did not differ between treatments ($F_{1, 36}$= 2.54, $P > 0.1$). The time calves spent eating solid feed in the home pen on the day before the neophobia tests averaged ± SD 3:19:35 ± 1:08:42 (h:mm:s) and again did not differ between treatments ($F_{1, 14}$=0.83, $P > 0.1$).

Figure 4. Least squares mean (±SE) a) intake of novel feed (g/test; as fed) and b) latency to eat novel feed (mm:s/test). Calves were assigned to housing either in a complex social group with the dam and other cows and calves or individual rearing. In Trial 1 (n=10 per housing treatment) calves were tested with exposure to a novel hay and in Trial 2 (n=8 per treatment) calves were tested with chopped carrots. Tests were 30 min/d for 3d. Analyses were based upon square-root transformed data; back-transformed data are presented.

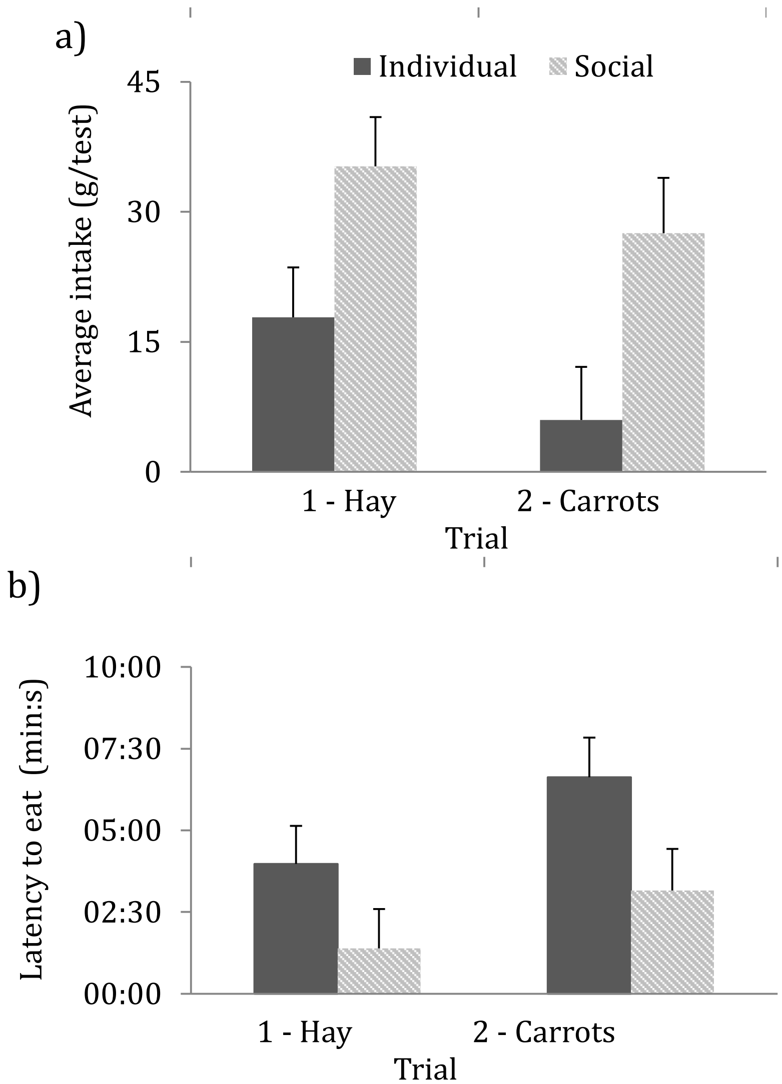


Table 3. Least squares mean (± SE) intake of novel feed (g/test) and latency to eat (min:s) during 3 consecutive days of testing. Calves were assigned to housing either in a complex social group with the dam and other cows and calves or individual rearing. In Trial 1 (n=10 per housing treatment) calves were tested with exposure to a novel hay and in Trial 2 (n=8 per treatment) calves were tested with chopped carrots. Tests were 30 min/d for 3d. Analyses were based upon square-root transformed data; back-transformed data are presented.

		Trial 1 - Hay		**Trial 2 - Carrots**	
Variables		**Individual**	**Social**	**Individual**	**Social**
Intake (g / test)	Days				
	1	17 ± 8.1	34 ± 8.1	6 ± 9.1	27 ± 8.6
	2	14 ± 8.1	47 ± 8.1	8 ± 9.1	26 ± 8.6
	3	22.5 ± 8.1	24 ± 8.6	5 ± 9.1	29 ± 9.1
Latency to eat (min:s)					
	1	2:47 ± 0:07	1:24 ± 0:06	7:02 ± 0:08	2:40 ± 0:07
	2	4:48 ± 0:07	1:16 ± 0:06	6:37 ± 0:07	2:51 ± 0:06
	3	4:20 ± 0:07	1:31 ± 0:07	6:26 ± 0:07	3:50 ± 0:06

Table 4. Least squares mean (±SE) latency (mm:s/test) to approach the feed, latency (mm:s/test) to approach the empty bucket, time (mm:s/test) spent eating and time (mm:s/test) spent manipulating empty bucket. Responses were measured for 30 min on 1 d only. Calves were assigned to housing either in a complex social group with the dam and other cows and calves or individual rearing. In Trial 1 (n=10 per housing treatment) calves were tested with exposure to a novel hay and in Trial 2 (n=8 per treatment) calves were tested with chopped carrots. Analyses were based upon square-root transformed data; back-transformed data are presented. P-values are shown for treatment (Treat), trial (Trial) and the interaction between treatment and trial (Treat*Trial).

	Trial 1 - Hay		**Trial 2 - Carrots**		**P-values**		
Time (min:s)	**Individual**	**Social**	**Individual**	**Social**	**Treat**	**Trial**	**Treat*Trial**
To approach the feed	1:39 ± 0:02	0:47 ± 0:02	1:40 ± 0:02	1:53 ± 0:02	0.35	0.15	0.17
To approach empty bucket	2:55 ± 0:41	3:02 ± 0:39	2:05 ± 0:42	2:52 ± 0:40	0.50	0.47	0.62
Eating	2:10 ± 0:08	4:48 ± 0:08	1:10 ± 0:08	2:10 ± 0:07	0.14	0.13	0.65
Manipulating empty bucket	2:45 ± 1:11	2:41 ± 1:11	5:58 ± 1:10	5:54 ± 1:07	0.95	0.01	0.99

4.4 Discussion

These results show that rearing in a complex social environment reduces food neophobia in dairy calves. Calves kept in a more complex social environment approached novel feed items more rapidly, spent more time in close contact with these items, and consumed a greater quantity of the feed compared to calves kept in the more conventional individual calf pens. These findings held true for two different types of novel feed tested in the current study. To my knowledge, this study is the first to demonstrate that early social experience reduces food neophobia in calves or indeed in any species. My results are consistent with earlier research in piglets showing that environmental enrichment before weaning (i.e. increased space allowance and provision of straw, wood shavings, peat and branches) increased the acceptance of piglets of a new diet and increased exploratory behaviour after weaning (Oostindjer et al., 2011a; b).

Previous work has shown that calves tested at 90 d of age were more reactive to environmental and social novelty if they had been housed individually for the first 3 mo. of life in comparison with calves that had been pair-housed over the same period (Jensen et al., 1997). A recent study has also shown that individual housing can impair cognitive performance and behavioural flexibility in dairy calves (Gaillard et al., 2014), and these differences may be due in part to the differences in reactivity.

De Paula Vieira et al. (2010) found that pair-housed calves consumed more solid feed before weaning when compared to calves that had previously been individually housed. This beneficial effect of a social rearing on intake of solid feed in the home pen may be have been due to social facilitation (i.e. the presence of other animals facilitating the expression of a behavioural response; Weiss and Miller, 1971). However, in the current study I tested calves individually in a test pen, so calves had no opportunity to observe and imitate the behaviour of other calves exposed to the novel feed. I conclude that the treatment differences in the current study were not due to social facilitation.

Calves that eat more solid feed in the home pen may gain more body weight, both because these animals will be larger and more familiar with solids I may expect these animals to also consume more of the novel feed in the test session. I was unable to quantify individual intake of (familiar) solid feed in the home pen for the complex socially housed calves, so thus I could not compare intakes of calves in the two treatments. However, treatments did not differ in BW or in the time calves spent eating solid feed on the day before the test. These results suggest that the treatment differences in response to the novel feeds cannot be explained simply on the basis of motivation to consume, or familiarity with, solid feed.

An alternative explanation is that the socially reared calves were more motivated to express exploratory behaviour; exploratory behaviours provide animals information about their environment and are likely to be more valuable in complex and variable environments. Consistent with this, Jensen et al. (1997) found that calves reared without social partners during the first 3 mo. of life showed delayed exploratory behaviour in comparison to pair raised calves. Similarly, de Paula Vieira et al. (2012a) found higher levels of exploratory behaviour in calves reared socially compared to individually reared calves. However, in the current study calves in the two treatments did not differ in latency to approach the feed or empty buckets, only time to eat the novel food and the amount eaten during the test. Thus the current results suggest that the treatment effects may be more specific to the avoidance of, and reluctance to taste, unfamiliar foods.

Over the 3 d of testing there were no differences in intake or in the latency to eat or approach the feed, suggesting that the neophobic response persists for at least this period. I had expected that the neophobic response would decline on d 2 and 3 d of testing; future work should test animals over a longer period to determine if and when intakes in the two treatments converge.

