EFFECTS OF THE EARLY SOCIAL ENVIRONMENT ON THE RESPONSES OF DAIRY CALVES TO NOVEL EVENTS

by

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Abstract

The pronounced responses of dairy calves to novel events such as weaning and mixing form an obvious welfare concern and represent an important challenge for the dairy industry. I hypothesized that providing calves a more natural social environment would reduce these responses. This thesis consists of 5 chapters, beginning with a general introduction (Chapter 1) and ending with a general discussion and conclusion (Chapter 5). Chapter 2 compares the effects of individual vs. pair housing on calf responses to weaning from milk as well as on the adjustment to a novel pen and novel social partners at mixing. This chapter shows that being housed with a social companion increases starter intake pre-weaning, has a buffering effect on vocal responses at weaning and improves the performance of calves after mixing when compared to calves housed individually. Chapter 3 describes the effects of housing dairy calves with an older companion on the development of feeding behavior before and after weaning from milk. This chapter shows that a weaned companion is an important social model during weaning, stimulating early intake of hay pre-weaning, starter intake post-weaning and improving growth relative to calves housed in groups of similar age. Chapter 4 describes the effects of the early social environment on the behavioral responses of dairy calves to environmental and social novelty. The results from this chapter show that individually housed calves are more reactive to both environmental and social novelty when compared to pair housed calves. Calves housed with an older companion are also more reactive to separation from group members but less reactive to the presence of an unfamiliar calf when compared to calves housed in groups of similar age. Chapter 5 discusses the results of this thesis and suggests that future research on the development of the affective and

cognitive abilities of dairy calves in different social contexts can improve the welfare of commercially reared dairy calves. Providing calves access to conspecifics of similar age or an older companion can minimize calf responses to weaning from milk and reduce responsiveness to environmental and social novelty during mixing.

Preface

I completed this thesis under the supervision of Dr. Daniel M. Weary. In addition to Dr. Weary my supervisory committee included Drs. Anne Marie de Passillé, Luiz Carlos Pinheiro Machado Filho and Marina A. G. von Keyserlingk.

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I was responsible for the study design, data collection, statistical analysis, interpretation and write-up of all manuscripts. I am grateful to my co-authors for their comments and edits on the manuscripts.

All the research conducted was approved by the UBC Animal Care Committee under the number: A08-0105.

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Dedication

I dedicate this thesis to all species and especially to the calves that made this dissertation possible. I truly hope that soon your preferences will be attended!

To my parents: Sebastião Roberto Vieira and Maria Carmo De Paula Vieira. You are the ones that truly inspire in me the determination and faith to pursue what is good, beautiful and true… I love you!

To all my family members (this includes the Weary's) and friends (from my childhood to those spread around the world), for always being there for me, and to Rogerio for connecting me to life. I love you all!

Chapter 1: General introduction

On many commercial farms, calves are separated from the dam soon after birth and housed alone in pens or in hutches. Little is known about the effects of the early social environment on calf development, and more specifically on how this affects their responses to novel events. Novel events in this dissertation are defined as any events that represent an immediate (real or perceived) threat to the individual (e.g. a calf being moved to a novel pen). These events may require mobilization and coordination of multiple physiological systems (usually accompanied by increased metabolic demand), and may necessitate behavioral changes.

In this chapter I describe the basis for my hypothesis that social experience early in life can have profound effects on affective and cognitive development, ultimately affecting calf welfare and growth, as well as calf responses to novel events such as weaning from milk and mixing with unfamiliar companions in a novel environment.

1.1. The effects of social bonding on calf development

Harry Harlow and his team completed some of the first studies on the effects of separation from a caregiver, for example, comparing monkeys raised by the mother with those 'raised' with an artificial terry cloth mother and isolated from other monkeys during the first 6 months of life (Suomi et al., 1973). These animals had altered social behavior as adult, including problems interacting socially with conspecifics and high levels of aggressive and fearful behavior (Harlow and Yudin, 1933; Seay et al., 1964; Seay and Harlow, 1965). These studies helped to provide the basis for the development of the 'Attachment Theory', initially introduced by John Bowlby in 1957, that gained popularity and recognition through the mid-1970's (see van der Horst, 2008).

Later studies have shown that the lack of a caregiver not only influences future social relationships, but can also compromise the development of the stress-regulatory system, including permanent changes in stress reactivity (e.g. Plotsky and Meaney, 1993). For example, increased attention from the dam (e.g. when infant rats are temporarily removed from the nest they receive additional grooming, licking and nursing by their mother when they are returned) results in better regulation of somatic growth and neural development, and enhanced hippocampal synaptic development and consequent spatial learning and memory (Caldji et al., 2011; Liu et al., 1997; Meaney et al., 1996). Moreover, nurturing behaviors are thought to regulate affective responses during development (Panksepp, 2005; 2010).

In social species, novel events such as separation and exposure to a novel environment can enhance the formation of long-lasting social attachments (e.g. Carter, 1998). It has been suggested that during development, threatening situations may encourage the young to return to a secure base or otherwise strengthen social bonds (Bowlby, 1969; Panksepp et al., 1985; Carter and Keverne, 2002). The maintenance of positive social networks likely enhances feelings of safety and reduces negative feelings during stressful events (Taylor et al., 2000).

When a cow is separated from her calf she becomes more active, more vocal and spends less time feeding and ruminating (Lidfors, 1996). Calves also respond to separation by increasing vocalizations and activity level; they also seem more fearful of handlers at separation (Flower and Weary, 2003). In nature, the cow-calf bond is maintained even after the calf is weaned from milk (e.g. Reinhardt, 2002). In commercial systems, dairy calves are typically separated from the dam in the hours after birth and reared individually for the first months of life. The effects of this social isolation have received little attention in the literature, but the work that has been completed does suggest that there may be multiple and long-lasting effects. For example, Flower and Weary (2001) recorded the behavioral responses of calves when they were first allowed to interact with another calf and the calves that were kept with the dams for two weeks were scored as being more interactive during the test than those separated 24 h after birth and reared in isolation.

Similarly to reports in laboratory animals (e.g. Seay and Harlow, 1965; Winslow, 2005), dam-reared calves also fight less and establish a dominance hierarchy earlier than artificially reared ones (on average 4-5 months vs. 9 months), possibly because their interactions are more stable (Reinhardt and Reinhardt, 1975). These results suggest that the lack of an older social companion may increase the risk of sustained agonistic interactions that are commonly reported in commercial agriculture (e.g. Bøe and Færevik, 2003).

Social bonding in cattle has mostly been studied in the context of the cow-calf relationship. However, calves may also develop social relationships with other conspecifics. For example, in piglets and sheep the strong reactions to separation from the dam can be attenuated by the presence of familiar littermates (Fraser, 1975; Porter et al., 1995). In horses, interactions with companions are thought to reduce fear reactions in young animals (Christensen et al., 2008). It also seems that calves prefer to be with a familiar rather than an unfamiliar calf when in a novel environment as they spend more time in the area where the familiar calf was placed and vocalize more when separated from the familiar calf (Færevik et al., 2006).

Little research to date has explored the benefits of social companions on alleviating stress in calves. In humans, social interactions are known to minimize the negative effects of exposure to stressful environments via social buffering (for review see Hennessy et al., 2009), reducing the risk of coronary heart disease, cardiovascular disease and improving immune function (e.g. Uchino et al., 1996; 1999). Similarly in cattle, epidemiological studies have associated stressful events such as mixing with an increased risk for developing infectious diseases (e.g. Ribble et al., 1995; Sanderson et al., 2008).

In addition to preventing the negative effects of persistent activation of the Hypothalamic-Pituitary-Adrenal (HPA) system (Sapolsky, 1998; Seeman and McEwen, 1996), positive social interactions with conspecifics can have positive effects that are mediated by the release of oxytocin, endogenous opioid peptides, vasopressin, norepinephrine, serotonin and prolactin (e.g. Kendrick et al., 1987; Martel et al., 1993; Nelson and Panksepp, 1998). Moreover, activity in dopaminergic reward pathways has been linked to socially affiliative behaviors modulated by oxytocin and vasopressin activity (for review see Skuse and Gallagher, 2009). In cattle, these social bonds may be especially important for heifers and cows as many of these hormones are related to the down-regulation of stress responses among females (e.g. Taylor et al., 2000).

1.2. The effects of social learning on calf development

In this thesis, social learning was defined as any socially influenced changes in behavior (such as local enhancement, emulation, social facilitation, etc.) including imitative learning (Zentall, 1996). Learning by observing or interacting with a social partner or its products is a cheaper way of acquiring valuable information when compared with asocial learning (Heyes, 1994). There are many social learning mechanisms that result in the transmission of behavior between individuals. For example, via local enhancement, a demonstrator attracts an observer to a specific location, which can lead to the observer learning about the objects at that location. Via emulation, i.e. by seeing a demonstrator interacting with objects in its environment, an observer becomes more likely to perform actions that bring about a similar effect on those objects (for review see Rendell et al., 2010).

Social learning can be influenced by a host of factors, ranging from whether a species is gregarious or solitary to whether the animals are competing for feed. In solitary species (e.g. rats and cats), social learning only takes place if there is competition. In contrast, in gregarious animals, excessive competition may actually inhibit social learning (Harlow, 1932). For example, scroungers, i.e. animals that parasitize the food discoveries of other individuals (the producers), were reported to prevent cultural transmission of food-finding behavior in pigeons (Giraldeau and Lefebvre, 1987).

In nature, cattle are gregarious animals and forage in groups. Cows of the same herd tend to feed, ruminate and rest at the same times (Miller and Wood-Gush, 1991; Rook and Huckle, 1995). The developing calf is gradually introduced into the group by the cow. Although calves' early social interactions are focused on the cow, over time the cow gradually increases the time and distance away from her calf, allowing fewer suckling bouts and terminating these more rapidly (Price, 1985). These behavioral cues provided by the dam gradually facilitate weaning at about 10 months of age (Reinhardt and Reinhardt, 1981). The calf initially starts grazing near the cow (Mirza and Provenza, 1992), but after the second week of life the calf increasingly distances itself from the dam and starts interacting with peers. These early social interactions with young conspecifics reach a peak between the 11th and 40th day of life (Vitale et al., 1986; Sato et al., 1987).

Besides young companions, older animals are also reported to graze nearby calf groups (e.g. Murphey et al., 2000, Sato et al., 1987), and thus can also influence calf development. Foraging with experienced social partners was shown to decrease fear of new feed items by young ruminants (e.g. Ralphs et al., 1994; Provenza and Burritt, 1991). For example, calves that had been trained to avoid eating a certain plant began to graze upon this when placed with cattle that were also grazing the same plant (Ralphs and Olsen, 1990).

Because in nature the developing calf learns to graze by observing the behavior of other conspecifics, dairy calves housed commercially may particularly benefit from social learning during weaning the period when they make the transition from a milk-based diet to one of solid feed. Dairy farmers typically encourage the intake of solid feed by restricting milk volume (e.g. Hodgson, 1971; Leaver and Yarrow, 1972; Huber et al., 1984), but milk restriction results in hunger (De Paula Vieira et al., 2008) and limits calf growth in the period following weaning (Weary et al., 2008). Moreover, before weaning calves are usually unable to properly utilize solid diets because their rumen is not fully developed. Therefore, it is critical that alternative practices that encourage voluntary intake of solid feed prior to weaning be developed.

It is known that when animals are fed in groups, feeding by one animal will often stimulate other animals to feed (Curtis and Houpt, 1983), in part because the sight of an individual engaged in feeding reveals the spatial location of the feed. Animals commonly respond to such information by engaging in feeding behavior or, if already feeding, by accelerating their feeding rate, especially when feed is limited. McQuoid and Galef (1992) demonstrated that hens exposed to another hen pecking at a specific location exhibited a strong tendency to peck in the same area. Also, according to Ross and Ross (1949), during social learning there are positive increments in any kind of learnt behavior that depend upon the arousal induced by the presence of other individuals. Bayer (1929), in a classic study, allowed a chicken to completely satiate itself by eating as much wheat as it wanted. He then introduced a hungry chicken that began to eat. The first chicken, although just satiated, resumed eating. Chickens peck at feed more quickly when other chickens are pecking; rats press a bar faster in the presence of other rats; cockroaches run at greater speeds when running alongside other cockroaches (e.g. Clayton, 1978). Studies in lambs and pigs also reported the effects of social learning in these farmed species (Wattanakul et al., 2005; Napolitano et al., 2003; and Hsia and Wood-Gush, 1984).

Social learning may be more likely to occur when prior experience is not enough to decrease uncertainty in unpredictable situations that require considerable behavioral flexibility, especially in rapidly changing environments (Galef et al., 2008; Dewar, 2004; Kendal et al. 2004). As social companions can influence the ability of a naïve animal to acquire a task (Lepoivre and Pallaud, 1985), it can be hypothesized that providing young calves an experienced social companion may help dairy calves to adopt novel feeding strategies at weaning. Although previous research reported increases in solid feed intake (Babu et al., 2004) and calf growth (Chua et al., 2002) for calves housed in groups, no research to date has identified what aspects of social learning are important to stimulate early intakes of solid feed at weaning.

