Current perspectives on the short- and long-term effects of conventional dairy calf raising systems: a comparison with the natural environment

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ABSTRACT: Although the neonatal and infancy period is short, it is well documented that the early neonatal environment is critical for appropriate physical, behavioral, and cognitive development that lasts into adulthood. Dairy calves are commonly removed from the dam shortly after birth and raised in individual housing and fed limited milk allowances (4 to 6 L/d) in commercial farms around the world (conventional raising). Individual housing was developed to promote health status and facilitate individual animal monitoring. However, it is associated with high labor demand, and early life social isolation is associated with cognitive and behavioral abnormalities. Recently, group housing and enhanced milk-feeding programs are being increasingly adopted by farms; these practices more closely resemble the social and nutritional environments in natural or seminatural environments when the calf is raised with the dam. Conventional raising may lead to short- and long-term effects when compared to calves raised with the dam or peers. Short-term effects of conventional raising include impaired social skills when introduced to novel peers, reduced consumption of novel feeds, increased activity in a novel environment, and signs of hunger associated with limited milk intake and poor growth during the preweaning period. Evidence also suggests that the long-term effects of conventional artificial raising systems include behavioral differences, such as lower social submissiveness, increased heart rate and cortisol when presented with a novel environment, and production differences such as milk yield and reproductive performance. However, research on the long-term effects of maternal, social, physical, and nutritional restrictions in early life is still limited and should be encouraged. More research is needed to determine the long-term effects of artificial raising systems (individual, group housing, dam-raised) on future behavior, cognition, performance, and health parameters in dairy calves.

Key words: group housing, heifers, individual housing, isolation, weaning

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INTRODUCTION

Dairy calves are commonly removed from the dam and raised artificially around the world. Calves are housed either individually, in pairs, or in groups, but individual housing is most common. According to dairy producer reported

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surveys, 60% of farms individually raise preweaned calves in western and central Europe (Marcé et al., 2010), 63% in the United States (United States Department of Agriculture [USDA], 2016), 88% in Quebec, Canada (Vasseur et al., 2010), and 70% in Southern Brazil (Hötzel et al., 2014). Individual housing for preweaned dairy calves was designed to limit or prevent direct contact between calves until the calf's immune system develops immunocompetence (Cortese, 2009); calves are especially susceptible to diarrhea in the first 3 wk of age (Cho and Yoon, 2014) and to bovine respiratory disease complex (BRD) within the first 8 wk of age (Griffin et al., 2010). BRD is known to have long-term impacts on fertility and survival to first lactation as a dairy heifer (Stanton et al., 2012); thus, individual housing has been argued as beneficial to minimizing the horizontal spread of disease (McGuirk, 2008). In addition, individual housing is suggested to decrease incidence of undesirable behaviors such as cross-sucking (Van Putten, 1982). However, the immediate maternal separation of calves into individual housing imposes artificial isolation of an inherently social species, involving the physical and social deprivation of contact with other calves or adults. The detrimental effects of such isolation in early life, especially on social development, have been described in a number of species including humans (Bornstein, 1989; Neigh et al., 2009), primates (Parker and Maestripieri, 2011), and cattle (reviewed by Costa et al., 2016b).

In addition to restricting or preventing maternal care and social interactions, young calves raised in artificial systems are typically fed a restricted milk allowance of about 10% of body weight (4 to 6 L/d), which encourages earlier consumption of solid feed and accelerated rumen development allowing for early weaning ages (as reviewed by Khan et al., 2011; Kertz et al., 2017).

The limit-feeding practice is prevalent today in many countries such as United States, Canada, Brazil, and Europe (e.g., Vasseur et al., 2010; Hötzel et al., 2014; Staněk et al., 2014; USDA, 2016), but is known to compromise preweaning growth (Jasper and Weary, 2002; Chapman et al., 2016) and restricted-fed calves are much more likely to experience prolonged hunger (De Paula Vieira et al., 2008; de Passillé et al., 2011). However, calves fed a limited milk diet have been shown to be more efficient at digesting solid feed around weaning than calves fed accelerated diets (Hill et al., 2016). This suggests that calves may have efficiency benefits in a conventional system. However, recent literature suggests calves fed higher planes of nutrition (up to 8.5 L/d) increase feed efficiency when weaning age is raised from 60 to 75 d (Lopreiato et al., 2018) or when gradual weaning or other techniques that encourage solid feed intake are used (de Passillé and Rushen, 2016). In summary, calves have been found to be more feed efficient when limit-fed milk, and will consume more solid feed before weaning, which is associated with rumen development.