All the tests were performed while calves were kept individually in the test pen. The calves were habituated to this procedure and to the test pen as they had received all their milk meals in this way from d 3 of age. However, it is possible that the brief period of social isolation in the test pen would be more of a stressor for the socially reared calved versus calves that were housed individually at all times. If this was the case I would expected that calves housed in the complex social environment would be more fearful (and thus less willing to approach the novel food) when tested in isolation, but my results show the opposite pattern. I conclude that the short period of isolation in the test pen did not cause increased fearfulness in the socially reared calves.

Delayed acceptance of new food items may be a welfare and production concern. Dairy cattle are often exposed to new feed types, including when first transitioned from milk to solid feed at weaning. In addition to changes in diet, dairy cattle may be exposed to a range of management practices that introduce novelty to the environment, such as changes in pen location, regrouping with new social partners, and new milking procedures. Each of these changes may be more problematic for both the animal and the farmer if cattle are fearful of novel conditions. The current study found that complex social housing reduced responses to novelty when calves were still young; it is not known if this effect persists as the calf ages. Future experiments should investigate the longer-term effects of different dairy calf housing systems on behavioural flexibility and if the effects found in this study can be generalized to other challenging situations in the lives of calves.

4.5 Conclusions

A complex social housing environment, where calves had access to their dam and other cows and calves, increased intake and decreased latency to approach and eat two different types of novel feeds. Delayed acceptance of new food items may be a welfare and production concern. Dairy cattle are often exposed to new feed types, individual rearing may reduce the calf's ability to adapt to changes in feed and perhaps other changes in their environment.

5 Dairy Heifers Benefit From Having an Older Experienced Cow Present When Learning How to Graze[4]

5.1 Introduction

In the North American dairy industry, indoor housing systems with zero grazing have become increasingly prevalent (Fulwider et al., 2008), with less than 5% of lactating dairy cattle having access to pasture at some point during the year (USDA, 2008). If pasture is used by producers it is frequently incorporated during the spring and summer months for growing heifers since pasture use results in reduced costs associated with purchased feed and reduction in labour (Hanson et al., 2013).

Beef calves are often born outside and spend much of their early life grazing with their mother and other social partners (Enríquez et al., 2011); in contrast, on intensive dairy farms calves are typically separated from the dam soon after birth (USDA, 2008; Vasseur et al., 2010), reared indoors and provided no access with pasture until at the earliest after weaning, and sometimes much later depending upon season and management on that farm. Lopes et al. (2013) found that providing grazing experience during the growing phase increased grazing time and positively affected milk production when dairy cows introduced to pasture after calving. However, most dairy replacement animals do not have the opportunity to graze when they are young, and often first-season grazing dairy heifers are placed on pasture without any companions.

These first-time grazers are thus faced with several challenges, including learning how to eat a novel feed type (Hessle, 2009), habituating to a novel environment (de Paula Vieira et al., 2012b), and often coping with new conspecifics (de Paula Vieira et al., 2010) as heifers are frequently comingled when put out onto pasture. There are numerous challenges associated with regrouping, particularly in terms of feeding and social behaviour (Hasegawa et al., 1997; see also review by von Keyserlingk and Weary, 2010). Thus the combined effects of regrouping and the introduction to a novel environment may be disruptive to the young heifers when transitioning from indoor housing to pasture.

[4] Costa, J. H. C., W. G. Costa, D. M. Weary, L. C. P. Machado Filho, and M. A. G. von Keyserlingk. 2015. Dairy heifers benefit from having an older experienced cow present when learning how to graze. J. Dairy Sci.

To my knowledge there has been limited research conducted on the challenges that naïve dairy replacement heifers face during the introduction to pasture, and acute effects have not been investigated. One possible solution to the challenges faced by first-time grazers is to provide experienced animals that can act as social models. Thus, the aim of this study was to investigate whether the presence of cows with previous experience on pasture would affect the development of grazing behaviour of naïve dairy heifers when first introduced to pasture.

5.2 Materials and Methods

This experiment was conducted between April 25th and July 4th 2013 at The University of British Columbia's (UBC) Dairy Education and Research Centre, located in Agassiz, British Colombia, Canada (49°N, 121°W). All procedures were approved by the UBC Animal Ethics Committee, and all animals were cared for according to the guidelines outlined by the Canadian Council on Animal Care (2009).

5.2.1 Animals

A total of 63 pregnant Holstein heifers (mean age ± SD 14.2 ±1.3 mo.; weight = 546 ± 60.7 kg; body condition score (BCS) (3.2 ± 0.5, range from 2.5 to 4; scored from 1 to 5 following Edmonson et al., 1989) with no previous experience on pasture and 21 non-lactating Holstein cows (2.6 ± 0.8 lactations; 751 ± 53.9 kg; BCS 3.5 ± 0.5, range from 2.5 to 4) were randomly assigned to 7 groups of 12 animals, each group had 3 non-lactating cows and 9 naïve heifers.

Each group was formed 3 wks. before introduction to pasture. All cows had some experience on pasture as growing heifers and in the case of the multiparous cows during the previous summers if they were non-lactating. All experimental animals regardless of age were housed for at least 6 mo. before the beginning of the experiment in a free stall barn with no access to the outdoors or to pasture during this time.

5.2.2 Experimental Design

The experimental period lasted 28 d per group, and groups were tested consecutively. During the first 21 d each group was housed indoors in a pen configured with 12 free stalls. On d 22 groups were sub-divided into two groups of 6 animals each: 1 with 6 naïve heifers and 1 with 3 naïve heifers and 3 experienced cows. Each sub-group was placed on pasture for 72h, starting at 0900 h. Treatment order was randomized: one sub-group was placed on pasture first on d 22 and the other sub-group stayed in the home pen until d 25 when they were granted access on pasture.

5.2.3 Housing and Management

Three experimental pens in a naturally ventilated free stall barn (width = 38 m, length = 156 m) with a north-south orientation and curtained sidewalls were used for this experiment. Each pen (width = 9.5 m and length = 12.3 m) had 12 free stalls (1.2 m center-to-center) separated a by free stall divider loops with a diameter of 0.89 m (Y2K stall dividers, Artex, Langley, British Columbia, Canada). The bed of each stall was 2.6 m long, and had a brisket board that was 1.7 m from the internal side of the curb (0.2 m height), providing a lying area of approximately 2 m^2/cow. The neck rail was positioned 1.2 m above the stall surface, and 1.2 m from the rear curb of the stall. The stall was covered with a geotextile mattress and bedded with approximately 5 cm of river sand. Alleys were scraped 8 times per day with an automatic scraper and crossovers were scraped by hand once per day.

The distance between the pasture and the barn varied according to the paddock used; the closest was 7 m and the farthest was 65 m from the barn. The pasture and the barn were connected via a 4.0 m wide path covered with bark mulch. The path was cleaned and checked for obstacles daily. Pasture composition was determined using eight haphazard 1 m^2 samples cut before the beginning of the experiment and the material was sorted into the species that were previously planted, the portions were weighted and relations determined. The pasture was approximately 45:40:10:5 *Festulolium* (tall fescue (*Festuca arundinacea*) x rye grass (*Lolium perenne* L.) cross): Orchard grass (*Dactylis glomerata* L.): Rye grass (*Lolium perenne* L.): white clover (*Trifolium repens*). The pasture was divided into 16 paddocks of 1400 m^2 each managed using a rotational grazing system, where each group was introduced to a new paddock. A water trough located adjacent to the fence in each paddock was filled with fresh water automatically. No shade was provided on pasture.

Weather conditions (air temperature, relative humidity, rainfall, and wind speed) were recorded automatically throughout the study by an Environment Canada weather station in Agassiz, BC, located adjacent to the research farm. During the course of the experiment (April to July 2013), the average ± SD daily temperature recorded was 15.7°C ± 3.6°C, minimum temperature was 10.7 °C ± 3.3°C, and maximum daily temperature was 20.6°C± 5.0°C. Precipitation averaged 3.8 mm ±

8.5 mm, (range from 0 to 45.2 mm/d), relativity humidity was 73.2 ± 9.3 %, (range from 34 to 99 %) and wind speed was 9.6 m/s ± 9.4 m/s, (range from 0 to 24 m/s).

Pasture samples were taken 1 h before the introduction of each new group. Each sample consisted of 6 sub-samples collected from the diagonal transects, a 0.25 m^2 patch was identified and clipped at 8 cm height. These sub-samples were pooled to create 1 representative sample per group. To calculate pasture mass, the sample weight was multiplied by the total area of the plot. Samples were dried at 55°C for 48 h to determine DM content. Dried samples were pooled, ground and sent for nutritional analysis (A&L Laboratories Inc., London, ON). During the experiment, pasture mass (averaged ± SD) 1900.09 ± 203.1 g/m^2 of fresh matter, 22.1 ± 2.3 % DM and (expressed as % DM) 22.1 ± 2.6 % CP, 57.1 ± 2.6 % NDF and 34.3 ± 2.3 % ADF.

A TMR was formulated following the National Research Council (NRC) guidelines (NRC, 2001) to meet or exceed the requirements of a 550 kg Holstein not producing milk, consisting of 31.2 % rye grass straw, 25.7 % corn silage, 23.1% alfalfa hay, 12.5 % concentrated mix and 7.5% grass silage, with an overall % DM of 48.7. TMR was offered ad libitum in the experimental pen and delivered daily at approximately 0800h; feed was pushed-up to the feed bunk 3 times per day at 1030h, 1600h and 2230h. Water was available ad libitum from a self-filling water trough located in the feed alley of each pen.