1.3. The effects of social isolation on calf development

Dairy calves are still housed individually in most farms. Individual housing was originally recommended as a way of preventing disease transmission between veal calves (e.g. Webster et al., 1985), but in well-managed commercial systems (e.g. where calves are fed a good quality colostrum soon after birth and higher milk volumes via teat, housed in small groups and efficient biosecurity measures are adopted), there is no clear advantage of housing calves individually versus in small groups (e.g. Chua et al., 2002; Hänninen et al., 2003; Losinger and Heinrichs, 1997). Moreover, calves' willingness to work to gain access to a social partner (e.g. Holm et al., 2002) suggests that social interactions are highly valuable to them.

Social deprivation not only influences the bonding, buffering and learning aspects of social living as previously discussed, but may also disrupt the social development of dairy calves (e.g. Jensen et al., 1997; Jensen et al., 1999; Veissier et al., 1994). In other species, social isolation of neonates can increase aggressive behavior, increase cognitive errors during discrimination tasks, and decrease brain development and plasticity (e.g. Schrijver et al., 2001; 2002; Fowler et al., 2002; Lipkind et al., 2002). Social isolation also increases locomotory activity (Dellmeier et al., 1985) and enhances the effects of reward-related stimuli (Jones et al., 1990).

On dairy farms, individually housed calves are eventually introduced into a group at mixing. During this time, calves have to adapt to environmental and social novelty. Previous studies in laboratory animals showed that when tested in a novel environment (e.g. an open-field), isolated animals are more reactive, anxious and emotional and therefore less likely to respond to novel environmental stimuli appropriately (e.g. Koch and Arnold, 1972; Sahakian et al., 1977). Furthermore, when introduced to novel social partners, they may also have a reduced ability to socially interact (e.g. Jensen et al., 1999), and more difficulty in coping with the novel social partners.

1.4. Thesis objectives

As discussed above, the postnatal social environment has been reported to have profound developmental effects in many species, therefore the overall objective of this thesis was to identify if social complexity early in life can influence calf responses to novel events such as the transition to solid feed, weaning from milk, mixing, environmental and social novelty.

Since the majority of dairy calves in North America are housed individually, I compared the effects of individual housing with the simplest possible group, a pair of similarly aged calves, on calf responses to novelty (Chapters 2 and 4). As dairy calves are also separated from the cow soon after birth, they may lack the benefits of an older social companion when dealing with novelty, especially in events that require considerable behavioral flexibility. Therefore, I also compared the developmental effects of being housed in a group with an older social companion and being housed in a group with companions of similar age (Chapters 3 and 4). These objectives were tested in a series of 3 experiments:

1.4.1. Experiment 1 (individual vs. pair housing)

The objective of the first experiment (Chapter 2) was to compare the effects of being housed with a social companion of similar age vs. being housed individually on calf responses to weaning from milk and to mixing.

1.4.1.1. Calf responses to weaning from milk

My first prediction was that via social learning pair housed calves would ingest more solid feed and gain more weight before and after weaning. My second prediction was that having a social companion would minimize calf responses to weaning from milk, in particular by decreasing the number of vocalizations.

1.4.1.2. Calf responses to mixing

I predicted that when introduced to a novel environment with novel social companions, individually housed calves would show a longer latency to feed within the first h of mixing and would gain less weight than pair housed calves, especially because in many species social isolation has been described to impair social and cognitive development.

1.4.2. Experiment 2 (group housed with an older companion vs. group housed with companions of similar age)

The objective of the second experiment (Chapter 3) was to compare the effects of being housed in groups with an older weaned social companion vs. being housed in groups with companions of similar age on the early development of solid feed intake and on the post-weaning responses of dairy calves.

1.4.2.1. Early development of solid feed intake

I predicted that an older weaned companion would serve as salient stimuli to draw calves' attention to the starter and hay feeders prior to weaning, increasing feeding time and feed intake via social learning.

1.4.2.2. Post-weaning responses

I also predicted that being housed with an older companion would increase solid feed intake, weight gain and reduce hunger during the post-weaning period.

1.4.3. Experiment 3 (individual vs. pair housing / group housed with an older companion vs. group housed with companions of similar age)

The aim of the final experiment (Chapter 4) was to test if the early social environment (being housed individually vs. being housed in pairs and being housed in groups of similar age vs. being housed with an older social companion) influenced the behavioral responses of dairy calves to novelty (environmental and social).

1.4.3.1. Environmental novelty

I predicted that individually housed calves would be more reactive to a novel environment when compared to calves housed in pairs due to a lower behavioral flexibility.

I also predicted that calves housed with an older companion would be more responsive to separation from group members when compared to calves housed in groups of similar age.

1.4.3.2. Social novelty

I predicted that individually housed calves would show reduced ability to socially interact and would be more reactive to unfamiliar calves when compared to calves housed in pairs.

I also predicted that calves housed with an older companion would be less reactive to unfamiliar calves when compared to calves housed in groups of similar age.

Chapter 2: Effects of pair versus single housing on performance and behavior of dairy calves before and after weaning from milk

2.1. Synopsis

This experiment tested the effects of pair versus single housing on the performance and behavior of dairy calves before and after weaning. Twenty-seven Holstein calves were separated from the dam within 6 h of birth, housed in individual pens for 4 d, and then assigned to either continued individual housing (n=9 calves) or pair housing (n=9 pairs). Calves had ad libitum access to starter, hay, and water via buckets. Pasteurized whole milk was fed via teat twice a day for 2 h at ad libitum volumes until d 36. During the milk-feeding period, paired calves showed higher intakes of starter than did the individually housed calves (averaging 93 vs. 59 ± 11 g/d per calf). Calves were weaned from milk from d 37 to 41 by progressive dilution of milk with water, and the teat was removed on d 49. Calves in both treatments vocalized in response to teat removal but this response was less in paired calves than in individually housed calves (84 vs. 194 ± 12 calls/2-h period per calf on d 49). On d 56, calves were moved to group pens, mixed with other calves, and observed for 15 d. Starter, water, and hay were available ad libitum via automatic feeders. Compared with calves previously housed in single pens, paired calves had a shorter latency to start feeding (9.1 ± 2.6 vs. 49.5 ± 4.1 h/calf), visited the starter feeder more frequently (41.6 ± 3.0 vs. 26.4 ± 3.3 visits/d per calf), spent more time at the feeder (87.8 ± 2.5 vs. 65.3 ± 2.9 min/d per calf), and consumed more starter (3.4 vs. 2.3 ± 0.2 kg/d per calf). Weight gains at mixing were higher for paired than for individually housed calves on d 2 and 3 after mixing (0.5 vs. −2.4 ± 0.3 kg/d per calf; and 0.8 vs. −0.9 ± 0.3 kg/d per calf, respectively). The results

indicate that pair housing during the milk-feeding stage reduces calf responses to weaning and improves performance after weaning when calves are housed in groups.

2.2. Introduction

Dairy calves are typically separated from the cow soon after birth and housed in individual pens or hutches. Little is known about how dairy calves might benefit from social housing. Work on laboratory animals has shown that during stressful events animals are often attracted to a social partner (Davitz and Mason, 1955; Morrison and Hill, 1967; Taylor, 1981), and that social interactions result in positive neurochemical signals during times of stress (Panksepp, 1998). Benefits of group housing on health and behavior have also been reported (e.g. improved immune function, lower stress-like cardiovascular responses and more time spent sleeping; Sharp et al., 2002; Bartolomucci, 2007), suggesting that grouping dairy calves during the milk-feeding phase may also provide benefits.

Previous work has shown that dairy heifers are less fearful when tested in the presence of a familiar social partner (Jensen et al., 1997; Jensen et al., 1999, Færevik et al., 2007). The lack of social partners early in life has also been reported to delay exploratory behavior (Jensen et al., 1997). Veissier et al. (1994), showed that individually housed calves had reduced ability to cope with unfamiliar animals during initial encounters at mixing. Moreover, within 2h after mixing, individually housed calves showed increased aggression and reduced play and grooming compared to group-housed calves.

One stressor faced by every dairy calf is weaning from milk to a solid diet. In response to weaning calves show increased activity and vocalizations, combined with a period of growth check (Weary et al., 2008). Chua et al. (2002) reported that calves that had been paired showed less of a growth check at weaning than did individually housed calves. This is the first study to investigate the effects of early social housing on the behavioral responses of dairy calves to weaning from milk.

Several studies have reported increased weight gains for group housed dairy calves when compared to individually housed calves during the milk feeding and weaning periods (e.g. Chua et al., 2002; Xicatto et al., 2002; Tapki, 2007), although some other studies have reported no effect (Færevik et al., 2007) or even increased weight gains for single housed calves (e.g. Terré et al., 2006). The higher weight gain for calves housed in groups is often attributed to social learning, an effect reported in many farm species (see Hsia and Wood-Gush, 1984; Napolitano et al., 2003; Wattanakul et al., 2005). The variability among studies may relate to differences in management (e.g. the number of animals per group, milk volume provided, duration of the feeding period and weaning method).

The objective of this experiment was to determine the effects of a social partner on calf performance and behavior. I predicted that, due to the effects of social learning, pair housed calves would eat more solid feed and gain more weight during the milk-feeding period. I also predicted that pair housed calves would show a reduced distress response and growth check at weaning from milk. Finally, I predicted that pair housed calves would ingest more starter and consequently gain more weight than the single housed calves when all calves were mixed after weaning.

2.3. Materials and methods

This study was conducted at the University of British Columbia's Dairy Education and Research Centre, Agassiz, Canada and was approved by the UBC Animal Care

Committee. Twenty-seven Holstein dairy heifers were allocated to individual (n=9) or pair housing (n=9 pairs), balanced by birth weight (mean ± SD; individual 46.8 ± 4.3 kg vs. pair 47.1 ± 4.1kg). Calves were separated from their dams and fed colostrum within 12 h of birth. Blood samples were collected from the jugular vein 24 h after the first feeding of colostrum and serum was analysed using a Reichert AR 200 Digital Handheld Refractometer (Reichert, Depew, USA). Only calves having a serum protein level greater than 5.5 g/dL were included in the study.

During the first 4 d of age, calves were housed individually in sawdust bedded pens measuring 1.2 m x 2.0 m and were fed a maximum of 6L of whole milk/feeding/calf twice daily. Calves were sedated and dehorned at 4 d of age using caustic paste. When calves were 5 d old they were subjected to a general clinical health examination. Only clinically healthy calves were included in this study.

2.3.1. Feed

During milk feeding calves had ad libitum access to pasteurized whole milk (a mixture of saleable and non-saleable milk) provided twice a day for 2 h at 7 am and 7 pm. Calves had free access to water, orchard grass hay and pelleted calf starter over the entire experimental period (Unifeed Calf Tex®, Chilliwack, BC, Canada). Milk samples were collected twice a week and analysed separately (Pacific Milk Analysis Lab, Chilliwack, BC, Canada). Starter and hay samples were collected daily and pooled weekly for analysis (Cumberland Valley Analytical Services, Maugansville, MD, USA). The chemical composition of the feed provided to the calves over the experimental period is illustrated in Table 2.1.

Table 2.1. Mean (±SD) chemical composition of starter, grass hay, and milk

Parameter	Starter [1]	Hay [2]	Milk [3]
DM (%)	89.5 ± 0.62	87.4 ± 3.1	ND [4]
CP (% DM)	20.67 ± 0.21	17.7 ± 2.34	3.2 ± 0.25
NDF (% DM)	18.6 ± 1.31	62.4 ± 2.66	ND
ADF (% DM)	11.0 ± 0.35	34.8 ± 1.59	ND
Fat (%)	ND	ND	3.72 ± 0.24
Ash (% DM)	7.63 ± 0.4	9.1 ± 1.1	ND
Lactose (%)	ND	ND	4.2 ± 0.06
Ca (% DM)	1.23 ± 0.03	0.37 ± 0.09	ND
Cu (ppm)	53.3 ± 8.4	21.3 ± 33.6	ND
P (% DM)	0.68 ± 0.01	0.29 ± 0.05	ND
Mn (ppm)	112.3 ± 2.5	86.3 ± 0.38	ND
K (% DM)	0.99 ± 0.02	3.32 ± 0.58	ND
Na (% DM)	0.49 ± 0.06	0.058 ± 0.05	ND
Fe (ppm)	417.3 ± 7.1	240.8 ± 72.4	ND
Zn (ppm)	305.0 ± 3.6	41.5 ± 13.7	ND
SCC (x 1000/mL)	ND	ND	857.7 ± 372.6
Net Energy Gain (Mcal/kg)	1.12 ± 0.02	0.83 ± 0.04	ND

[1] Pelleted starter diet (Unifeed® Calf Tex, Chilliwack, BC, Canada).

[2] Orchard grass hay.

[3] Mixture of saleable and non-saleable whole milk.

[4] ND = not determined.

2.3.2. Milk feeding and weaning periods

Milk was provided via a teat twice a day at ad libitum volumes per 2 h feeding (see von Keyserlingk et al., 2006). Daily milk intakes were recorded by measuring the amount of milk ingested at each feeding. Daily (24-h) starter and water intakes were determined each morning. The milk feeding equipment was washed and disinfected with a 5000 ppm hypocloride solution after each feeding. Water and starter buckets were cleaned daily. Individual pens measured 1.2 m x 2.0 m. Pair housed calves were provided twice the area (2.4 m x 2.0 m). Sawdust was added to the pens every other day with the bedding completely replaced and the walls washed once a week. Milk weaning was carried out gradually by dilution with water at a rate of 10% per feeding over the course of 5 d, beginning in the morning of d 37. Calves continued to receive water via artificial teats from d 42 until d 48. On d 49, the teats were removed but calves remained in their pens until d 55 with free access to hay, starter and water provided via buckets. All calves were housed in the same area and calves were able to hear and see other calves, however no other type of social contact was possible for the individually housed calves. Each calf had access to its own milk teat, hayrack, water and starter buckets.