These imposed maternal, social, physical, and nutritional restrictions in the early life of a dairy calf (e.g., individually housed calves on limited diets) will be referred to as conventional practices for the purpose of this review. These restrictions on many commercial facilities around the world are a significant departure from how a young calf would be raised in seminatural environments. Under seminatural conditions, calves are raised by the dam in a complex social and physical environment of other conspecifics, milk intake in the first months of age is virtually *ad libitum*, and weaning is dictated by the dam, often between 7 and 14 mo of age (as reviewed by Reinhardt and Reinhardt, 1982). There is growing scientific evidence that conventional practices may have short- and long-term consequences for the welfare, health, and productivity of the growing heifer and adult cow. For instance, individual housing has been shown to result in poor social skills when faced with an unfamiliar calf (De Paula Vieira et al., 2012), increased fearfulness of novel environments and novel feeds (De Paula Vieira et al., 2012; Costa et al., 2014), and learning deficits (Gaillard et al., 2014; Meagher et al., 2017) compared to calves housed with another calf, multiple calves, or their dams. Furthermore, calves that were fed a restricted diet and who also had poor growth during the preweaning period were associated with reduced first-lactation milk production as adults (Heinrichs and Heinrichs, 2011; Soberon et al., 2012). This research suggests that current calf management practices may be raising calves that are quite different from those raised more closely resembling their natural social and nutritional environments. Consequently, these calves as mature adults may fall short of their biological potential, with compromised affective states and opportunity to express their natural behavior during their lives.

The aim of this review was to discuss the short- and long-term consequences of the artificial environment and diet on the dairy calf. First, we describe conventional practices of raising dairy calves in different countries and draw parallels with how calves would be raised in natural or seminatural environments. Finally, we summarize the short- and long-term effects that are associated with dairy calves raised in conventional systems and provide some suggestions for revising the practices of intensive production systems by incorporating our knowledge of the natural environments and the needs of young cattle.

CONVENTIONAL CALF-RAISING PRACTICES COMPARED TO IN NATURE

Maternal Environment

Near to calving, seminaturally housed cattle will seek isolation from the herd (Lidfors et al., 1994). This is similar to dairy cattle housed in confinement, though it is speculated that calving difficulty (Rørvang et al., 2017) and social rank and personality (Rørvang et al., 2018a) influence access to calving in a private area. Cattle's desire to seek social isolation prior to calving has been referred to in a "hider-follower" paradigm (as reviewed by Rørvang et al., 2018b). Indeed, this hypothesis speculates that ungulate species that avoided herd disturbances (hiders) had higher reproductive success than those calving within the herd. Hider species give birth either under cover as seen in mountain sheep (Jewell, 1973) or through increased spatial herd distance as seen in Australian Bush Goats (Allan et al., 1991), or a combination of the two as seen in cattle (Lidfors et al., 1994). After birth, and during the first days of life, the dam hides the vulnerable calf in bushes (Vitale et al., 1986) or tall grasses (Langbein and Raasch, 2000) while she grazes within view of the calf. During this period of isolation, direct dam–calf grooming and frequent vocalizations are exchanged, which strengthen the cow–calf bond (as reviewed by von Keyserlingk and Weary, 2007).

In typical confined systems, however, the opportunity for maternal care is extremely or completely limited. Dairy calves are removed from the dam usually within 24 h of life, but often within hours after birth. As in natural conditions, grooming and vocalization exchanges occur between cow–calf pairs and are thought to strengthen the bond (Jensen, 2011). For this reason, it is often recommended to separate the calf as soon as possible to minimize imprinting, and thus limit stress associated with separation (Flower and Weary, 2001; Stěhulová et al., 2008). Indeed, research shows that when calves are left with the dam for 4 to 7 d, compared to just 1 d, calves vocalized more often, sniffed the air more often, and stood longer, suggesting more stress after the removal process (Stěhulová et al., 2008). When calves are separated at later ages, separation stress appears to be largely associated with nutritional dependence on the cow. For instance, calves that were able to suckle from their dam at night and separated at 6 wk of age showed reduced locomotor play and increased vocalizations when in a novel arena compared to calves that were separated at birth and fed 12 L/d of milk from an automated milk feeder (Rushen et al., 2016). Vocalizations are often expressed as an indicator of hunger when milk is removed (De Paula Vieira et al., 2008), so this behavior could be related to milk restriction at the time of separation from the dam. This was shown in a study where calves that drank more from the milk feeder after separation had fewer vocalizations and more play behaviors (Johnsen et al., 2018). In addition, calves appear to show less abnormal signs of nonnutritive oral behaviors such as cross-sucking and tongue rolling when raised with the dam compared to calves raised on high milk allowances from an automated feeder (Fröberg and Lidfors, 2009). Calves also showed a pessimistic bias in a cognitive bias test after removal from the dam, suggesting they experience a low mood in response to separation (Daros et al., 2014). This evidence suggests that calves that are nutritionally dependent on the dam exhibit greater signs of hunger during separation, abnormal nonnutritive oral behaviors and negative judgment bias.