Fresh TMR samples were taken on the second and last day of each replication immediately after the feed delivery. Samples were pooled to create 1 representative sample. Samples were dried at 60°C for 48 h to determine DM content and then ground and sent for nutritional analysis at A&L Laboratories Inc. (London, ON). The TMR contained on average 46.4 ± 2.4 % DM and (expressed as % DM) 13.3 ± 1.7 % CP, 49.1 ± 2.1 % NDF and 31.6 ± 1.9 % ADF.

5.2.4 Measurements

The animals were weighed and blood sampled. This procedure was carried out weekly during the 3 wks. before introduction to pasture and again 12h before and 72h after introduction to pasture. Blood was analyzed for glucose following Wittrock et al. (2013), using a hand-held electronic glucometer (Precision Xtra blood glucose kit; Abbott Diabetes Care, Alameda, CA) and BHBA (Precision Xtra blood ketone kit; Abbott Diabetes Care) concentrations following the procedures described by Iwersen et al. (2009) for blood ketone analysis. Animals were gait scored (as described by Flower and Weary 2006) on a scale of 1 to 5; subjects with a gait score ≥ 3 were not included in the experiment.

5.2.5 Behaviour

The focal animals' behaviours were observed via continuous recording (Martin & Bateson 2007) during the first hour immediately after animals were introduced to pasture, recording the number of stomps, agonistic interactions, vocalizations and defecations (Table 5). During the next 3 h (i.e. 4 h in total) continuous recording were used to record latency to first graze and nibble the grass, and time spent nibbling, grazing, ruminating, walking and alert. Within each sub-group, 3 heifers were identified as the focal animals and each animal was observed by a separate observer. Three observers collectively developed the data sheets and the descriptions of the behaviours and tested the definitions during a pilot trial. In a minute base inter-reliability test, average paired Kappa coefficient was 0.74.

Table 5. Behaviour of the naïve heifers observed immediately after introduction to pasture on this study.

Behaviour	Description
Nibbling	Animal comes into contact with the grass, sniffs and/or performs small, quick bites.
Grazing	Animal grabbing and ingesting forage, may be stationary or moving forward for a period of at least 5 consecutive minutes in which the animal consumed grass.
Ruminating	Chewing with lateral jaw movements with the head at the same level or above its body, lying or standing.
Walking	Animal moving, with the head above the grass.
Alert	Animal stationary, lying or walking with head up and ears positioned forward.
Stomp	Animal lifts and kicks one or both hind legs
Agonistic Interaction	Displacements and/or threats associated with a conflict between two individuals

5.2.6 Statistical Analyses

Number of stomps, agonistic interactions, vocalizations and defecations, latency to graze and nibble, glucose and BHBA blood concentration were considered as dependent variables and were compared between treatments. The group was considered the experimental unit; data from each individual (n=3) within a group were averaged. Prior to all analyses, data were checked for normality using the UNIVARIATE procedure in SAS (version 9.3; SAS Institute Inc., Cary, NC) and probability distribution plots. Since data were not normally distributed, treatments were compared using the non-parametric exact Mann-Whitney test. Results throughout the text are present as median and Q1-Q3 of the median, significance was declared at $P < 0.05$.

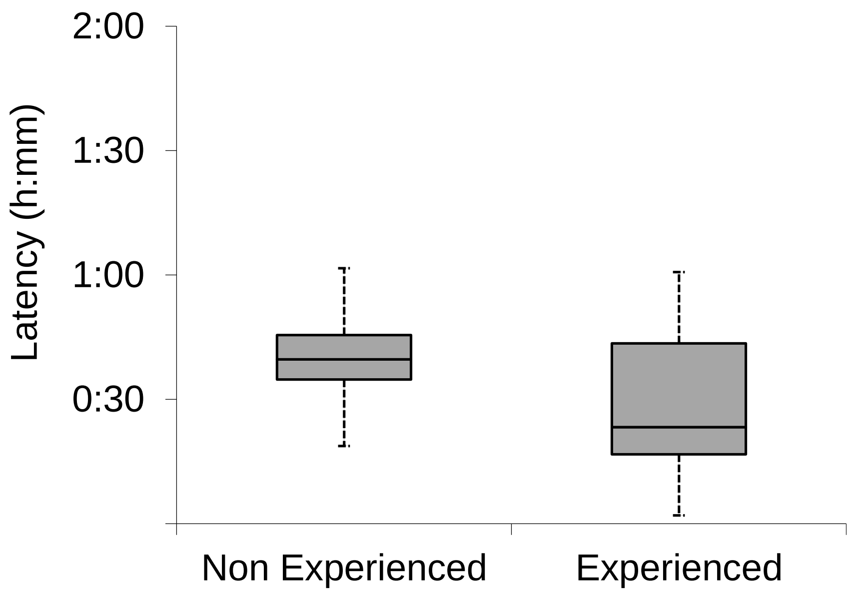
5.3 Results

Less than 30 min after heifers from both treatments were introduced to pasture they began to nibble the grass (Fig. 5a; W(10)= 21.0, Z= -1.25, $P = 0.24$). Soon after, heifers grouped with pasture-experienced cows began to graze, but the heifers within the naïve group took an additional hour before they began grazing (Fig. 5b; W(10)= 15.0, Z= -2.50, $P = 0.01$).

During the first hour after heifers were introduced to pasture, animals in the Experienced treatment showed fewer stomping events (W(11)= 58.5, Z= 2.28, $P = 0.02$) and vocalizations (W(11)= 57.0, Z= 2.07, $P = 0.03$). Number of agonistic interactions did not differ between treatments (Fig. 6; W(11)= 45.0, Z= 0.36, $P = 0.72$). Heifers in both treatments rarely defecated during the first hour on pasture (Experienced: 0.33 (0-1) (Median (Q1-Q3); Non-Experienced 0 (0-0.33); $P = 0.21$).

Figure 5. Latency (h) to a) nibble and b) graze, shown separately for naïve heifers with or without the presence of grazing experienced cows (n=7 per treatment). The lower and upper ends of the boxes indicate the 25th and 75th quartiles, respectively. The quartiles ± 1.5 the inter-quartile range are indicated by the whiskers. The line across the middle of the box identifies the median.

a)



b)

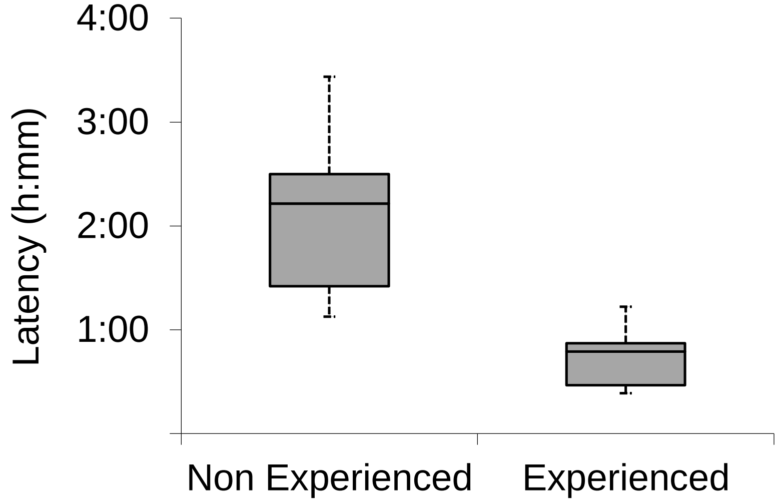
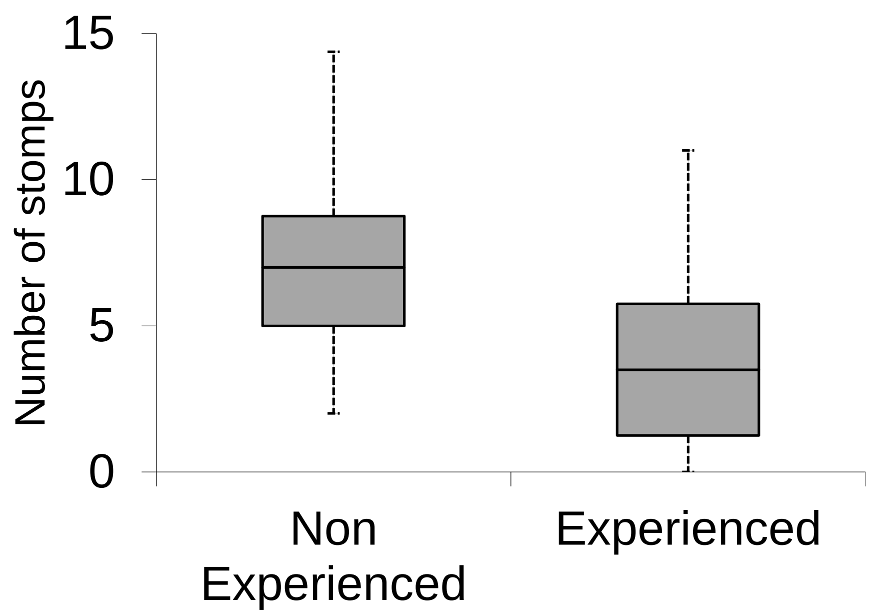
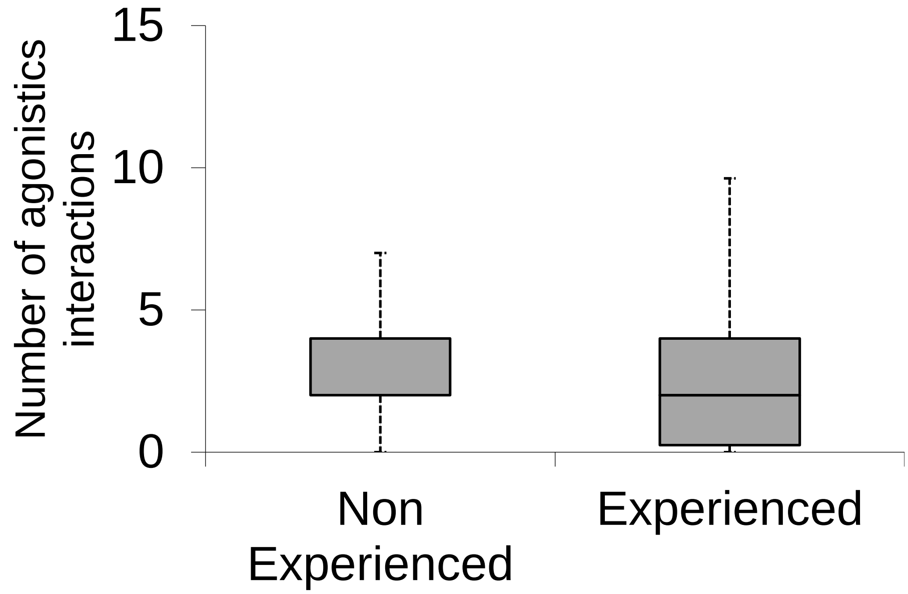