Calves were weighed and health checked every other day before the morning feeding. Health checks consisted of 1) diarrhoea scoring of calves (1=normal feces; 2=plaques but not watery; 3=watery and body temperature < 39.5°C; 4=watery and body temperature ≥ 39.5°C), and 2) clinical examination of the respiratory system (absence of nasal discharges and/or pathological sounds of pulmonary infection during auscultation). When calves were diagnosed as ill, they were treated according to current veterinary practices adopted on farm (e.g. by administering antibiotic drugs and electrolytic solutions).

The number of vocalizations was monitored by direct observations from d 42 until d 55. Calves were observed for 1 h during the morning and evening feedings totaling 2 h/d of observations.

2.3.3. Mixing period

On d 56 calves were moved to a group pen and monitored for 15 d. The experiment ended on d 70. There were 6 replications of the mixing period and each group consisted of 6 calves: 3 older calves and 3 focal calves from this study (1 previously housed as an individual and 2 from a single pair). The group pen measured 7.0 m x 5.0 m and was equipped for free access to water and hay (intakes not measured). A CF1000CS-Combi automatic feeder (De Laval, Tumba, Sweden) measured intakes of calf starter. Visits to the starter feeder were defined as beginning when the calf's entire body was inside the feeder allowing automatic recognition of calves' transponders. BW was recorded automatically at every visit to the drinker. Sawdust was added once a week to the group pen, and pens were cleaned when the group was moved on d 70.

2.3.4. Statistical analyses

2.3.4.1. Milk feeding and weaning periods

The effect of housing (single versus pair) on milk intake, starter intake, water intake, BW and vocalizations was tested by obtaining the mean value of the pen (i.e. based on a single calf per pen for the individual treatment, and the mean of the two calves per pen in the pair treatment), on each experimental day. These data were normally distributed and checked for homogeneity of variance. Because delivery of the liquid diet varied during weaning, I separated the analysis for the pre-weaning and weaning phases into 4 periods: 1) milk feeding (from d 1 until d 36), 2) milk dilution (from d 37 until d 41), 3) water via teat (from d 42 until d 48) and 4) no liquid via teat (from d 49 until d 55). Vocalizations were analysed for periods 3 and 4 as they were recorded only from d 42 until d 55. The effect of treatment (1 d.f.) was tested separately for each period and each variable using PROC MIXED in SAS (version 9.1, SAS Institute Inc., Cary, NC) with 16 error d.f. Least squares means and standard errors were determined using the LSMEANS statement in the MIXED procedure. Unless specified otherwise, means are reported ± SE.

2.3.4.2. Mixing period

The effect of previous housing type at grouping (1 d.f.) on the average time spent at the starter feeder, number of visits to the starter feeder, starter intake and growth rate was tested by obtaining the daily mean value per calf (or pair for the previously paired calves). The effect of treatment was tested using PROC MIXED of SAS (version 9.1, SAS Institute Inc., Cary, NC) with 10 error d.f. Least squares means and standard errors were determined using the LSMEANS statement in the MIXED procedure. All data was normally distributed and checked for homogeneity of variance. The analysis for growth rate was carried out in 2 different ways. The analysis of weight gain over the entire 15 d period did not include the effect of d. Growth check was greatest during the first 2 d after mixing, so I analysed changes in BW over this period including d in the model. Unless specified otherwise, means are reported ± SE.

2.4. Results

2.4.1. Pre-weaning and weaning periods

2.4.1.1. Milk and water intakes via teat

Milk intake increased over the pre-weaning period (Figure 2.1). For example, intake increased from (mean ± SD) 7.3 ± 1.6 kg/calf on d 2 to 10.7 ± 1.7 kg/calf on d 36. Average intakes of milk were similar in pair and single housed calves (mean ± SD; 9.6 ± 1.8 kg/d/calf; $P=0.36$), even at the end of the milk-feeding period (mean ± SD; 12.6 ± 3.5 kg/calf on d 41).

When water was provided via teat there was a tendency for pair housed calves to ingest more water (15.2 vs. 12.7 ± 0.5 kg/d/calf; P=0.05) compared to individually housed calves.

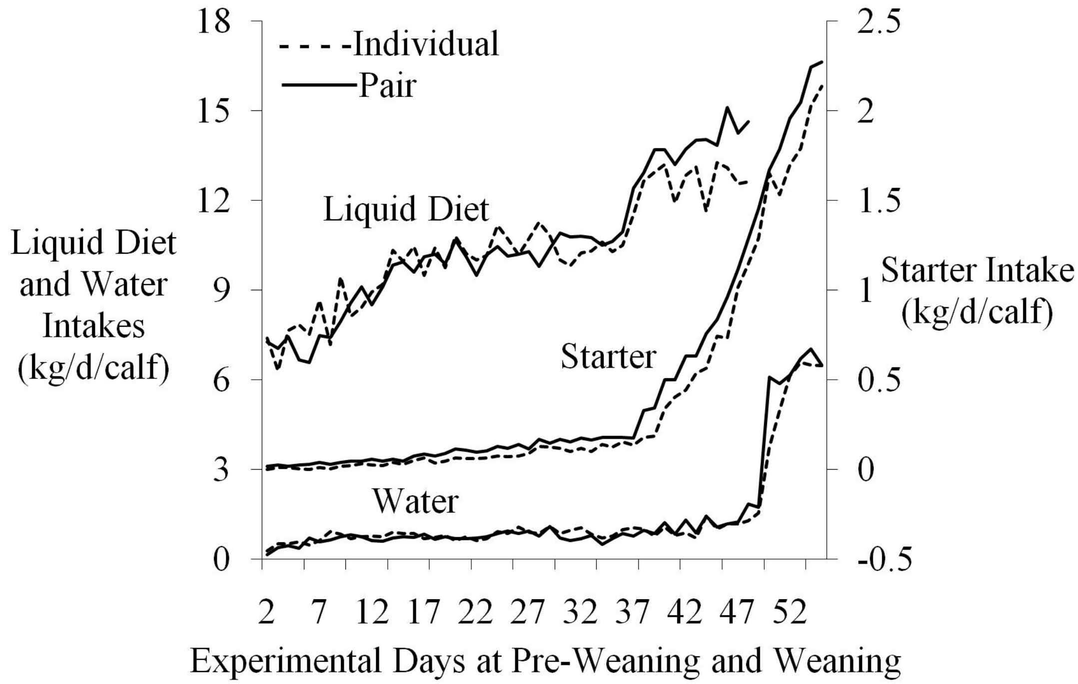


Figure 2.1. Mean intake of starter (kg/d/calf), liquid diet (kg/d/calf; milk, diluted milk and water provided via teat) and water (kg/d/calf; provided via bucket) for calves housed in pairs (n = 9 pairs) or individually (n = 9 calves) during the milk feeding (day 1 until day 36) and weaning (day 37 until day 55) periods

2.4.1.2. Water intake via bucket

During the pre-weaning period, water intake increased gradually over time for both single and pair housed calves (mean ± SD; 0.2 ± 0.1 kg/calf on d 2 to 0.9 ± 0.7 kg/calf on d 36; Figure 2.1) with no difference in intakes between treatment groups (mean ± SD; 0.7 ± 0.5 kg/d/calf; P=0.54). Water intakes also did not differ during the dilution phase (mean ± SD; 0.93 ± 0.6 kg/d/calf; P=0.99), but intakes were higher in the pair housed calves when only water was available from the teat (1.7 vs. 1.0 ± 0.16 kg/d/calf, respectively; P=0.03). When the teat was removed water intake via buckets was again similar between the two treatments (mean ± SD; 5.5 ± 1.6 kg/d/calf; P=0.10).

2.4.1.3. Starter intake

Starter intake over the pre-weaning period was higher for pair housed calves (93 vs. 59 ± 11 g/d/calf; P=0.04; Figure 2.1). Starter intake increased with calf age, from (mean ± SD) 25 ± 30 g/d/calf during the first 2 wks to 145 ± 93 g/d/calf during the last week of the pre-weaning period. Starter intake during milk dilution averaged (mean ± SD) 0.3 ± 0.2 kg/d/calf (P=0.22) and was highly variable, ranging from 150 ± 100 g/calf on d 37 to 450 ± 300 g/calf on d 41. When only water was provided via teat, starter intakes averaged (mean ± SD) 0.8 ± 0.3 kg/d/calf (P=0.11) over the entire period, ranging from (mean ± SD) 0.5 ± 0.3 kg/calf on d 42 to 1.2 ± 0.4 kg/calf on d 48. When the teat was removed, calves consumed an average (mean ± SD) of 1.9 ± 0.4 kg/d/calf of starter (P=0.2), ranging from (mean ± SD) 1.4 ± 0.4 kg/calf on d 49 to 2.3 ± 0.5 kg/calf on d 55.

2.4.1.4. Weight gain

There was no difference in BW between the 2 treatment groups during the pre-weaning and weaning periods. Calves averaged (mean ± SD) 61.0 ± 4.7 kg/calf during the milk feeding period (P=0.73), 79.7 ± 6.5 kg/calf during milk dilution period (P=0.88), 82.0 ± 6.0 kg/calf (P=0.48) when water was provided via teat, and 88.3 ± 6.7 kg/calf (P=0.43) after the teat was removed.

2.4.1.5. Number of vocalizations

Individually housed calves vocalized 3-times more than did pair housed calves over the period from d 42 until d 48 (7.6 vs. 2.1 ± 0.7 calls/calf/2-h period; P<0.001; Figure 2.2). The number of vocalizations remained high on the days after the removal of the milk teat (d 49 until d 55) with individually housed calves again vocalizing more often than pair housed calves (75.7 vs. 29.4 ± 6.0 calls/calf/2-h period/d; P<0.001).

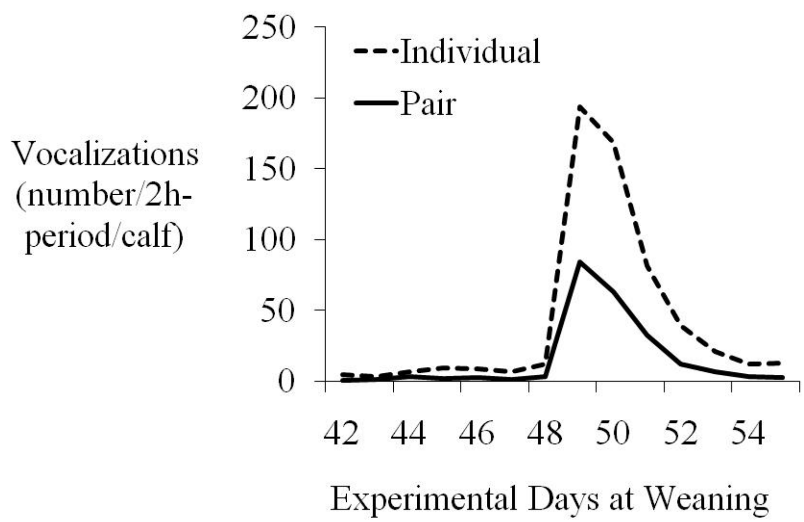


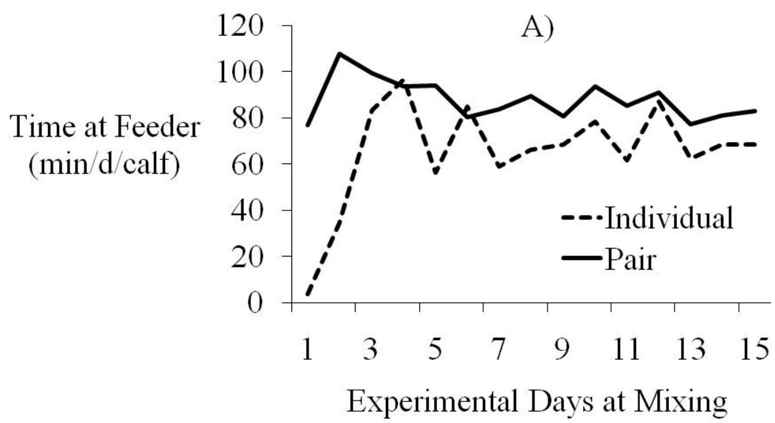
Figure 2.2. Mean number of vocalizations (2-h period/d/calf) for pair (n = 9 pairs) and individually (n = 9 calves) housed calves during weaning (d 42 until d 55)

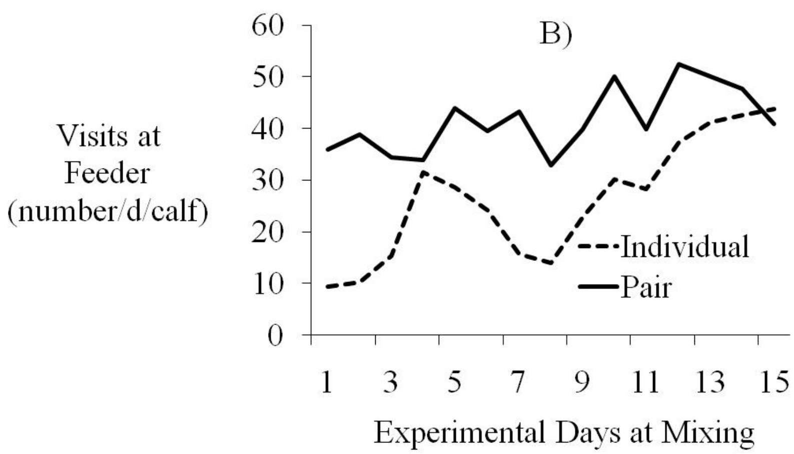
2.4.2. Mixing period

The latency for calves to first visit the starter feeder was shorter for the calves that were previously pair housed versus individually housed (mean ± SD; 9.1 ± 2.6 h vs. 49.5 ± 4.1 h/calf). Paired calves spent more time at the feeder (87.8 ± 2.5 vs. 65.3 ± 2.9 min/d/calf; P<0.001; Figure 2.3 A), visited the feeder more often (41.6 ± 3.0 vs. 26.4 ± 3.3 visits/d/calf;

P=0.008; Figure 2.3 B) and consumed more starter (3.46 vs. 2.3 ± 0.2 kg/d/calf; P=0.002; Figure 2.3 C). Pair housed calves began eating starter on d 1 while single housed calves consumed no starter on d 1 or 2. Starter intake of pair housed calves was (mean ± SD) 1.2 ± 0.6 kg/calf on d 1 and 2.4 ± 0.5 kg/calf on d 2. On d 3, starter intake averaged (mean ± SD) 3.0 ± 0.7 kg/calf for pair and 0.4 ± 0.9 kg/calf for single housed calves.

Weight gains at mixing were higher for paired than individually housed calves at d 2 (0.5 vs. -2.4 ± 0.3 kg/calf; P<0.004) and d 3 (0.9 vs. -0.9 ± 0.3 kg/calf; P=0.02). Over the remainder of the mixing period, there was no effect of treatment on weight gain, with calves gaining on average (mean ± SD) 0.5 ± 0.21 kg/d/calf (P=0.7; Figure 2.3 D).





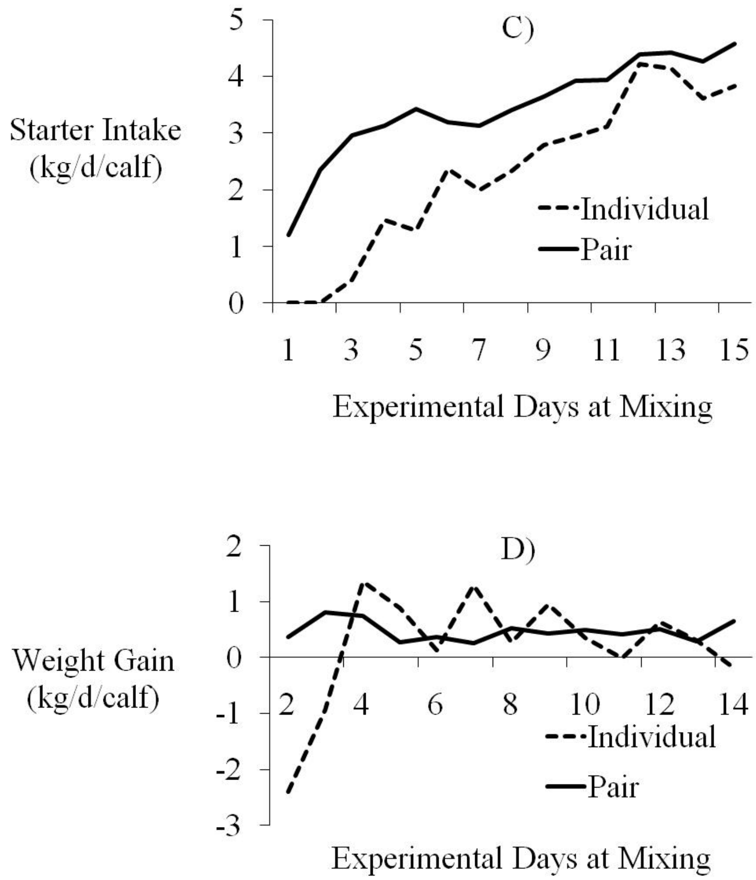


Figure 2.3. The effect of mixing (d 56 until d 70) for pair (n=6 pairs) and individually (n=6 calves) housed dairy calves on: A) mean duration of visits to the starter feeder (min/d/calf), B) mean number of visits to the starter feeder (number/d/calf), C) mean starter intake/visit (kg/d/calf) and D) mean growth rate (kg/d/calf)

2.5. Discussion

Pair housing did not influence weight gains during the milk feeding and weaning periods in this study. Previous studies that reported increased weight gains for group housed calves (e.g. Chua et al., 2002; Xicatto et al., 2002; Tapki, 2007) varied in management practices and experimental design (e.g. feeding frequency, number of animals, milk volume and duration of the feeding period), so readers should interpret differences among these studies with care.

Pair housed calves ingested more starter during the pre-weaning period than did individually housed calves, but intakes in both treatments were within the range previously reported for calves fed higher milk volumes (e.g. Jasper and Weary, 2002). The higher starter intake in the pair housed calves may be attributed to social learning. Although, I only noted increased starter intake in the pair housed calves during the milk feeding period, others (e.g. Babu et al., 2004; Hepola et al., 2006) have reported similar effects over a longer feeding period.

At weaning, individually housed calves showed a stronger vocal response than did paired calves. The number of vocalizations peaked on d 49, when the teat was no longer available. Stronger vocal responses to weaning have been linked to the lack of access to the feeding system, rather than the lack of milk per se (Budzynska and Weary, 2008). The reduced responses of the pair housed calves may be due to social buffering effects described in other species (Kikusui et al., 2006; Hennessy et al., 2009); to my knowledge this is the first evidence of social buffering in response to weaning distress in cattle.

The results of this study suggest that the paired calves may have higher behavioral flexibility, i.e. ability to modify behavior in response to a changing environment such as mixing with unfamiliar calves in a novel environment. Paired calves spent more time at the feeder, visited the feeder more often, and started ingesting concentrate from the computerized starter feeder more rapidly than did individually housed calves, such that the paired calves ingested more solid feed and gained more weight. The differences in feeding behavior at mixing may be explained by the socially inexperienced single housed calves having to cope with learning how to use the feeder as well as learning how to cope with conspecifics. In contrast, the pair housed calves were able to draw on previous social experiences with the familiar companion. This may have also enabled them to socially learn the feeding behavior of the calves in the group that had previous experience with the feeding system. Differences in response may also have been due to cognitive differences due to early social experiences of paired calves. Social isolation in rats seems to disrupt brain development, resulting in behavioral and neurochemical changes (Schrijver and Würbel, 2001) that reduce measures of cognitive performance. Studies are now required to understand the role that different housing systems may play in affecting the social and cognitive development of dairy calves.

2.6. Conclusion

Pair housing during the milk-feeding period reduced behavioral responses to weaning and improved performance of calves grouped after weaning.

Chapter 3: Presence of an older weaned companion influences feeding behavior and improves performance of dairy calves before and after weaning from milk

3.1. Synopsis

In commercial dairy production calves are typically separated from the dam at a young age. This practice may interfere with developmental processes mediated by social interactions that occur between the calf, their dam and older social partners. The aim of this study was to test the prediction that calves housed with an older weaned companion would show earlier intakes of solid feed before weaning, and higher growth rates during and after weaning, compared to calves housed with calves of their own age. Forty-five dairy calves were separated from the dam and housed individually for approximately 7 d. Afterwards calves were assigned to pens composed of groups of either 3 young calves, or 2 young calves and an older weaned calf. Group pens were equipped with automatic milk, water, starter, hay feeders and scales. Weaning was by gradual reduction of milk volume over 5 d, from d 36 to d 40. During the pre-weaning period (d 1 to d 35) the number (8.8 vs. 5.1 ± 0.5 visits/d/calf) and duration (13.2 vs. 8.2 ± 1.1 min/d/calf) of visits to the hay feeder was higher for calves housed with an older companion, and calves in this treatment consumed more hay (57.9 vs. 25.6 ± 4.7 g/d) than did calves housed in groups of similar age. Starter intake did not differ between treatments before weaning, but the number of visits (15.2 vs. 9.4 ± 0.6 visits/d) and the time spent at the starter feeder (6.5 vs. 3.4 ± 0.5 min/d) was higher for calves housed with an older weaned companion. During the weaning period (d 36 to d 40), calves housed with an older companion spent more time at the starter feeder (22.1 vs. 12.9 ± 1.9 min/d) and made fewer unrewarded visits to the milk feeder (17.0 vs. 26.1 ± 1.9 visits/d) than did calves housed in groups of similar age. During the post-weaning period (d 41 to d 55) calves housed with an older weaned companion spent less time at the hay feeder (32.5 vs. 58.5 ± 5.5 min/d), more time at the starter feeder (41.4 vs. 28.2 ± 3.7 min/d) and consumed more starter (1.8 vs. 1.3 ± 0.1 kg/d). Calves housed with an older weaned companion gained more weight during the pre-weaning (0.89 vs. 0.76 ± 0.03 kg/d) and post-weaning (1.4 vs. 1.1 ± 0.05 kg/d) periods. I conclude that housing young calves with an older weaned companion stimulates feeding behavior and growth before and after weaning from milk.

3.2. Introduction

On commercial dairy farms calves are typically separated from the cow soon after birth and housed in single pens or in groups of similar age. The lack of access to a more experienced social partner may influence the early development of feeding behavior, especially the early intake of solid feed. Young animals seem more dependent on social learning to locate and select edible feedstuffs than are adults (Galef, 1977).

The calf's ability to find the teat and suckle successfully is influenced by the cow's behavior (Hafez and Lineweaver, 1968), and as the calf ages the cow behaves in ways that discourages milk intake (e.g. the cow gradually increases the time and distance away from her calf, allows fewer suckling bouts and decreases nursing time; Reinhardt and Reinhardt, 1981; Vitale et al., 1986). This stimulates the calf to sample alternative feeds. For example, within the first few weeks of life, calves start sampling solid feed in the company of grazing adults (Key and MacIver, 1980; Nolte et al., 1990). Foraging with experienced social partners is known to decrease food neophobia and facilitate acceptance of novel foods

(Lynch et al., 1983; Galef and Stein, 1985), and young grazers copy the dietary choices of adult members of the group helping them avoid poisonous substances (Mirza and Provenza, 1994). Providing calves a novel diet in the presence of their dam biases calves' preference towards that diet for at least 12 weeks after first exposure (Fukusawa et al., 1999).

Social learning of feeding may be particularly beneficial before and after weaning, the period when calves make the transition from a milk-based diet to solid feed. Calves that consume little solid feed before weaning are more likely to experience poor growth and prolonged hunger until intake of solid feed meets their requirements for maintenance and growth (De Paula Vieira et al., 2008; de Passillé et al., 2011).

The aim of this study was to test the prediction that young calves housed with an older weaned companion would ingest more solid feed before weaning, improving weight gains during and after the weaning period.

3.3. Materials and methods

This study used 54 Holstein dairy heifers housed at the University of British Columbia's (UBC) Dairy Education and Research Centre, Agassiz, Canada. The animal care protocol was approved by the UBC Animal Care Committee.

3.3.1. Pre-experimental period

All calves used in this study (including the older companions) were female and subjected to the same management practices during the early age. All calves were separated from their dams and fed colostrum within 8 h of birth. To assess the efficiency of passive immune transfer, blood samples were collected from the jugular vein of each calf within 24 h after the first feeding of colostrum, and serum was analysed using a Reichert AR 200 digital hand-held refractometer (Reichert, Depew, NY). Only calves having a serum protein level >5.5 g/dL were included in the study. After colostrum feeding the umbilical cord of all calves was treated with a 7% iodine solution. All calves were sedated and dehorned at 4 d of age using caustic paste (see Vickers et al., 2005). During this period all calves were housed individually in sawdust-bedded pens measuring 1.2 m × 2.0 m and provided 8 L of whole milk divided in 2 meals/d. Calves had free access to water, hay and starter during this period. Prior to group housing all calves were subjected to a general clinical health examination by a veterinarian and only clinically healthy calves were included in this study. The older weaned companion calves were previously housed in groups of 3 animals and were habituated to feed from the automatic feeders before being housed with the younger calves.

3.3.2. Experimental period

When younger calves were 8 ± 2.5 d of age, they were assigned to pens composed of either groups of 3 young calves (n = 9 groups), or groups of 2 young calves and an older weaned calf (n=9 groups). Groups were balanced by weight (mean ± SD; group of 3 young calves 46.6 ± 5.4 kg vs. group of 2 young calves 46.9 ± 5.6 kg housed with an older weaned calf 121.5 ± 8.4 kg). Older weaned companions were 85 ± 5.5 d old when group housed with the younger calves. The group pens measured 7.0 m × 5.0 m and were equipped with automatic feeders.

The young calves were allowed access to 8 L/d of pasteurized whole milk (a mixture of saleable and non saleable milk) provided by a CF1000CS-Combi automatic feeder (DeLaval, Tumba, Sweden); this feeder also provided free access to a textured calf starter

(93% DM) that contained 57.5% concentrate pellets, 14% flatted barley, 13% flatted oats, 10% steamroll corn and 3.5% molasses (Unifeed Ltd., Chilliwack, BC, Canada).