4:00
3:00
2:00
1:00
Latency (h:mm)
Non Experienced
Experienced

Figure 6. The number of a) stomps, b) agonistics interactions and, c) vocalization for naïve heifers with or without the presence of grazing experienced cows observed during the first hour immediately after introduction to pasture (n=7 per treatment). The lower and upper ends of the boxes indicate the 25th and 75th quartiles, respectively. The quartiles ± 1.5 the inter-quartile range are indicated by the whiskers. The line across the middle of the box identifies the median.

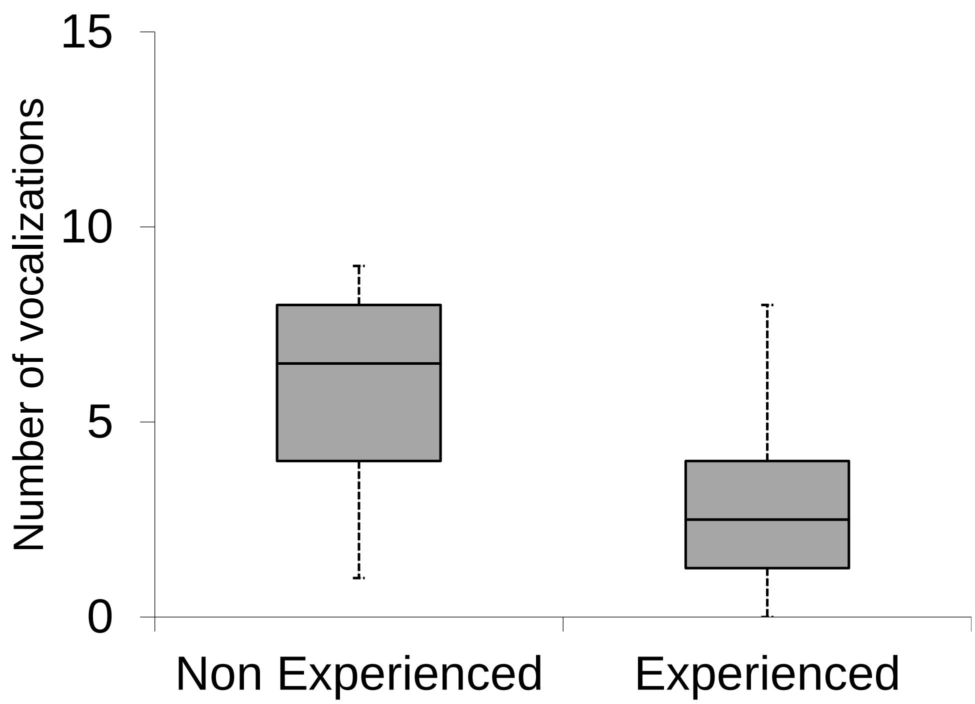
a)



b)


15
10
5
0
Number of agonistics interactions
Non Experienced
Experienced

c)


15
10
5
0
Number of vocalizations
Non Experienced
Experienced

Despite differences in latency to start to graze, total time spent grazing did not differ during the first 4 h on pasture (Experienced: 40:58 (29:34 – 44:28) (min:s); Non-Experienced 27:01 (20:26 – 38:29) ; W(12)= 64.0, Z= 1.40, $P = 0.16$). Time spent nibbling tended to be higher for Non-experienced than Experienced animals during the first 4 h on pasture (Experienced: 07:37 (03:10 – 13:07) (min:s); Non-Experienced 19:06 (11:13 – 49:07); W(12)= 37.0, Z= -1.92, $P = 0.06$). All other behaviours observed (ruminating, walking, and alert) were similar in the two treatments (Table 6). Body weight and blood parameters (glucose and BHBA) also did not vary with treatment (P <0.10; Table 7).

Table 6. Median (Q1 – Q3) time spent ruminating, walking and alert (min:s) for naïve heifers with or without the presence of grazing experienced cows (n=7 per treatment) observed during the first 4 h after animals were introduced to pasture.

Time (min:s)	Non-Experienced	Experienced	*P-values*
Rumination	00:15 (0:07 – 0:27)	00:08 (00:03 – 00:19)	0.25
Walking	47:20 (29:19 –59:24)	39:47 (21:04 – 57:14)	0.84
Alert	37:25 (28:20 –55:30)	46:27 (11:10 – 58:24)	0.60

Table 7. Median (Q1 – Q3) of the difference before and 3d after the animals were introduced to pasture on this study of body weight, glucose (Wittrock et al., 2013) and BHBA (Iwersen et al., 2009)) for naïve heifers with or without the presence of grazing experienced cows (n=7 per treatment). P-values are for the test of treatment.

Variables	Non-Experienced	Experienced	*P-value*
Body weight (kg)	- 16.66 (-23.33 – -6.67)	- 25 (-33 – -6.67)	0.77
Glucose (mmol/L)	6.16 (-0.33 – 13)	6.16 (-0.67 – 13)	0.14
BHBA (mmol/L)	-0.07 (-0.07 – -0.33)	0 (-0.10 – 0.16)	0.75

5.4 Discussion

Heifers kept in a group with experienced cows began grazing more rapidly than did naïve heifers kept with only naïve conspecifics. These results are consistent with the findings of Hessle (2009) who found that the presence of experienced animals increased grazing activity when providing calves first contact with semi-natural grassland.

Previous work has found that naïve calves are more efficient at finding preferred food locations when provided with experienced steers as social models (Ksiksi and Laca, 2000). Another study found that grazing activity increased on the first day when 10-mo old dairy steers were turned out on semi-natural grasslands with experienced cattle. However, this study did not show increased grazing times, grazing efficiency or live weight gains after a month on pasture compared to control calves (Hessle, 2009). Heifers that were raised on pasture with just one species of grass but grouped with animals that were habituated to tropical pastures that included the presence of shrubs and trees, showed a higher use of shrubs and trees, and consumed a higher diversity of plants in comparison to animals introduced without a social model (Velázquez-Martínez et al., 2010). In contrast, another study (Bailey et al., 2000) failed to find any improvements in foraging ability of yearling heifers grouped with experienced conspecifics.

Interestingly, I observed no treatment difference in the latency to start nibbling grass; all animals had experience eating feed from the ground in the freestall pens, so accessing feed from the ground in the new pasture environment would not be novel, but the ability to collect and ingest grass was a novel behaviour for the animals. I speculate that the more rapid learning of heifers with experienced animals is associated with social learning. Social learning is defined as learning that is influenced by observation of, or interaction with another individual, and has been described as an influential factor affecting the feeding behaviour of many farmed species (Keeling and Hurnik, 1996; Launchbaugh and Howery, 2005). The major benefit of social learning is that the naïve animals experience increased efficiency and reduced risks associated with testing and exploring novel environments (reviewed by Bandura, 1977).

Naïve animals provided with social models are generally more efficient in ingesting forage in a new environment, suffer less from predation and ingest fewer toxic plants compared to those not provided with a social model (Provenza and Cincotta, 1993; Launchbaugh and Howery, 2005). In the current study I did not record the behaviour of the experienced animals. I encourage future work to investigate the influence of the behaviours performed by the social model on the naïve animals. Providing access to the dam has been shown to be important in the development of neonatal grazing behaviour, but other dominant individuals in the group may also be influential (Thorhallsdottir et al., 1990; Howery et al., 1998). In the current study age and experience were confounded; future work should investigate if the age of the experienced social models affects the first experiences observed of the naïve heifers when provided access to pasture for the first time.

The benefits of providing a social model appear to be concentrated in the first hours following introduction to pasture. Despite the differences in latency to first graze, all heifers began grazing within their first 4 hours on pasture. Over the study, heifers housed together with experienced cows had no differences in weight gains, BHBA or blood glucose compared to heifers not provided a social model. These results are consistent with earlier work. For example, Hessle (2009) found that the company of experienced animals did not increase live weight gain of 10 mo. old calves after a month on pasture. Similarly, when heifers were transferred from a grass monoculture pasture to a diverse plant species environment, with or without the presence of experienced animals, weight gain was positive for both treatments (Velázquez-Martínez et al. 2010). More recent work by Lopes et al. (2013) found that previous grazing experience as a heifer affected behaviour and milk production of cows during the first days on pasture but not when averaged over a 2 mo. period.