Calves were trained by a caretaker to use the milk feeder. This training was carried out in the morning and afternoon of each of the first 3 d of the experimental period. A barrier at the entrance to the milk feeder prevented the older weaned companions from gaining access to this feeder but allowed access by the smaller calves. Weaning was carried out gradually starting on d 36, with a reduction of milk volume by 1.6 L/d. From d 41 onward, milk was no longer provided. Chopped orchard grass hay (95% DM) of a mean particle size of 1.2 ± 0.4 cm (calculated using the Penn State Particle Separator) and water (water intakes and visits were not measured) were also provided automatically (Insentec, Marknesse, Holland). Visits to the feeders were defined as starting from the time when the calf's transponder was detected by the feeder. Calves were weighed automatically at every visit to the milk feeder and water drinker by scales located underneath them (Smart 1, Westernscale Inc., Port Coquitlam, BC, Canada).

During the entire experimental period older weaned companions visited the starter feeder (mean ± SD) 24.4 ± 8.1 times/d. These visits lasted 54 ± 18.6 min/d and calves consumed 3.6 ± 1.4 kg/d of starter. Visits to the hay feeder lasted 24 ± 12 min/d and older weaned calves performed 25.7 ± 17.8 visits/d. Older companions consumed 0.5 ± 0.3 kg/d of hay throughout the experiment.

Health checks were performed every 2 d consisting of 1) diarrhea scoring of calves (1=normal feces; 2=plaques but not watery; 3=watery) and cleanliness of the rump (1=clean, 2=some fecal soiling; 3=heavily soiled with fecal matter), 2) clinical examination of the respiratory system (presence or absence of nasal discharge and pulmonary sounds using an stethoscope), 3) body temperature and, 4) inspection of the umbilical cord. Calves diagnosed as ill were rechecked daily and treated according to standard operating procedures developed by the herd veterinarian (e.g. administration of antibiotics, anti-inflammatory drugs, electrolytic solutions and topical iodine solution as required). Of the 27 calves housed with same age companions, 11 were diagnosed with an inflammation in the umbilical cord and 12 were diagnosed as having diarrhea scores of 3 (some calves had a combination of the two conditions). Of the 18 calves housed with an older social companion, 4 were diagnosed with an inflammation in the umbilical cord and 6 were diagnosed as having diarrhea scores of 3. Again, some calves had a combination of the two ailments. No calves showed clinical signs of respiratory diseases. I found no treatment difference (as tested using a Fisher's Exact Test) for any of these health measures, but readers should be cautioned that the study was not designed to assess health outcomes and a larger sample of calves would be required for meaningful analysis.

3.3.3. Statistical analyses

Average daily gains were calculated for each of the younger calves from the slope of the regression between BW and age. These values were then averaged to calculate a mean value for each of the 18 test groups. The effect of treatment (1 df) on gains, average intake, time and number of visits to the drinker and the milk, starter and hay feeders were tested with group as the experimental unit (i.e. 16 error df) using the MIXED procedure in SAS (version 9.2, SAS Institute Inc.). The model specified day as a repeated measure and also tested day and the day by treatment interaction. Residuals from the model were plotted against the predicted values to verify assumptions of normality and homogeneity of variance. Data were analysed separately in 3 periods: pre-weaning (d 1 to d 35), weaning (d 36 to d 40) and post-weaning (d 41 to d 55).

3.4. Results

3.4.1. Milk intake and visits to the milk feeder

Milk intakes were similar for groups housed with an older weaned companion and groups housed with calves of similar age. During the pre-weaning period the duration and total number of visits to the milk feeder did not differ between treatments. During the weaning period, the total number of visits and the number of unrewarded visits to the milk feeder was lower for calves housed with an older weaned companion (Figure 3.1).

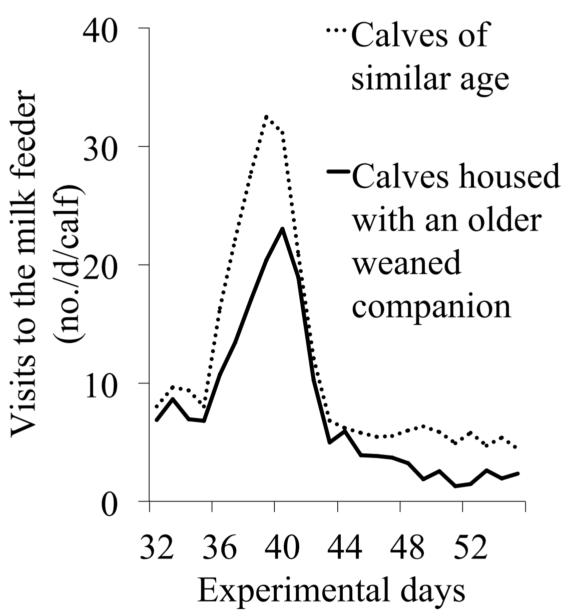


Figure 3.1. Mean number of visits to the milk feeder (no./d) for calves housed with an older weaned companion (n=9 pens; 2 young calves/pen) and for calves of similar age (n=9 pens; 3 young calves/pen) during the weaning (d 36 to d 40) and post-weaning periods (d 41 to d 55)

During the post-weaning period the average time spent at the milk feeder decreased, but did not differ with treatment (Table 3.1).

Table 3.1. Mean intake of milk (kg/d), number of unrewarded visits (no./d), number (no./d) and duration (min/d) of visits to the milk feeder for calves housed with an older weaned companion (n=9 pens; 2 young calves/pen) and for calves of similar age (n=9 pens; 3 young calves/pen) during the pre-weaning (d 1 to 35), weaning (d 36 to d 40) and post-weaning (d 41 to d 55) periods

	Calves with an older companion	**Calves of similar age**	**SE**	***P*-value**
Pre-weaning period (d 1 to d 35)				
Milk intake (kg/d)	7.6	7.6	0.1	0.64
Unrewarded visits to the feeder (no./d)	8.8	9.2	0.5	0.6
Total visits to the feeder (no./d)	14.3	14.8	0.6	0.53
Duration (min/d)	69.3	69.8	3.0	0.88
Weaning period (d 36 to d 40)				
Milk intake (kg/d)	3.8	3.8	0.1	0.8
Unrewarded visits to the feeder (no./d)	17.0	26.1	1.9	0.0043
Total visits to the feeder (no./d)	20.3	29.6	2.0	0.0045
Duration (min/d)	123.2	152.5	22.2	0.37
Post-weaning period (d 41 to d 55)				
Unrewarded visits to the feeder (no./d)	4.7	7.0	1.3	0.22
Duration (min/d)	1.0	1.0	0.1	0.91

3.4.2. Starter intake and visits to the starter feeder

During the pre-weaning period, calves housed with an older companion visited the starter feeder more often and spent more time at the feeder than did calves housed in groups of similar age. Starter intake did not differ between treatments and increased with calf age (P=0.0001) from (mean ± SD) 24.2 ± 15.9 g/d during the first 2 wk to (mean ± SD) 197.2 ± 87.9 g/d during the rest of the pre-weaning period (Figure 3.2).

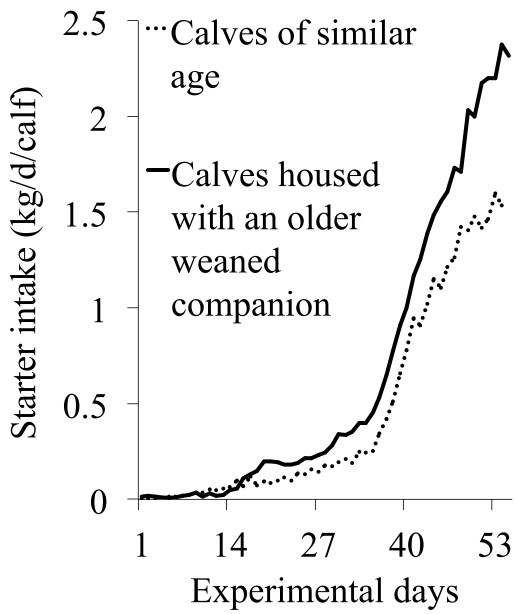


Figure 3.2. Mean intake of starter (kg/d) for calves housed with an older weaned companion (n=9 pens; 2 young calves/pen) and for calves of similar age (n=9 pens; 3 young calves/pen) during the pre-weaning (d1 to d 35), weaning (d 36 to d 40) and post-weaning (d 41 to d 55) periods

During the weaning period, starter intake did not differ between treatments but calves housed with an older companion spent more time at the starter feeder than did calves housed in groups of similar age. During the post-weaning period, calves housed with an older companion also spent more time at the starter feeder and consumed more starter when compared to calves housed in groups of similar age (Table 3.2).

Table 3.2. Mean intake of starter (g/d), number (no./d) and duration (min/d) of visits to the milk feeder for calves housed with an older weaned companion (n=9 pens; 2 young calves/pen) and for calves of similar age (n=9 pens; 3 young calves/pen) during the pre-weaning (d 1 to 35), weaning (d 36 to d 40) and post-weaning (d 41 to d 55) periods

	Calves with an older companion	Calves of similar age	SE	*P*-value
Pre-weaning period (d 1 to d 35)				
Starter intake (g/d)	156.2	99.8	30.5	0.21
Total visits to the feeder (no./d)	15.2	9.4	0.6	0.0001
Total duration at the feeder (min/d)	6.5	3.4	0.5	0.001
Weaning period (d 36 to d 40)				
Starter intake (g/d)	765.3	541.9	96.7	0.12
Total visits to the feeder (no./d)	24.9	20.7	1.9	0.15
Total duration at the feeder (min/d)	22.1	12.9	1.9	0.003
Post-weaning period (d 41 to d 55)				
Starter intake (g/d)	1794.5	1296.6	86.3	0.001
Total visits to the feeder (no./d)	29.0	25.8	1.3	0.08
Total duration at the feeder (min/d)	41.4	28.2	3.7	0.03

3.4.3. Hay intake and visits to the hay feeder

Hay intake during the pre-weaning period was higher for calves housed with an older weaned social companion (Figure 3.3); these calves also spent more time at the hay feeder and visited the feeder more often during this period.

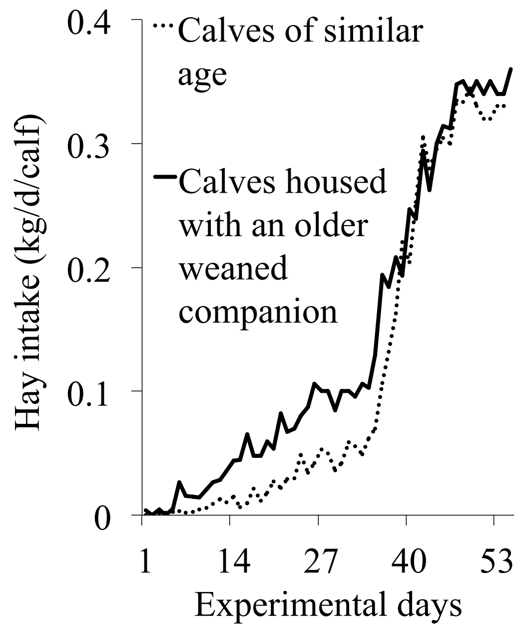


Figure 3.3. Mean intake of hay (kg/d) for calves housed with an older weaned companion (n=9 pens; 2 young calves/pen) and for calves of similar age (n=9 pens; 3 young calves/pen) during the pre-weaning (d1 to d 35), weaning (d 36 to d 40) and post-weaning (d 41 to d 55) periods

During the weaning period, hay intake, number of visits and time spent at the hay feeder were similar for the two treatments. During the post-weaning period, hay intake and the number of visits to the hay feeder did not differ between the two treatments, but calves housed with an older companion spent less time at the hay feeder when compared to calves housed in groups of similar age (Table 3.3).

Table 3.3. Mean intake of hay (kg/d) for calves housed with an older weaned companion (n=9 pens; 2 young calves/pen) and for calves of similar age (n=9 pens; 3 young calves/pen) during the pre-weaning (d1 to d 35), weaning (d 36 to d 40) and post-weaning (d 41 to d 55) periods

	Calves with an older companion	Calves of similar age	SE	*P*-value
Pre-weaning period (d 1 to d 35)				
Hay intake (g/d)	57.9	25.6	4.7	0.0002
Total visits to the feeder (no./d)	8.8	5.1	0.5	0.0001
Total duration at the feeder (min/d)	13.2	8.2	1.1	0.004
Weaning period (d 36 to d 40)				
Hay intake (g/d)	205.3	161.3	31.1	0.33
Total visits to the feeder (no./d)	21.3	16.5	3.9	0.39
Total duration at the feeder (min/d)	32.8	38.6	4.5	0.37
Post-weaning period (d 41 to d 55)				
Hay intake (g/d)	292.1	306.6	27.0	0.70
Total visits to the feeder (no./d)	25.0	28.6	2.7	0.35
Total duration at the feeder (min/d)	32.5	58.5	5.5	0.005

3.4.4. Growth rate

Calves housed with an older weaned companion gained more weight during the pre-weaning (0.89 vs. 0.76 ± 0.03 kg/d, P=0.01) and post-weaning (1.4 vs. 1.1 ± 0.05 kg/d, P=0.009) periods when compared with calves housed with same aged calves. During the weaning period, weight gain did not differ among treatments (0.45 vs. 0.37 ± 0.16 kg/d, P=0.7).