One previous study found that mixing younger cattle with older animals on pasture increase the number of aggressive social interactions which in turn may reduce time spent grazing (Philips and Rind, 2001). In the current study I found no effect; heifers put out on pasture for the first time with or without the presence of older experienced animals engaged the same number of agonistic interactions. These results may be explained by the use of groups that had been stable with no new animals introduced for over 4 weeks before testing. Regrouping is known to cause increased competitive behaviour in cattle, and heifers are frequently subjected to aggressive behaviours following grouping with older cows (Neisen et al., 2009).

5.5 Conclusion

Providing heifers with pasture-experienced social companions when first introduced to pasture promotes a more rapid onset of grazing. The presence of habituated older experienced companions may improve the ability of heifers’ to adapt to pasture.

6 Understanding Sorting Behaviour in Weaned Dairy Calves. [5]

6.1 Introduction

Domestic ruminants balance their intake of high-energy grain components with forage that helps buffer the rumen against the acidic byproducts of carbohydrate fermentation (Krause and Oetzel, 2006). Unlike grazing cattle that spend between 7 and 13 h per day grazing, adult dairy cows in intensive production systems typically spend only 3 to 5 h per day feeding (Dado and Allen, 1994; Hosseinkhani et al., 2008). In indoor systems, both dairy and beef cattle are generally fed a TMR once or twice daily (Krause and Oetzel, 2006). The TMR generally contains forage and grain components that vary in physical (i.e. particle size) and nutritional attributes (Coppock et al., 1981). Cattle often selectively consume small, energy-dense grain particles (Leonardi and Armentano, 2003; Miller-Cushon and Devries, 2009) when offered a TMR. Feed sorting in cattle can result in unbalanced nutrient intake and increases the risk of digestive disorders including ruminal acidosis (DeVries et al., 2008). Many studies have reported feed sorting in adult dairy cattle (Leonardi and Armentano, 2003) but there is now a small and growing literature on feed sorting in young cattle.

Feeding behaviour in developing calves is influenced by the transition from milk to solid feeding, as calves become acquainted with solid feeds and their post-ingestive consequences (Provenza and Balph, 1987). Recent research suggests that feeding patterns developed early in life are likely to be retained into adulthood (Greter et al., 2010). Early feed exposure also has been shown to affect adult feed preferences in ruminants (Arnold and Maller, 1977; Squibb et al., 1990; Nolte et al, 1990). Young animals are believed to develop feeding habits through social interactions and mimicry of their peers and dam (Mirza and Provenza, 1994; Galef and Laland, 2005).

Recently, Miller-Cushon and DeVries (2011) found that calves fed either concentrate or hay during weaning selectively consumed the familiar feed when switched to a mixed ration. Calves fed separate components (forage and concentrate) before weaning, compared to those fed a mixed ration, showed reduced feed sorting after weaning (Miller-Cushon et al., 2013). How calves were transitioned between feeds also affected sorting. For example, a gradual dietary transition over 7 d

[5] A version of Chapter 6 has submitted for publication: Costa, J. H. C., N. A. Adderley, D. M. Weary and M. A. G. von Keyserlingk. Understanding sorting behaviour in weaned dairy calves.

resulted in more sorting compared with calves transitioned abruptly to a novel feed (Miller-Cushon et al., 2015).

The objectives of this observational study were to: (a) describe sorting in dairy calves, and (b) determine if sorting changes when supplementary concentrate was no longer available. Removing access to supplementary concentrate likely increases the value of the grain acquired through sorting the TMR. Thus we predicted that calves would sort for grain within the TMR when supplementary concentrate was not available.

6.2 Materials and Methods

This experiment was conducted between October 2012 and May 2013 at the University of British Columbia's (UBC) Dairy Education and Research Centre in Agassiz, British Columbia, Canada (49°N, 121°W). UBC's Animal Care Committee (Animal Use Protocol # A12-0337) approved the procedures used in this study. All the animals were cared for according to the guidelines outlined by the Canadian Council of Animal Care (2009).

6.2.1 Animals and Housing

Eighteen Holstein dairy bull calves were enrolled in the study. Calves were separated from their dam immediately after birth, weighed (44.0 ± 6.1 kg BW [mean ± SD]), and housed in sawdust-bedded pens (1.2 mx 2.0m) with no visual, but auditory contact with other calves. Within 6 h of birth, calves were fed by bottle at least 4 L of colostrum with >50 g/L of IgG. Serum from blood samples collected from the jugular vein 24 h after the first feeding of colostrum were analyzed using a Reichert AR 200 Digital Handheld Refractometer (Reichert, Depew, USA). All calves had serum protein >5.5 g/DL. Pens were cleaned and new sawdust replaced once per week.

6.2.2 Milk Delivery, Solid Feeding and Weaning

Calves were bottle-fed 8L/d of pasteurized whole milk divided in 2 feedings, at approximately 0800h and 1630h from birth until 28 d of age. From d 29 to 49, calves were fed 6 L/d, using the same procedure as described above. Milk volume was reduced by 20 %/d from d 50 to d 55, with milk weaning occurring on d 55. Calves remained in the experiment until d 71. Starting at 3 d of age all calves had ad libitum access to water, TMR (described in Table 8) and calf starter (Hi-

Pro Medicated Calf Starter, Chilliwack, BC, Canada; Table 8). TMR and calf starter were fed for a target orts of 1 kg; feeding was increased by 0.5 kg when orts dropped below this threshold. Over the study TMR orts averaged ± S.D. 1.3 ± 0.7 kg and calf starter orts 1.6 ± 0.9 kg. Feeding level (% orts) was compared between test days to ensure that it was not a confounding factor, as sorting can be affect by the % of orts (see Miller-Cushon and DeVries, 2010). Feed refusals were removed daily before fresh feed and water delivery at approximately 0830h. Daily calf starter and TMR intakes were determined each morning by disappearance.

6.2.3 Feed Sampling and Analysis

Representative samples of both the offered feed (taken immediately before feeding) and orts (after 24 h of feed access) were taken. Sorting was assessed after weaning when calves were 65 d old and had access to both TMR and calf starter, and again at 70 d of age the first day after which concentrate was no longer available. On both days sorting was measured over a 24 h period. A Penn State Particle Separator (PSPS) with 3 screens (19, 8, and 1.18mm) and a bottom pan was used to separate samples for particle size analysis into long (>19mm), medium (<19, >8mm), short (<8, >1.18mm) and fine (<1.18mm) fractions (Kononoff et al., 2003) (see Table 8 for distribution of particle sizes in the TMR).

Samples for nutrient and DM analysis were oven dried at 55°C for 48 h. Dried samples were ground to pass though a 1-mm screen and sent to A&L Canada Laboratories Inc. (London, ON) for analysis of DM (135°C; AOAC International, 2000L method 930.15), ADF (AOAC International, 2000: method 973.18), NDF with heat-stable α-amylase and sodium sulphite (Van Soest et al., 1991), and CP (N x 6.25; AOAC International 2000: method 990.03; Leco FP-528 Nitrogen Analyzer, Leco, St. Joseph, MI).

Table 8. Chemical [dry matter (DM), crude protein (CP), acid detergent fibre (ADF) and neutral detergent fibre (NDF)] and particle size composition of concentrate and total mixed ration (TMR) [mean % ± SD; DM basis].

Item	Concentrate[1]	TMR[2]
Chemical composition[3]		
DM %	89.5 ± 0.7	49.1 ± 1.5
CP, % of DM	20.6 ± 1.13	16.9 ± 0.95
ADF, % of DM	7.84 ± 0.45	20.4 ± 1.77
NDF, % of DM	16.5 ± 0.39	31.8 ± 2.68
Particles[4]		
Long particles	—	12.8 ± 3.6
Medium particles	—	35.7 ± 2.57
Short particles	—	37.6 ± 3.6
Fine particles	—	13.9 ± 1.58

[1] Hi-Pro Medicated Calf Starter (Chilliwack, BC, Canada); medicated with a coccidiostat [50 mg/kg of Lasalocid Sodium]).

[2] TMR containing 26.1% corn silage, 14.8% grass silage, 10% alfalfa hay, and 49% concentrated mix on DM basis.

[3] Values obtained from chemical analysis of feed samples (A&L Laboratories).

[4] Particle separated, using a Penn State Particle Separator, into 4 fractions: long (>19mm), medium, (<19, >8mm), short (<8, >1.18mm), and fine (<1.18mm).

6.2.4 Data Analysis

Sorting behaviour was quantified as the actual intake of each fraction (long, medium, short and pan), expressed as a percentage of the predicted intake of each fraction (Leonardi and Armentano, 2003), the predicted intake of each fraction was calculated as the product of the DMI of the feed offered multiplied by the DM percentage of that fraction in the fed TMR. Values >100% indicated sorting for that particle size and values <100% indicated sorting against that particle size.

Prior to analysis, data were checked for normality using the UNIVARIATE procedure in SAS and probability distribution plots. All analyses were performed with SAS (version 9.3; SAS Inst. Inc., Cary, NC) using the calf as the experimental unit. The predicted intake of each particle size fraction, expressed as a percentage, and the relative percentage of NDF, ADF and CP in the orts, were tested in both studies for a difference from 100 using t-tests.

6.3 Results

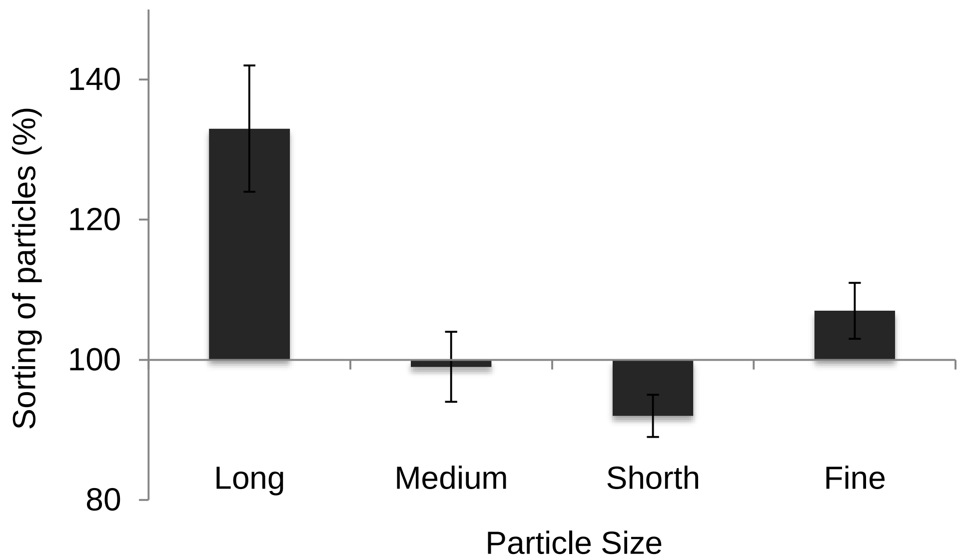
At 65 d of age calves preferentially sorted the TMR for long particles, consuming more of these particles than expected by chance (134 ± 9 %; $T_{1,11}$ = 3.65; P = 0.004; Fig. 7a). Conversely, calves only consumed 92 ± 3 % ($T_{1,11}$ = -2.62; P = 0.02) of the predicted intake of small particles. Intake of medium and fine particles did not differ from that predicted, with calves consuming 99 ± 5 % ($T_{1,11}$ = -0.13; P = 0.90) and 107 ± 5 ($T_{1,11}$ = 1.57; P = 0.14) of predicted intake, respectively. At this age calves consumed the diet in such a way that there was no change in the CP content of the TMR (106 ± 4 %; $T_{1,11}$ = 1.25; P = 0.24) after 24 h (Fig. 8). Likewise, ADF and NDF were consumed in expected proportions (100 ± 6 %; $T_{1,11}$ = -0.03; P = 0.9792 and 99 ± 4.90 %; $T_{1,11}$ = -0.24; P = 0.8110, respectively).

Calves 65 d of age showed no evidence of sorting the calf starter offered ad libitum; we also found no difference in CP (97 ± 7 %; $T_{1,11}$ = -1.35; P = 0.20), or ADF and NDF (98 ± 7 %; $T_{1,11}$ = -1.06; P = 0.31 and 101 ± 5 %; $T_{1,11}$ = 0.80; P = 0.44, respectively), between the offered calf starter and the orts.

At d 70 when free access calf starter was no longer available, intake of fine particles exceeded the predicted value (113 ± 4 %; $T_{1,10}$ = 3.15; P = 0.01; Fig. 7b). Consumption of large particles was as expected, with calves consuming an average of 101 ± 11 % ($T_{1,10}$ = 0.07; P = 0.95) of predicted intake. Likewise, calves did not sort for or against medium and small particles, consuming 99 ± 6 % ($T_{1,10}$ = 0.25; P = 0.80) and 97 ± 4 % ($T_{1,10}$ = -0.68 ; P = 0.51) of predicted intake of medium and small particles, respectively. At d 70 sorting was also apparent in the assessment of the dietary components of the TMR (Fig. 8). Sorting decreased the CP content of the TMR (93 ± 2 %; T1,17 = -2.94; P = 0.01) and increased the NDF content (to 113 ± 5 %; T1,17 = 2.51; P = 0.02). Calves offered only TMR also consumed less ADF (112 ± 7 %; T1,17 = 1.77; P = 0.094).

Figure 7. Mean ± SE intake of the particle fractions of a total mixed ration (TMR) (expressed as a % of predicted intake) when calves were offered a), TMR and a separate grain source at 65 d, and b) TMR only at 70 d. Results are from individually housed calves (n = 18). Analyses were based upon the predicted intake of each particle fraction measured as disappearance after 24 h feeding. Particles were separated into 4 fractions: long (>19mm), medium, (<19, >8mm), short (<8, >1.18mm), and fine (<1.18mm).

a)



b)

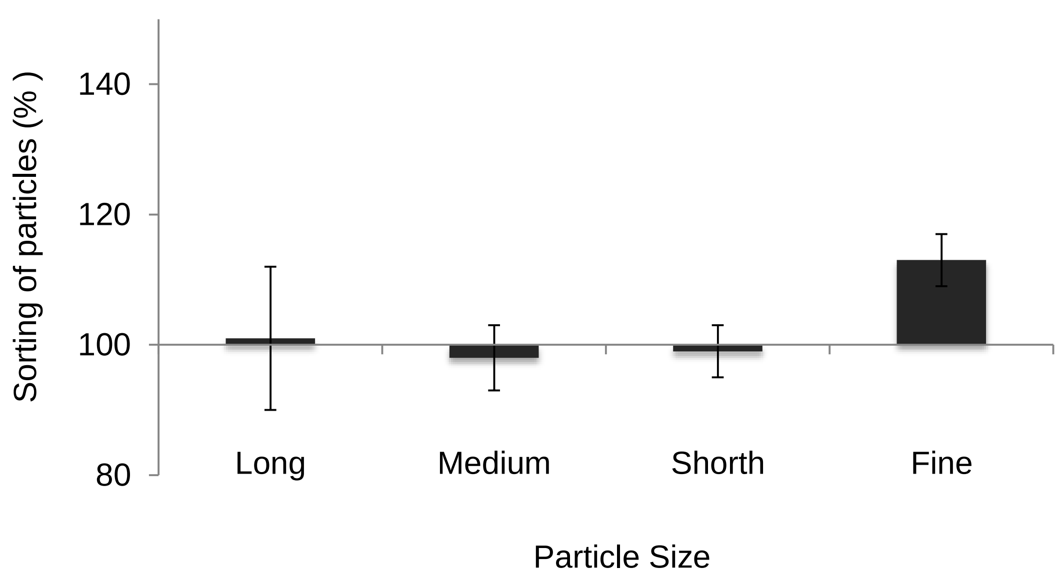
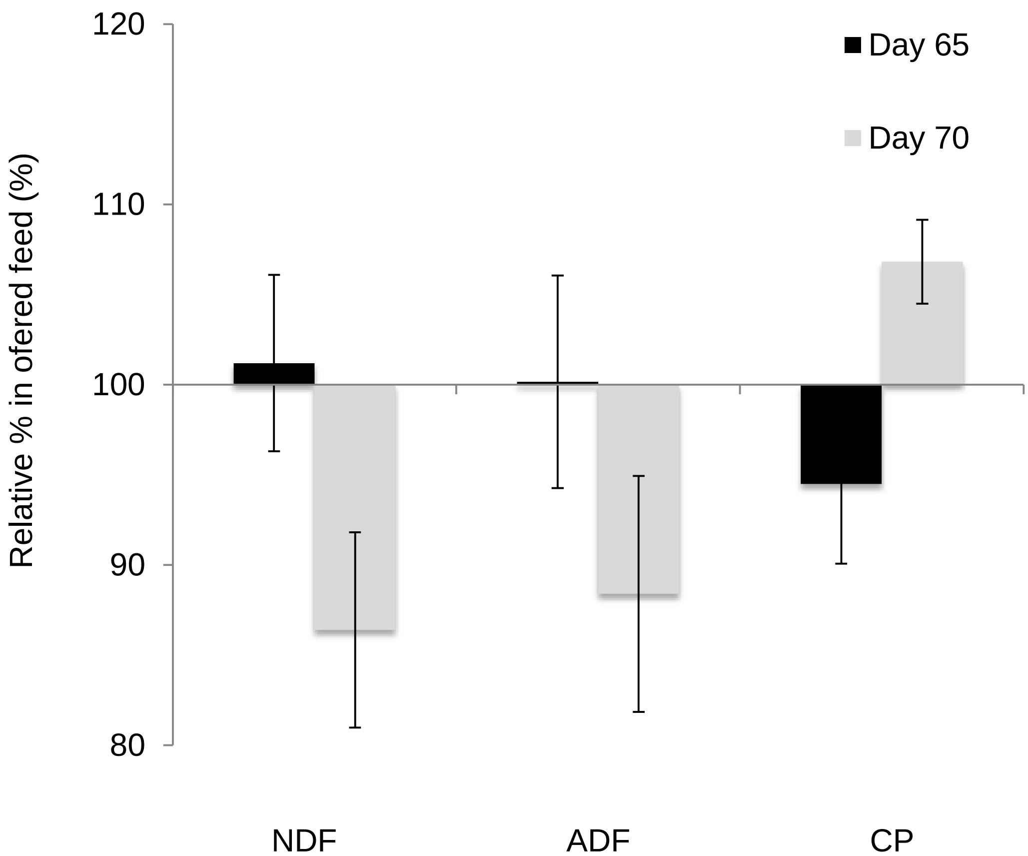


Figure 8. Mean ± SE neutral detergent fibre (NDF), acidic detergent fibre (ADF), and crude protein (CP) in the TMR fed to calves compared with orts. Results are for individually-housed calves (n=18) provided access to TMR and concentrate at 65 d, and TMR only at 70 d.