3.5. Discussion

During the pre-weaning period, calves housed with an older weaned companion visited the hay and starter feeders more often and spent more time at the feeders than did calves housed in a uniform age group. As calves in both treatments consumed similar amounts of milk and starter pre-weaning, the higher intake of hay by calves housed with an older weaned companion may have contributed to their slightly higher weight gains pre-weaning. It has long been believed that feeding calves hay before weaning reduces starter intake and calf growth (Stobo et al., 1966; Warner et al., 1956) but more recent work suggests that the opposite may be true, at least for calves fed higher quantities of milk. For these calves it seems that hay intake does not decrease weight gain (Khan et al., 2011). Moreover, hay intake enhances rumen weight and capacity and increases rumination relative to calves that do not have access to hay. The presence of an older companion may have increased the availability of microorganisms in the environment, allowing earlier inoculation of fauna and flora in the digestive tract of these calves (Pounden and Hibbs, 1948). The consequences of this early inoculation on feed digestibility and calf growth are not well understood. I encourage more work on how early rumen inoculation (flora and fauna) may interact and trigger rumen development, especially for calves fed high milk volumes and provided forages during the pre-weaning period.

This increased affinity for solid feed early in life, by calves provided the company of an older weaned companion, could be the result of social learning (Galef, 1993; Galef and Giraldeau, 2001). For example, local enhancement (a non-imitative process defined as attraction of observers to a location at which conspecifics are behaving; Thorpe, 1956) may explain the increased exploratory behavior (e.g. higher number and duration of visits to the starter and hay feeders) observed in calves provided the company of an older weaned companion. Olfactory stimulation, independent of imitation, may also explain these results. For example, in rats some information about feed is transferred between individuals via the feed odors in the breath of the demonstrator animal (Galef, 1994); young calves may have also been influenced by the odors of hay and starter on the breath of the older companion, triggering them to experiment with feeds of similar smell. Young calves may have also imitated the behavior of the older weaned companion, but this explanation requires some understanding by the young calf of the goals (e.g. at weaning it is necessary to ingest alternative feeds) or the consequences (e.g. to avoid hunger) of the behavior being observed (Tomasello, 1990). The current study was not designed to distinguish among these different types of social learning but I encourage future work to understand the mechanisms at play.

Throughout their development, dairy calves are exposed to a range of management practices (e.g. introduction to new feeding systems, regrouping, social isolation, abrupt weaning and other changes in diet) that require considerable behavioral flexibility in order to adapt. Work on behavioral plasticity that allows calves to adapt to stressful events is only just beginning (Chapter 2), and the extent to which lack of behavioral plasticity can result in the maladjustment of dairy calves to commercial systems is not well documented. Because social learning is more likely to occur when prior experience is not enough to decrease uncertainty in unpredictable situations that require behavioral flexibility (Galef et al., 2008; Dewar, 2004; Kendal et al. 2004) future studies that assess the mechanisms and potential benefits of social learning in dairy calves are also required.

In this experiment, calves were expected to go from a milk-based diet to one based only on solid feed over a 5-d period starting at about 5 wk of age. Calves provided an older weaned companion seem to have adopted more successful feeding strategies that allowed improved weight gains after weaning. For example, during the post-weaning period calves housed with an older companion spent more time at the starter feeder. Consequently they consumed more starter and gained more weight. In contrast, calves housed with companions of similar age visited the milk feeder more often during the weaning period. Because the visits to the milk feeder were mostly unrewarded during this period, performing this behavior provided no real benefits to the calves. Calves fed less milk (i.e. 4 L/d versus 8 L/d) also visit the milk feeder more frequently, even when these visits result in no extra milk (De Paula Vieira et al., 2008), indicating that these visits are associated with hunger.

The higher post-weaning weight gains of calves provided an older weaned companion may be a consequence of higher hay intakes during the pre-weaning period. These higher intakes may have allowed calves to develop a better functioning rumen (e.g. by increasing rumen capacity and rumination; Hibbs et al., 1956; Tamate et al., 1962; van Ackeren et al., 2009), so that after weaning calves housed with an older companion were better able to utilize the starter. It is known that when milk is no longer provided solid feed intake increases abruptly (Khan et al., 2011). The effects of this higher intake of starter on calf rumen metabolism and morphology is not well described in the literature, but I speculate that calves provided the company of an older companion may have been less affected by the negative effects of low rumen pH such as rumenitis and papillae branching (Nocek et al., 1984; Suárez et al., 2006 a, b). I encourage future studies on the early ruminal development of young dairy calves fed higher milk volumes that test specific properties of solid diets (e.g. palatability, digestibility, rumen growth and capacity) that are relevant at triggering early rumen development pre-weaning and minimize rumen overload post-weaning.

3.6. Conclusion

This is the first study to report the benefits of social learning on the behavior and performance of dairy calves before and after weaning from milk. Providing young calves an older weaned companion increases solid feed intake and improves growth rate before and after weaning from milk. Future work needs to determine the social learning mechanisms at play that result in these benefits.

Chapter 4: Effects of the early social environment on the behavioral responses of dairy calves to novel events

4.1. Synopsis

Providing young animals the opportunity to engage in more complex social interactions is hypothesized to improve their capacity to cope with changing environments. To test the effects of the early social environment on the behavioral responses of dairy calves to novelty I compared 1) individual vs. pair housing and 2) group housing with companions of similar age vs. group housing with a more experienced conspecific. Fifty-four dairy calves were separated from the cow soon after birth and housed individually (n=6 calves) vs. in pairs (n=6 pairs), or in pens composed of groups of 3 young calves (n=6 groups) versus in groups of 2 young calves and an older calf (n=6 groups). At 65 to 69 d of age calf responses were tested in an environmental novelty test and a social novelty test. Individually housed calves were more active (i.e. spent less time standing, 201.4 vs. 280.3 ± 30.5 s/test; and more time running, 83.2 vs. 57.3 ± 19.1 s/test) and more reactive (i.e. defecated more frequently, 1.3 vs. 0.6 ± 0.2 events/test) when tested in the novel arena, compared with pair housed calves. During the social novelty test, individually housed calves spent less time running (51.8 vs. 96.4 ± 11.6 s/test), showed a longer latency to socially interact (111.1 vs. 20.4 ± 21.7 s/test) and spent more time involved in social interactions (130.7 vs. 79.7 ± 19.0 s/test) with the unfamiliar calf than did pair housed calves. Individually housed calves were also more reactive to the presence of an unfamiliar calf as indicated by increased rates of defecation (2.3 vs. 0.7 ± 0.5 events/test) and kicking (2.2 vs. 0.7 ± 0.4 events/test) compared with pair-housed calves. Calves housed in groups with an older companion were more

reactive to the novel environment than were calves housed in groups of similar age: they defecated (1.0 vs. 0.6 ± 0.2 events/test) and vocalized (23.6 vs. 15.3 ± 3.8 events/test) more during the test. These calves also spent less time exploring (266.3 vs. 355.0 ± 27.4 events/test) and had a lower frequency of kicking (0.1 vs. 2.0 ± 0.5 events/test) when tested with an unfamiliar calf. I conclude that calves housed individually are more reactive to environmental and social novelty when compared to calves housed in pairs and that calves housed with an older companion are less reactive to a novel calf when compared to calves housed in groups of similar age.

4.2. Introduction

In nature calves' early social interactions are focused on the cow, but as lactation progresses the cow increases the time and distance away from her calf, allowing fewer suckling bouts and terminating these more rapidly (Price, 1985). Initially calves start grazing near the cow (Mirza and Provenza, 1992), but over the first few weeks of life the calf increasingly distances itself from the dam and interacts with other calves (Vitale et al., 1986; Sato et al., 1987) and older cattle (e.g. Murphey et al., 2000, Sato et al., 1987). In contrast to this complex social environment that calves experience in more natural settings, on many dairy farms calves are separated from the dam soon after birth and housed individually in pens or in hutches.

Providing calves the opportunity to engage in social interactions may allow for the development of better cognitive and social abilities. Research on other species has shown that social isolation of neonates can increase aggressive behavior, increase cognitive errors during discrimination tasks, and decrease brain development and plasticity (e.g. Schrijver et al., 2001; 2002; Fowler et al., 2002; Lipkind et al., 2002). Animals that have been reared in social isolation tend to be more reactive, anxious and emotional and thus less likely to respond to novel environmental stimuli appropriately than animals raised with a companion (e.g. Koch and Arnold, 1972; Sahakian et al., 1977).

Existing evidence suggests that early social experiences can influence calf responses to novelty. For example, individually housed calves vocalize more at weaning from milk, take longer to learn to use automatic systems and experience a more severe growth check when moved to a large group pen than do calves housed in pairs (Chapter 2). Individually housed calves also show stronger fear responses to novel situations (Jensen et al., 1997). The simplest possible group is a pair of similarly aged calves, thus the first objective of this study was to test if calf responses to environmental and social novelty are reduced in pair housed versus individually housed calves.

Calves may also benefit from access to older social partners, in part because older social companions may provide more salient social cues. In Chapter 3, I demonstrated that group housing with an older social companion increased solid feed intake pre-weaning and body weight gains before and after weaning; these results suggested that calves housed with an older companion were better able to learn to consume solid feed and this in turn improved their responses to weaning from milk when compared to calves housed in groups of similar age. Thus, the second objective of this study was to test if calf responses to environmental and social novelty are reduced when calves are housed with an older companion versus housing with a group of similarly aged calves.

4.3. Materials and methods

This study used 54 Holstein dairy heifers housed at the University of British Columbia's (UBC) Dairy Education and Research Centre, Agassiz, Canada. This animal use was approved by UBC's Animal Care Committee.

4.3.1. Pre-testing

Calves were separated from their dams and fed colostrum within 8 h of birth. To assess the efficiency of passive immune transfer, blood samples were collected from the jugular vein 24 h after the first feeding of colostrum, and serum was analysed using a Reichert AR 200 digital hand-held refractometer (Reichert, Depew, NY). Only calves having a serum protein level >5.5 g/dL were included in the study. After colostrum feeding the umbilical cord was treated with a 7% iodine solution. Calves were sedated and dehorned at 4 d of age using caustic paste (see Vickers et al., 2005).

Prior to 9 d of age, all calves were housed individually with free access to water, hay and starter. Calves were then assigned to one of four treatments: 1) individual housing (n=6 calves), 2) pair housing (n=6 pairs), 3) group housing in groups of 3 young calves (n=6 groups), and 4) group housing in groups of 2 young calves and an older calf (n=6 groups). Older companions averaged 83 ± 5.4 days of age when mixed with the younger calves. Calves were assigned pseudo-randomly to treatment, balancing for body weight on d 9. These weights averaged (±SD) 44.9 ± 5.6 kg for individual housing, 44.8 ± 5.7 kg for pair housing, 45.9 ± 5.7 kg for group of 3 young calves, and 46.4 ± 5.8 kg for the group of 2 young calves housed with an older companion (weighing on average 120.4 ± 8.3 kg).

The individual pen measured 1.2 m x 2.0 m and the pair pen measured 2.4 m x 2.0 m. Group pens measured 7.0 m × 5.0 m. The older companion calves had lived in the group pens for approximately 10 weeks before assigning younger calves to this treatment.

All of the young calves were allowed access to 8 L/d of pasteurized whole milk (a mixture of saleable and non saleable milk) either by bottle (for calves housed individually and in pairs) or by a CF1000CS-Combi automatic feeder (DeLaval, Tumba, Sweden) that also provided free access to a textured calf starter (for the two group treatments). Calves housed individually and in pairs received free access to starter via bucket. The starter offered for all calves (93% DM) contained 57.5% concentrate pellets, 14% flatted barley, 13% flatted oats, 10% steamroll corn and 3.5% molasses (Unifeed Ltd., Chilliwack, Canada). All calves had free access to water and chopped orchard grass hay (95% DM) with a mean particle size of 1.2 ± 0.4 cm as measured using the Penn State Particle Separator. Group housed calves received water and hay automatically (Insentec, Marknesse, Holland), while calves housed individually and in pairs received these via water buckets and individual hayracks suspended on the wall of the pen.

Calves were trained by a caretaker to use the bottle and milk feeders. This training was carried out in the morning and afternoon of each of the first 3 d of the experimental period. Weaning was carried out gradually starting on d 36, reducing milk volume by 1.6 L/d. From day 41 onward, milk was no longer provided.

4.3.2. Testing

Tests were chosen to measure calf reactivity to environmental and social novelty. Testing started when calves were approximately 65 d of age. Repeated exposure provides a method for assessing habituation to the test, so calves were tested daily (from 09:00 h to 12:30 h) during 3 consecutive days for the environmental novelty test. The social novelty test was performed on the days 4 and 5 (from 10:00 h to 10:30 h). Calves were examined by a veterinarian on a daily basis and none showed signs of disease on any test day. For all tests calves were walked to a test arena with concrete flooring (covered with approximately 3 cm of sawdust bedding) measuring 30.0 m x 5.0 m. Feces and soiled bedding were removed from the test arena after each calf was tested.

For the environmental novelty test: each replication consisted of testing calves from all 4 treatments (8 calves/replication) alone in the arena, once/d over 3 d following a randomized testing order.

For the social novelty test: individual vs. pair housing, I selected 3 calves (1 from the individual housing treatment, 1 from the pair housing treatment and 1 calf from the group of similar age) of similar weight from each of the 6 replications. The calf from the group of similar age (a non-focal calf; data from this calf was not included in the analysis) was the unfamiliar calf for both individually (focal calf; tested once) and pair housed calves (focal calf; tested once). The unfamiliar calf was tested twice over d 4 and d 5, and treatment order was alternated for each replication. For the social novelty test: calves housed with an older companion vs. calves housed in groups of similar age, 4 calves from each of the 6 replications (all focal calves, each tested once) from both treatments were tested on d 4 and d 5. Within each replicate a calf from one treatment was used as an unfamiliar test calf for the other treatment, and vice-versa. All the calves used in these tests had been previously habituated to the test arena for 3 d during the novel environment testing. All of the unfamiliar calves had been group-housed calves (either housed with an older companion or housed in groups of similar age) prior to testing.

Behavior of each focal calf in both tests was video recorded continuously for the 900 s test using camcorders (DCRSR100 HDD Handycam Camcorders, Sony Corp., Park Ridge, NJ). Video recordings were analysed continuously by one trained observer blind to treatment using Observer software (Noldus Inc., Wageningen, Netherlands), starting when the focal calf's back legs entered the arena. Inter-observer reliability was evaluated for all behaviors studied by comparing records with a second trained observer blind to treatment in 16 environmental novelty and social novelty tests; correlations averaged (±SD); 0.78 ± 0.07. Intra-observer reliability was carried out by comparing records assessed independently by the same observer, again for both environmental and social novelty tests 16 times; correlations averaged (± SD) 0.89 ± 0.05.

4.3.2.1. Environmental novelty test

Behaviors recorded were: time (s) spent standing inactive, walking, running, exploring (i.e. sniffing and/or licking the walls and floor of the arena while standing or walking), and number of defecation bouts, backing-off events (i.e. an abrupt movement in a reverse direction from the area being explored and/or a sudden neck movement like a startle reflex while exploring) and vocalizations. Calves were separated from their group mates during testing, so responses may have also reflected the effects of physical separation from pen mates. To assess the effect of separation I also recorded vocalizations by the companion calves that remained in the home pens (including the older companion). Test calves were not in visual contact with their pen mates while in the test arena but the calves were able to hear one another.

4.3.2.2. Social novelty test

Behaviors recorded included all those described above as well as time (s) involved in social interactions with the unfamiliar calf (i.e. licking and/or sniffing the unfamiliar calf while standing or walking) and latency to initiate social interaction, as well as number of head-head contacts, kicks (directed by the focal calf towards the unfamiliar calf) and synchronous running events (focal calf starting a running bout within 1 s of the start of a bout by the unfamiliar calf).

4.3.3. Statistical analyses

Durations and numbers of behaviors were summed per test and averaged for the similarly aged calves in each pen (i.e. one calf in the individual treatment, the 2 calves in the pair treatment, the 3 calves in the same aged treatment, and the 2 similarly aged calves in groups with an older calf) yielding a total of 72 observations for the environmental novelty test (6 pens for each of 4 treatments, tested over 3 d) and 48 observations for the social novelty test (6 pens for each of 4 treatments, tested over 2 d; 12 of these observations were not included in the analysis as they were originated from the unfamiliar calf used in the test for the pair and individually housed calves). The effect of treatment was tested using the MIXED procedure in SAS (version 9.2, SAS Institute Inc.) with an autoregressive covariance structure. The model specified day as a repeated measure and pen as the subject. Residuals from the model were plotted against the predicted values to verify assumptions of normality and homogeneity of variance. Specified contrasts were used to compare 1) individually vs. pair housed calves, and 2) calves of similar age vs. calves housed with an older companion. For all results, I report the mean value of each behavior/test if no effect of day was found. When an effect of day was found, I report the mean value for each of the test days. Day by treatment interactions were tested but never significant and hence are not reported below. During the social novelty test calves did not perform backing-off events so this variable is not reported below. Unless specified otherwise, means are reported ± SE.

4.4. Results

4.4.1. Individual vs. pair housing

4.4.1.1. Environmental novelty test

During the environmental novelty test, individually housed calves were more active than pair housed calves as shown by less time spent standing and more time running (Table 4.1). The time calves spent running reduced over the three test days from an average of 136 s on d 1 to 41 s on d 3 (± 19.1 s; $P<0.0001$).

Individually housed calves were also more reactive than pair housed calves during this test, as indicated by the increased rates of defecation and a higher number of backing-off events. Rates of defecation and backing-off events were higher on d 1 than on subsequent days. Defecation events averaged 1.6 events on d 1 and 0.6 events on d 3 (± 0.2 events; $P<0.0001$). Backing-off events averaged 4.7 events on d 1 and 2.3 events on d 3 (± 0.1 events; $P=0.03$). These effects of day suggest that calves habituated to the test arena.

Pair housed calves vocalized more frequently during the test, likely in response to separation from their pen mate

Table 4.1. Behavioral responses (mean ± SE) of individually (n=6 calves) vs. pair housed calves (n=6 pairs) during the environmental and social novelty tests

	Individual	**Pair**	**SE**	***P*-value**
Environmental novelty test				
Exploring (s/test)	531.9	470.2	38.6	0.06
Standing (s/test)	201.4	280.3	30.5	0.03
Walking (s/test)	81.5	92.2	16.2	0.41
Running (s/test)	83.2	57.3	19.1	0.03
Defecation (no./test)	1.3	0.6	0.2	0.0002
Backing-off (no./test)	4.7	1.6	0.1	0.0007
Vocalizations (no./test)	7.7	14.3	3.0	0.03
Social novelty test				
Exploring (s/test)	262.1	358.2	22.1	0.0007
Standing (s/test)	302.2	232.0	30.2	0.07
Walking (s/test)	153.3	133.8	20.7	0.52
Running (s/test)	51.8	96.4	11.6	0.02
Social Interactions (s/test)	130.7	79.7	19.0	0.05
Latency to socially interact (s/test)	111.1	20.4	21.7	0.0093
Defecation (no./test)	2.3	0.7	0.5	0.05
Head-head (no./test)	2.2	18.0	4.4	0.04
Kicks (no./test)	2.2	0.7	0.4	0.03
Vocalizations (no./test)	1.3	6.0	1.3	0.05
Synchronous running (no./test)	0.5	1.8	0.4	0.04

4.4.1.2. Social novelty test

Calves housed individually explored less, ran less and tended to spend more time standing inactive than did calves housed in pairs. Individually housed calves also showed a longer latency to initiate a social interaction (i.e. lick and/or sniff) with the unfamiliar calf, but once social interaction was initiated these calves were more persistent. Individually housed calves also performed fewer head-head contacts, kicked and defecated more, vocalized and initiated fewer synchronous running events than did calves housed in pairs.

4.4.2. Groups housed with an older companion vs. groups of similar age

4.4.2.1. Environmental novelty test

There was no effect of treatment on time spent running (Table 4.2), but there was an effect of day. Running reduced over the three test days from an average of 113 s on d 1 to 35 s on d 3 (± 12.4 s; $P<0.0001$). Calves housed with an older companion defecated more frequently and tended to spend less time exploring and more time standing than did calves housed with same aged group mates.

Table 4.2. Behavioral responses (mean ± SE) of younger calves housed with an older companion (n=6 pens; 2 young calves/pen) vs. calves housed in groups of similar age (n=6 pens; 3 young calves/pen) during the environmental and social novelty tests

	Calves with an older companion	**Calves of similar age**	**SE**	***P*-value**
Environmental novelty test				
Exploring (s/test)	355.9	415.7	38.4	0.07
Standing (s/test)	390.0	325.1	37.6	0.06
Walking (s/test)	87.2	97.6	15.6	0.51
Running (s/test)	67.0	61.5	12.4	0.63
Defecation (no./test)	1.0	0.6	0.2	0.03
Backing-off (no./test)	0.4	0.7	0.3	0.78
Vocalizations	23.6	15.3	3.8	0.0097
Social novelty test				
Exploring (s/test)	266.3	355.0	27.4	0.02
Standing (s/test)	364.8	272.6	39.3	0.06
Walking (s/test)	109.6	128.4	20.1	0.85
Running (s/test)	79.4	72.6	26.7	0.63
Social Interactions (s/test)	79.9	71.4	18.6	0.53
Latency to socially interact (s/test)	40.6	38.4	19.6	0.9
Defecation (no./test)	0.9	0.7	0.3	0.57
Head-head (no./test)	3.5	7.3	1.3	0.06
Kicks (no./test)	0.1	2.0	0.5	0.02
Vocalizations (no./test)	11.9	12.8	2.4	0.7
Synchronous running (no./test)	2.2	1.8	0.8	0.6

During this test, calves housed with an older companion vocalized more than did calves housed in groups of similar age (Figure 4.1; Table 4.2). When one calf was tested in the test arena, the calves that remained in the home pen sometimes vocalized. The rate of these vocalizations was higher for young calves housed with an older companion versus calves housed with similarly aged calves (3.7 vs. 0.5 ± 0.7 events/test; P=0.0013). The older social companion was also vocal, averaging (± SD) 11.2 ± 9.2 calls/test.

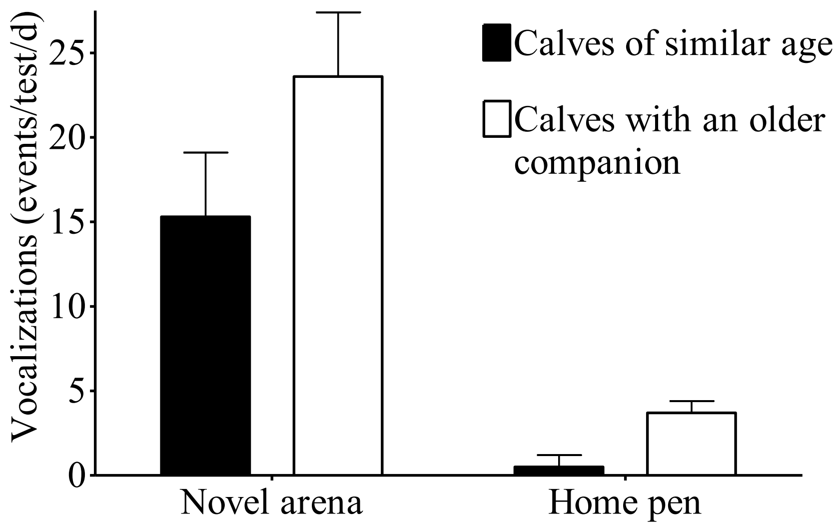


Figure 4.1. Number of vocalizations (mean ± SE; events/test) during the environmental novelty test and in the home pen for younger calves housed with an older companion (n=6 pens; 2 young calves/pen) vs. calves housed in groups of similar age (n=6 pens; 3 young calves/pen)

4.4.2.2. Social novelty test

Calves housed with an older companion spent less time exploring the arena and tended to stand more than did calves housed in groups of similar age. Calves housed with an older companion kicked less frequently at the unfamiliar calf and tended to perform fewer head-head contacts than did calves housed in groups of similar age.

4.5. Discussion

4.5.1. Individual vs. pair housing

Individually housed calves were more reactive during the environmental novelty test as indicated by more time spent standing and running and a tendency to spend more time exploring the arena, and more defecation and backing-off events during exploration relative to calves housed in pairs. These findings agree with previous work on laboratory animals (e.g. Sahakian et al., 1977, Gentsch et al., 1988, Hall et al., 1997; Varty et al., 2000) and calves (Warnick et al., 1977; Jensen et al., 1997; Jensen et al., 1999) that reported a higher sensitivity to a novel environment for individually reared animals. 'Isolation-syndrome'-like behaviors are thought to arise because socially deprived animals overreact to novel environmental stimuli, perhaps because of heightened anxiety or emotionality (e.g. Koch and Arnold, 1972; Sahakian et al., 1977) associated with changes in brain development (Lipkind et al., 2002; Schrijver et al., 2001; 2002; Suomi et al., 1971).

An alternative explanation for the increased reactivity of individually housed calves is that access to the test arena may have been more rewarding for these calves. Research on laboratory animals has shown that isolation enhances the effects of reward-related stimuli (Jones et al., 1990). The home pens of the individually housed calves were half the size of those used for the pair-housed calves, reducing the opportunity for locomotory play, perhaps making access to the large test arena particularly valuable for these calves. Calves from both conditions spent a considerable portion of their time running in the test arena, especially on the first day of testing, a result consistent with previous work on the effect of access to space on locomotory play (e.g. Dellmeier, 1985; Jensen, 2001; Sisto and Friend, 2001).

The results of the social novelty test showed that individually housed calves were more reactive to the unfamiliar calf, as evidenced by increased defecation and less time spent running and exploring the arena. These calves also showed reduced synchronous running, fewer head-head contacts, and an increased latency to initiate social interactions. These results are consistent with previous work showing deficits in social behavior for calves reared individually (e.g. Jensen et al., 1997; Jensen et al., 1999; Veissier et al., 1994). It is not clear if these deficits in social behavior decline with social experience later in life; I encourage future research on the ontogeny of social behaviors in dairy calves.