6.4 Discussion

Calves sorted TMR for specific particle fractions. When given ad libitum access to both TMR and calf starter at 65 d of age, calves showed a preference for long particles consisting primarily of forage. Miller-Cushon and DeVries (2011) found that calves fed hay before weaning initially demonstrated a preference for forage particles when switched to a mixed ration containing (DM basis) 40% hay and 60% concentrate, but developed a preference for grain particles within 4 wk of this change in diet. An initial preference for forage has been associated with feed familiarity and developing sorting skills (Miller-Cushon and DeVries, 2011). However, unlike the study of Miller-Cushon and DeVries (2011), calves in the present study were fed TMR from birth, so it seems unlikely that their sorting behaviour is due to feed neophobia or a lack of the requisite motor skills to obtain fine particles. Our results are consistent with some earlier findings. For instance, Forbes and Kyriazakis (1995) found that sheep consumed an appreciable amount of forage when offered a choice between forage and concentrate. Since ruminants are believed to learn through physiological post-ingestive feedback mechanisms (Provenza, 1995), our results suggest that calves fed both a TMR and free choice calf starter from birth learn to balance consumption of grain and forage in ways that mitigate the effects of lower rumen pH. Interestingly, calves in the present study did not change the relative proportions of ADF, NDF, and CP in the orts, despite sorting for longer particles.

Given that the calf starter was provided as a pellet it is not surprising that the calves were not able to sort for specific components within the calf starter. In contrast to texturized calf starter, pelleted calf starter has been suggested to decrease sorting behaviour (Hutgens, 2001; Moran, 2012), although to our knowledge no research has specifically addressed this issue.

Following the removal of free-access calf starter, calves modified their sorting behaviour, preferentially sorting for fine particles in TMR. Orts were also lower in CP and higher in ADF and NDF, relative to the fed TMR. Preferential consumption of fine, high-energy particles has been reported in previous studies on cows (Leonardi and Armentano, 2003; DeVries et al., 2008). DeVries and von Keyserlingk (2009) also reported that young dairy heifers sorted for concentrate when offered concentrate and hay or when concentrate was top-dressed on the hay. This type of sorting is expected to maximize the energy intake (Provenza and Balph, 1987; Hughes, 1993), so young calves may also be expected to prefer grain particles to hay when choice is presented (Webb et al., 2014a). In this study we only noted sorting for grain within the TMR when the supplementary (and easy to access) grain source was removed. Another study found that sorting behaviour in calves may depend on availability of other feed sources, as calves selected the diet for forage before weaning and for the grain portion of the diet after weaning (Miller-Cushon et al., 2013). Together, these results indicate that calves are able to vary their investment in sorting behaviour depending upon the accessibility of other sources providing the same nutrients. Indeed, this result suggests that sorting tasks may be designed to provide a naturalistic test of how hard calves are willing to work for access to different dietary components in different circumstances. Calves worked for roughage when supplied with a high energy diet comprising of milk replacer and concentrate, we conclude that these findings support the idea that ruminants are able to make choices based on rumen function and possibly also based on their motivation to chew and ruminate.

Provision of forage to young dairy calves has long been controversial, due to the concerns that it may displace concentrate intake and thereby impair rumen development (Hill et al., 2008). Many calves are not provided access to forage until they are completely weaned from milk, leaving concentrate as the only source of solid feed before weaning (Kertz et al., 1979). The results from the present study, showing that calves select forage from a mixed diet, suggest that calves have the desire to access forage in early life. These results and those from Miller-Cushon et al. (2013), together with experimental work showing that calves are highly motivated to access forage (e.g. Webb et a., 2014b), suggest that calf welfare would be improved by providing calves access to forage early in life.

The design of the current study followed normal calf rearing procedures, with calves initially provided free access to starter and then transitioned to a mixed diet with forage. However, this design confounds diet with age, and it is at least possible that some of the changes in sorting we observed were due to the 5 extra days of age (70 d vs. 65 d), rather than the removal of the concentrate. Future studies should test the effects of diet independent of calf age to rule out this possibility. We also encourage future work on how the development of sorting in calves affects the expression of this behaviour in adult cattle. Finally, we have suggested above that sorting may provide a naturalistic approach for assessing calf (or cow) motivation for dietary components; we encourage future work to compare this naturalistic approach with more traditional methods of testing motivation in animals.

6.5 Conclusion

Calves offered TMR and concentrate preferentially consumed long particles. When offered only TMR, calves preferentially consumed fine particles contained within the TMR. These results indicate that young calves are able to sort a TMR and that they can modify their sorting behaviour in response to changes in feed offered. Sorting for longer particles suggest that calves are motivated to consume forage when also provided free access to concentrate.

7 General Discussion and Conclusions

The overall objective of my research was to contribute to the understanding of the effect of the social environment on dairy calves, specifically the development of feeding behaviour, feed preferences, food neophobia, nutrition and the development and motivations behind sorting behaviour. I investigated practices that contribute to the development of strategies to minimize negative impacts of diet and environmental changes on pre-weaned and weaned dairy calves and heifers. In this chapter, I discuss the thesis' findings and its contributions to the available knowledge on these subjects. I will also discuss the strengths and the limitations of the work and provide suggestions for future research directions.

7.1 Thesis Findings

The review of the existing literature on the effects of early social contact and isolation, and in particular the effects of social housing on dairy calves was presented in the Chapter 2. This review summarized the detrimental effects of social isolation on a range of species, showing that dairy calves reared in isolation have deficient social skills, difficulties in coping with novel situations and poor learning abilities. The review identified many gaps in the literature; some of these gaps were addressed in the subsequent research chapters.

One important focus of the review was on the effects of social rearing on increased solid feed intake and hence higher weight gains before and after weaning. In Chapter 3, I assessed the effects of early (at 3 d of age) versus late pairing (at 42 d of age) of dairy heifers on feeding behaviour and weight gain before and after weaning. I found that calves paired soon after birth had the highest intake of solid feed and the highest BW gains in comparison with late paired and individually housed calves. This work provides a scientific basis for the recommendation that dairy calves be housed socially starting at a young age.

Previous work has shown that animals that are socially housed from a young age are better able to cope with novelty and are less fearful (i.e. Duve et al., 2012). Some aspects of these effects have been investigated in dairy cattle, but no previous work had addressed the effects of social rearing on the ability to transition to new types of feed. In Chapter 4, I investigated the effects of complex social housing on neophobic responses to new food items and the ability of dairy calves to transition to new types feed. My findings indicate that housing dairy calves in a complex social group reduces food neophobia. More generally, this study contributed to a series of studies showing that calves reared in more complex social environments may be better able to transition to other changes in their environment, relative to calves raised individually.

Chapter 5 also addressed the effects of social environment on coping with dietary changes, but in older animals and in a different context. I chose an issue that has always piqued my curiosity: how naïve dairy heifers learn to graze when first introduced to pasture. The study investigated whether being grouped with experienced dairy cows would affect the development of grazing behaviours in näive animals. I found that providing heifers with pasture-experienced social companions when first introduced to pasture promotes a more rapid onset of grazing. More generally, this study provides a scientific basis for the recommendation to group naïve heifers with known, older experienced companions to improve the transition to pasture and perhaps other new environments.

In Chapter 6, I focused on one specific aspect of feeding behaviour: feed sorting. Dairy cattle are often fed a mixed diet but are able to sort the mixture, selectively consuming particular fractions of the diet. In some cases sorting can lead to digestive disorders that threaten welfare and productivity. How sorting behaviour develops is poorly understood. The work presented in the final part of my dissertation showed that calves were able to sort TMR at a young age (65 d of age) and that they can adjust their behaviour in response to hunger for grain and forage components. This study showed that calves offered TMR and supplementary concentrate throughout the milk-feeding period preferentially consumed long particles from the TMR. When offered only a TMR, calves preferentially consumed fine particles. These results indicate that young calves are able to sort a TMR and can modify their sorting behaviour in response to changes in feed offered. Sorting for longer particles is evidence that calves are motivated to consume forage when offered supplementary concentrate. These results show that calves have the ability to control and manipulate feeding in relation to their preferences and needs from a young age.

The studies presented in this thesis collectively addressed a number of gaps in the literature regarding raising dairy calves; the findings provide evidence that calves raised in a social environment early in life experience benefits related to feeding behaviour, performance and ability to cope with novelty. Also, I found that experienced companions could mitigate some of the stressors present when young cattle are presented with novel situations. Finally, I showed that calves have feed preferences and are able to sort mixed rations from an early age and that the presence of other feed types influence this motivation. Together, the evidence presented in this thesis added to the existing body of literature showing the benefits of social housing and feed management for calves. I argue that the results of this thesis, and the growing body of literature demonstrating the detrimental effects of social isolation in the early life of dairy calves support that the current standard practice of housing dairy calves individually should be discontinued and that calves should instead be housed in small groups.

7.2 Limitations and Future Research Directions

During the process of reviewing the relevant literature and writing Chapter 2, I came across much evidence of the detrimental effects of the lack of social companions early life in the life. Some of the research was conducted decades ago (i.e. Harlow et al., 1965; Bowlby, 1969), while some was more recent, such as that on the cerebral pathways of social isolation stress (i.e. Zlatković et al., 2014). Detrimental development effects of social isolation have been widely demonstrated in mammals and birds, but recent research has also reported effects on lizards (isolation reared lizards were more submissive, adopted darker and duller colours and performed less well in a foraging task; Ballen et al., 2013).

The effects of social isolation in early life are especially relevant for dairy calves, as these animals are commonly raised in social isolation. I found many important gaps in the literature regarding the effects of social isolation on the lives of dairy calves. Chapter 3, 4 and 5 explored and identified beneficial effects of a complex social environment when calves are developing and coping with a novel situation. Unfortunately, time prevented me from investigating other gaps identified in my review. Two important gaps that were not addressed in this thesis are 1) the persistence of the beneficial effects of a complex social environment in early life, 2) the practical effects of social support and social buffering in dairy cattle, and 3) the identification of sensitive periods during which calves must be socialized to avoid deleterious negative effects on cognition and behavioural flexibility.

The majority of work to date has focused on the short-term effects of social isolation; work investigating the longer-term effects has only begun. Future studies should investigate the persistence of the negative effects of social isolation on cognition and behavioural flexibility. The lack of work in this area is likely due, in part, to the length of time required and the challenges associated with maintaining adequate controls. However, this information would be fundamental to understanding the effects of individual housing in the dairy industry. The link between social isolation early in life and aggressive behaviour, regrouping and behavioural flexibility of adult dairy animals should be investigated in future work. Longer-term effects of social isolation have been demonstrated in other species (i.e. Harlow et al., 1965; Haller et al., 2014) and would likely also be found in cattle.

Research on the longer-term effects of social deprivation on cognitive impairment is also encouraged. Future experiments should investigate the longer-term effects of different dairy calf housing systems on behavioural flexibility, for example the ability to learn the milking routine.

Secondly, social buffering, or the ability of social partners to decrease the impact of stressors during a challenge (Cohen and Wills, 1985) has received little attention in cattle, even though there is considerable potential for these mechanisms to improve welfare. Social support has beneficial effects on humans (for reviews see Kikusui et al., 2006 and Hennessy et al., 2009), rats (Kiyokawa et al., 2014a), guinea pigs (Hennessy et al., 2000), and pigs (Reimert et al., 2014). Some work has occurred on dairy cattle (e.g. testing the acute effects of providing known social companions to cattle learning how to eat a novel feed type, habituating to a novel environment, and coping with new conspecifics; Hessle, 2009; de Paula Vieira et al., 2012a), but this work lacks the controls necessary to distinguish between social support and other mechanisms (Rault, 2012). One potential area of application is in reducing distress associated with routine husbandry procedures such as dehorning. I predict that social support can mitigate the negative affective states associated with dehorning, environmental changes and other potentially fearful situations. I see considerable potential for the use of social companions to support cattle facing challenges.

One limitation of the review presented in Chapter 2 was the lack of a meta-analysis; this analysis can be a useful to synthesize the data and provides a statistical basis for inferences (Petticrew and Roberts, 2006). Unfortunately, at the current time there is an inadequate number of comparable published studies to allow for a meaningful meta-analysis. I encourage future authors to consider the use of meta-analyses as more research on these topics is published.

One of the conclusions of the review presented in Chapter 2 is that the social environment can have profound influences on total food intake, diet and persistence of solid feed intake of calves. Provision of social companions facilitates increased intake of solids during the milk-feeding phase and weaning, which results in performance differences in the majority of trials. These effects were confirmed in the experiments presented in Chapter 3 and 4. One limitation of chapters is that I could not identify the exact age at which calves would be most affected by social companions. Future studies should investigate if there is a critical stage during which calves must be socialized to avoid these deficits. Sensitive periods have been studied extensively in humans (Knudsen, 2004) and rodents (Fone and Porkess, 2008). Behavioural inflexibility has been associated with individual housing of dairy calves (Galliard et al., 2014) and this has been shown to be reduced if calves have social contact with peers at a young age (Meagher et al., 2015). Thus, the existence and length of the sensitive period in which calves require social contact should be investigated.

The increased intake of solids for socially housed calves, as reported in Chapter 3, may be due to social facilitation, social learning or some combination of both. Social facilitation can be defined as "the initiation of a particular response while observing others engaged in that behaviour" (Galef, 1988); in this way the stimulus of an animal eating or approaching the feed would increase the likelihood of the other calf in the same pen performing the same behaviours. Social learning can be defined as learning that is influenced by observation of, or interaction with, another individual (Keeling and Hurnik, 1996). In the previous literature on the development of feeding behaviour in farmed species some authors have implicated social facilitation (e.g. Ralphs et al., 1994) and other authors have suggested social learning (e.g. Launchbaugh and Howery, 2005), but in my view it is not possible to distinguish between these mechanisms based on the studies in this thesis. I encourage future studies to distinguish between the effects of social facilitation and social learning through the use of more elaborate controls, such as a two-action and control designs, where social learning is tested by exposing two groups of naïve animals to different demonstrators, each trained on one of two feeding patterns and a control with no demonstrator (Whiten and Mesoudi, 2008). This method has been used to prove the use of social learning in rats (Heyes and Dawson, 1990) and to confirm experimentally that the famous ‘milk bottle’ innovation found in wild blue tits can be acquired via social learning (Aplin et al., 2013).

7.2.1 Coping with Novelty

Social isolation during development can impair cognition in cattle, especially during a reversal-learning task (Gaillard et al., 2014; Meagher et al., in press). This impairment in reversal learning indicates a lack of behavioural flexibility, and thus a reduced ability to respond appropriately to changes. Although calves have to learn solid feeding behaviour early in life, diet changes are common in the life of modern dairy cattle, including when first transitioned from milk to solid feed at weaning. Delayed acceptance of new food items may be a welfare and production concern (Launchbaugh et al., 1997). I investigated the reluctance to eat novel feed in young dairy cattle in relation to the social environment that calves were raised in. To my knowledge, this study is the first to demonstrate that early social experience reduces food neophobia in calves or indeed in any species.

The work presented in Chapter 3 has some key limitations. First, the complex social environment that the calves were raised in intentionally confounded several features: calves were kept with cows, other calves and in a very spacious and complex environment compared to the singly housed animals. I could not investigate the effects of each of these features independently. Secondly, further research should investigate if the reluctance of isolated calves to eat a novel feed can be generalized to other challenging situations in the lives of calves. Another important limitation is that tests were conducted when calves were still very young; it is not known if this effect persists as the calf ages.

A variety of tests can be used to assess behavioural and physiological responses to novel stimuli, including “open field”, “novel object” and “human interaction” tests. These tests have been criticized on several grounds, especially in the lack of applicable biological relevance (Forkman et al., 2007). Behavioural tests that are more relevant to the nature of specific species are required. One example of a biologically relevant behavioural test is the food neophobia test used in this thesis to assess adaptability to novelty in dairy calves. A second example of a more naturalistic test was the use of sorting behaviour to assess motivation to access feed components, as described in Chapter 6 of this thesis. The relationship between food neophobia and fear responses in other behavioural tests has been explored in sheep (Villalba et al., 2009). The authors measured general fear responses in sheep to a novel environment and response to separation using an open-field test and related these to readiness to eat novel foods. They reported a relationship between behaviour in the open-field test and reluctance to eat new foods, suggesting individuals that are more responsive to social isolation (as measured by number of bleats) are more fearful of novel foods. However, food neophobia when investigated in adult cows, food neophobia tests showed no inter-test relationship with novel object or unfamiliar person avoidance tests (Herskin et al., 2004). Further research should investigate and identify consistent differences between individuals and correlate within-individual responses across different behavioural tests (i.e. novel object, novel environment and human approach tests) in relation to food neophobia, or other biologically relevant tests.

7.2.2 Social Companions

The effects of experienced social companions on the development of foraging in young ruminants has been demonstrated (e.g. Key and MacIver, 1980; Nolte et al., 1990); naïve animals provided with social models are generally more efficient in ingesting forage in a new environment, suffer less from predation and ingest fewer toxic plants compared to those not provided with a social model (Provenza and Cincotta, 1993; Launchbaugh and Howery, 2005). Upon reviewing the findings of Chapter 5, it was clear that one major limitation was that I did not record the behaviour of the experienced animals during the first introduction to pasture. I encourage future work to investigate the influence of the behaviours performed by the social model. In the current study, age and experience were confounded; future work should investigate if the age of the experienced social models affects the behaviour of the naïve heifers.

7.2.3 Sorting Behaviour

Young calves may prefer grain particles to hay when the choice is presented (Webb et al., 2014). However, in Chapter 6, sorting for grain in the TMR occurred only when access of grain was removed. Though Chapter 6 documents sorting behaviour in dairy calves, longer-term studies are needed to assess how sorting and preferences for feed components change as the calf matures.

7.3 General Conclusion

Social housing of dairy calves is associated with benefits regarding early solid feed intake, behavioural flexibility and buffering the negative effects of novelty. In this thesis I demonstrated that social contact can result in higher solid feed intakes and weight gain in the pre-weaning period (Chapter 3), less reluctance to eat novel feed (Chapter 4), and ease in coping with environmental changes (Chapter 5). I also reviewed additional factors that are associated with social housing (see Chapter 2). Moreover, I showed that calves have feed preferences and are able to sort a mixed feed from an early age and that the presence of other feed types influences this motivation (Chapter 6). Finally, three main areas are discussed for future research: persistence of the negative effects of social isolation on cognition and behavioural flexibility, the applied use of social support to mitigate the negative affective states associated with fearful situations, and the identification of sensitive periods during which calves must be socialized to avoid deleterious negative effects on cognition and behavioural flexibility.

The results presented in this thesis, together with the growing body of literature demonstrating detrimental effects of social isolation on dairy calves must be considered in any discussion of how best to house dairy calves on commercial dairy farms. Given the increased awareness of animal welfare by both dairy producers and the general public, including specific concerns associated with social isolation, these results are of special relevance in informing new practices and policies that support the transition to group-housing for dairy calves.

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