4.5.2. Groups housed with an older companion vs. groups of similar age

To my knowledge, this is the first study to test the effects of housing calves with an older companion on responses to environmental and social novelty. Calves reared in groups with an older companion vocalized more frequently when in the test arena than did calves housed in groups of similar age. Pen mates housed with an older companion also vocalized more in the home pen while their companion was being tested than did pen mates of calves housed in groups of similar age. Vocalizations in this context are likely an indicator of separation distress, analogous to the vocal responses of calves after separation from the dam (e.g. Flower and Weary, 2001). If this interpretation is correct these results suggest that calves reared with an older companion form stronger social bonds with their pen mates, perhaps especially the older calf and vice-versa. Calves may have also been responding the high rates of vocalizations produced by the older companion calf. Higher separation responses by these calves might also explain the increased rates of defecation.

When introduced to an unfamiliar calf in the social novelty test, calves reared in same aged groups were more reactive than calves housed in groups with an older companion; specifically, these calves were more likely to kick at the unfamiliar calf and to engage in head-head interactions. Previous studies comparing animals that were housed with the dam vs. artificially reared reported reduced aggression among mothered animals (Seay and Harlow, 1965; Winslow, 2005) as well as higher dominance later in life (Bouissou et al., 2001); the results of the current study suggest that rearing calves with older companions may have similar effects. We especially encourage research that tests if social relationships with the older companions were aversive or not for the young calves, as the types of social interaction early in life (e.g. rejection, aggression) are known to also affect neurological development (e.g. Maestripieri et al., 1997; 1999; 2005). For example, there is evidence that in adulthood offspring from nurturing mothers have increased hippocampal synaptic density and enhanced performance in paradigms that test hippocampal dependent learning and memory (Bredy et al., 2003 a, b; Liu et al., 2000) while the neurons of offspring from less nurturing mothers are more vulnerable to apoptosis (Weaver et al., 2004; 2006).

4.6. Conclusion

Calves are typically reared individually. Preventing access to more complex social environments may leave calves less able to cope with novelty, stressful events and perhaps especially social interactions. Calves housed individually are more reactive to environmental and social novelty when compared to calves housed in pairs. Rearing calves with an older companion appears to strengthen the social bonding within the group and may have additional benefits in terms of the development of social behavior. More research is required on the longer-term effects of the early social environment and the degree that these effects can be reversed via social experience later in life.

Chapter 5: General discussion

In this chapter, I will discuss the contribution that the results of this thesis make to the available knowledge on the effects of early social interactions on how calves respond to environmental and social stressors (reviewed in Chapter 1). I also provide ideas for future research aimed at understanding and improving the quality of life of commercially reared dairy calves.

5.1. Social bonding: buffering effects and possible early regulation of affect

On many dairy farms the calf is separated from the cow soon after birth (e.g. Flower and Weary, 2001). Because calves are often housed individually during the first weeks of life, they are prevented from any opportunity to develop a social bond with either the dam and or other conspecifics. From a nutritional perspective, allowing calves to maintain a social bond with the cow may provide little advantage if calves are fed high volumes of milk. However, preventing calves from developing social bonds with others may influence how well they cope with change throughout their lives (Chapter 1).

In Chapter 2, I demonstrated that the presence of a social companion could modulate the responses of dairy calves to weaning. For example, calves housed individually vocalized three times more at weaning than did calves housed in pairs. Vocalizations are thought to provide an index of the affective state of the animal during separation (e.g. Knutson et al., 2002) and the higher number of vocalizations performed by individually housed calves during weaning may be costly from an energetic standpoint (e.g. Weary and Fraser, 1995). To my knowledge, this result provides the first evidence of social buffering in dairy cattle.

The results reported in Chapter 4 suggest that the social bond among calves housed with an older companion was stronger than that of calves housed in groups of similar age, as the former were more vocal when separated from a pen mate. This is the first study to suggest that social bonds are stronger when calves are housed with an older social companion. One alternative explanation is that older calves are simply more vocal, and the higher responses by the young calves were in response to the high vocal rate by the older partner. More work will be required to distinguish among these explanations. I especially encourage research that tests if social relationships with the older companions were aversive or not for the young calves, as the types of social interaction early in life (e.g. rejection, aggression) are known to also affect neurological development (e.g. Maestripieri et al., 1997; 1999; 2005). For example, there is evidence that in adulthood offspring from nurturing mothers have increased hippocampal synaptic density and enhanced performance in paradigms that test hippocampal dependent learning and memory (Bredy et al., 2003 a, b; Liu et al., 2000) while the neurons of offspring from less nurturing mothers are more vulnerable to apoptosis (Weaver et al., 2004; 2006). Rodent pups that receive reduced maternal attention also exhibit lower maternal care towards their own offspring (Kikusui et al., 2005).

In Chapter 4, I showed that calves housed with an older companion were less reactive towards an unfamiliar calf, kicking less and tending to engage in fewer head-head interactions than did calves housed in groups of similar age. In gregarious species, social instability during the prenatal and postnatal period results in more aggressive and anxious female daughters (Sachser et al., 2011). Because the dams from both treatments were housed under similar conditions during gestation, differences between the treatments are likely due to modulation of behavior during the postnatal period. Studies on the long-term effects of social complexity experienced early in life are now required, especially because they may imply a reduction in the high levels of competition among animals that are commonly observed on modern farms.

Increased locomotory activity by individually housed calves during the environmental novelty test may have been due to a higher motivation to exercise (e.g. Dellmeier, 1985; Jensen, 2001; Sisto and Friend, 2001). Alternatively, higher time spent running may reflect an inability to inhibit behavior in a highly rewarding (but novel) situation. Research on laboratory animals often interprets the higher locomotion in a novel environment and aggression towards an unfamiliar calf (e.g. in Chapter 4 individually housed calves kicked more than did pair housed calves) as 'isolation-syndrome-like behaviors'. These behaviors have been interpreted as a sign of anxiety (e.g. Ago, 2007; Hall et al., 2000) and depression (e.g. Isovich et al., 2001). To date, no research has examined the effects of social isolation on the affective states of dairy calves. I predict that isolation reared animals will show an increased sensitivity to amphetamine and reward-related stimuli that are dopamine-dependent when compared to calves that have been socially housed (Jones et al., 1990).

Nurturing by the dam can influence the regulation of affect in developing animals (e.g. Panksepp, 2005; 2010). I suggest that future studies should aim at understanding these effects in calves. One way to assess affective states in calves might be via a cognitive bias testing (e.g. Mendl et al., 2009). Based on the literature discussed in Chapter 1, I predict that calves housed with the cow would be more likely to respond positively (i.e. optimistic) to ambiguous stimuli, when compared to calves housed alone or calves housed in groups of similar age.

I also encourage future research on the effects of these early social experiences on the animals' resilience in coping with stressful events later in life. Any general reduction in reactivity to stress may also reduce activation of the HPA axis, potentially enhancing immune functioning and thus reducing the risk of disease (Chapter 1).

5.2. Learning during development: asocial and social learning

In nature, the young calf relies on the dam's milk as its main source of nutrients. The development of natural grazing behavior is socially learnt via interactions with the cow and other herd members, helping the calf to become nutritionally independent from the dam's milk. Early social interactions are also important for the behavioral development of dairy calves. However, because dairy calves are typically separated from the cow at an early age and housed individually, this perhaps reduces their ability to adjust to solid feed at weaning and to adjust to new social companions when they are eventually grouped (typically after weaning).

In Chapter 2, I demonstrated that during the first two weeks of life, calves consume little starter, but after this period starter intake gradually increases. Having a social companion of similar age improves starter intake during the pre-weaning period. I attributed this higher intake of starter to social learning via social facilitation, a non-imitative learning process that is stimulated by the mere presence of a conspecific (Zajonc, 1965).

In Chapter 3, I also described the effects of social learning on the development of feeding behavior and on calves' adaptation to weaning, this time comparing calves housed in groups of similar age and calves housed with an older weaned companion. I concluded that being housed with an older companion was beneficial for the young calves, in part because this improved solid feed intake before weaning (and these higher intakes pre-weaning were likely responsible for higher intakes post weaning). The improved familiarity with solids before weaning likely facilitated the transition at weaning, reducing hunger during this period (as evidenced by their reduced persistence at the milk feeder when milk volume was gradually decreased). The higher intake of hay pre-weaning also suggests that hay consumption was important to the calves. This is an important finding, especially because many farmers do not provide calves with access to hay before weaning (for review see Khan et al., 2011).

I attributed these social learning effects to local enhancement, the facilitation of learning that results from drawing attention to a location in which conspecifics are behaving, placing the young calves in a position to learn something that they would not otherwise learn. However, other types of social learning as well as true imitation (i.e. the copying of a novel or otherwise improbable behavior; Thorpe, 1963) could also be influencing calves' behavior. Although social facilitation cannot be directly separated from imitative learning, one can readily control for it by comparing the rate of task acquisition by a group exposed to the target behavior with that of a group exposed to the mere presence of another animal (Zentall, 1996).

According to Tomasello (1990), not all social learning about behavior is imitation and not all social learning about the environment is local enhancement. Imitative learning should be distinguished from mere mimicry (the animals ability to perceive and conceive a correspondence between the behavior of others and its own behavior). Imitation involves some understanding of the demonstrator's goal and purpose (see Call and Tomasello, 2008).

Also, local enhancement (social learning about the environment) should be distinguished from emulation in which the observer learns about the dynamic properties of environmental objects, not merely to attend to their static features via trial and error learning (e.g. during emulation, by watching a tool actually used by a social companion, animals learn about cause and effect relations between tool and goal and incorporate this knowledge into their own attempts at tool use; Tomasello, 1990).

There have been few studies to date that provide insight into mechanisms that young calves use to learn about their asocial (e.g. when locating feed resources) and social environment (e.g. 'understanding' the behavioral strategies of other calves may be beneficial when there is high competition for resources). In Chapter 2, I described that during mixing, calves previously housed individually showed a longer latency to ingest starter than did calves previously housed in pairs. This lower intake of solid feed during mixing was likely due to the individually housed calves having to adjust to both the novel pen and novel social partners. If this was due to the individually housed calves not being able to read the behaviors of the resident calves to locate feed resources is unclear. Perhaps because the pair housed calves were in the presence of a socially bonded companion (e.g. Færevik et al., 2006), they were more comfortable exploring the novel environment. Pair housed calves also have better social skills (e.g. Jensen et al., 1999) when interacting with the resident calves and were thus more likely to benefit from social learning. This interpretation is consistent with the results from Chapter 4, showing that, when in the presence of an unfamiliar calf, individually housed calves spent less time exploring the test arena, defecated more frequently and were more reactive to an unfamiliar companion.

The results of Chapter 3 suggest that dairy calves require more salient cues that signal feed delivery in automatic systems. As previous studies have shown that heifers can be trained by operant conditioning to approach a feed source after receiving an acoustic signal (Wredle et al., 2004), I believe this could be used to signal variation in milk provision during weaning so that it could happen gradually. Moreover, group-reared calves could be trained to individually recognize reward cues, reducing competition for access to the milk, starter and hay feeders.

Social isolation is known to impair cognitive development (as discussed in Chapter 1), so it is also possible that calves housed individually took longer to operate the automatic feeders (to receive the calf starter, the calf needs to operate an electronic switch). To test if individual housing affects cognitive development, I suggest that future experiments be aimed at testing behavioral flexibility between calves housed in pairs and calves housed individually. Isolation rearing appears to cause impairment in many rule-based tasks, including reversal learning (Krech et al., 1962). When isolated rats are tested in food motivated learning tasks, they show no impairment in the acquisition of the task. However, when they are required to adopt a different strategy, they are not able to do so (Morgan, 1973), and persist using the previously rewarded behavior (Morgan et al., 1977). For example, Birrell and Brown (2000) developed a task for rats of digging in scented bowls for food rewards hidden in different substrates. The rats needed to follow one of the cues (e.g. scent) to find the reward. The training then changed, but still using the same type of cue (e.g. a new scent); this is known as intra-dimensional (ID) or affective shifts. In the final stage of training rats were exposed to an extra-dimensional (ED) or attentional shift. The rats now had to learn to follow another cue (e.g. digging medium). Isolated rats show lower performance, especially on the attentional shift task (e.g. Schrijver and Würbel, 2001).

During development, calves also need to learn about the behavior of conspecifics as they are usually group housed after weaning. It has been claimed that mirror neurons in the premotor cortex (Gallese et al., 1996) provide part of the neural basis for social cognition that allows animals to mimic the actions of other, and perhaps also aids in the understanding of their intentions, sensory experiences and emotions via embodied stimulation mechanisms (Gallese et al., 2004; Rizzolati and Craighero, 2004). For example, in work on humans when one perceives others expressing a basic emotion such as disgust, the same brain areas are activated and the other subjectively experiences the same emotion (Wicker et al., 2003). In Chapter 4, I found that synchronous running was higher for pair housed calves when compared to calves housed individually. The pair housed calves also showed more head-head contacts. The higher levels of these mirroring behaviors for the social housed calves suggest that these behaviors take some experience to develop. I suggest that these mirror behaviors are important for the socialization process and possibly social bonding among conspecifics.

5.3. Conclusion

My thesis shows that social rearing can minimize responses to novel events, and that social complexity may allow calves to better regulate affect. Having a more experienced social companion during stressful events, such as weaning, increases voluntary intake of solid feed, perhaps due to improved skills in social learning. It is not clear if the lack of early social rearing leads to long-term changes in behavior. Future research should aim at evaluating the type of learning deficits that result from individual rearing, and whether these and other deficits can be reversed. The results of this thesis support the use of group housing systems for young calves.

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