Social Environment

After several days of isolation with the dam, the young calf returns to the herd and becomes integrated with other young calves and adults of the group in natural settings (Bouissou et al., 2001). From about 2 wk of age, calves begin to distance themselves more from the dam and interact closely in small groups of calves (Vitale et al., 1986). This transition period from maternal care to greater independence from the dam is an important period of learning for the young calf. Early contact with other conspecifics allows calves to benefit from social learning, where the dam, other adults, and dominant young peers serve as social models. For instance, young ruminants will develop feeding patterns that resemble those of social models in the herd, selecting and avoiding food sources appropriately (Provenza and Balph, 1987; Provenza et al., 2003). Calves will also learn from others about the social hierarchy of the herd; in feral Chillingham cattle, dominant individuals only use threats to maintain stability within the herd and dominant bulls will rule the herd by 2 yr of age (Reinhardt et al., 1986), and lower ranking cattle maintain friendships through frontal head play (Reinhardt et al., 1986; Vitale et al., 1986). With freedom of movement under natural or seminatural conditions, calves will often be seen engaging in play behaviors, especially social play accompanied by play fighting, galloping, bucking, and kicking (Reinhardt and Reinhardt, 1982). Play behaviors are thought to be an important source of locomotor and emotional development in mammals, which prepares the individual for coping with unexpected events and loss of control in the future (Spinka et al., 2001).

In contrast, in commercial systems that separate the calf from the dam, calves are most often placed in individual housing until weaning (e.g., Canada (Vasseur et al., 2010), Brazil (Hötzel et al., 2014), United States (USDA, 2016)). Typically, individual housing offers visual and auditory contact with peers, but tactile contact is often prevented to limit transmission of pathogens (McGuirk, 2008). The fact, the level of contact between animals affects behavioral responses to a novel social situation; calves raised individually with only bar contact to neighbors spent less time interacting (sniffing, liking) with a novel peer and displayed more frontal pushing than calves raised with a peer (Duve and Jensen, 2011). Calves are also highly motivated for social contact; a study showed that calves will work hard to gain full body contact with another calf compared to just head–head contact through a barrier (Holm et al., 2002). Consequently, the prevention of social contact severely limits the use of social models in learning appropriate feeding and social behaviors in a group; for instance, calves that were housed in pairs had increased solid feed intake (Costa et al., 2015) and were quicker to engage in social contact and social play with unfamiliar calves upon mixing after weaning (De Paula Vieira et al., 2012). In addition, individual stalls are generally limited in size, which will also restrict the expression of behaviors typical of young calves such as locomotor play behavior (Jensen, 1999). Indeed, when calves housed in smaller individual stalls were provided temporary access to a large arena, they showed more play behavior, kicking, and running than calves who were housed in larger individual stalls (Rushen and de Passillé, 2014). This "rebound" in behavior after a prolonged period of prevention suggests that the expression of play behavior is internally motivated, and is especially pronounced when individually housed for longer periods of time (Jensen, 1999). Together this evidence suggests that calves raised conventionally have limited social and exercise opportunities when compared to the seminatural environments.

Nutritional Environment

In natural and seminatural environments, the diet of the young calf is at first entirely dependent upon milk from the dam. The calf suckles 8 to 12 times daily, spending approximately 10 min suckling at each visit, and these suckling visits to the dam decrease with age (Lidfors and Jensen, 1988). These meal patterns are similar in confined systems that maintain suckling cow–calf pairs (Lidfors et al., 2010). Daily milk consumption of dairy calves left with the dam reaches around 8 to 13 L/d (de Passillé and Rushen, 2006). Calves, like other ungulates, largely depend on milk consumption for nutrition during the first 3 wk of life and are hormonally primed for gluconeogenesis and glycolysis to digest milk-based nutrition at this time (Hammon et al., 2012). To appropriately digest milk, an esophageal groove is stimulated to shunt milk directly to the abomasum when suckling occurs (Hegland et al., 1957). This process is thought to protect the rumen from disturbance so that it can establish microflora essential for digesting forages. The complex environment of natural or seminaturally raised calves likely plays a role in sequential development of the ruminal microflora, which becomes established within a just a few days of age (Bryant and Small, 1960); in particular, the dam is hypothesized to be the first source of microbiota inoculation for the calf's rumen (Becker and Hsiung, 1929). Therefore, aside from nutritional dependence, the calf may also physiologically depend on the dam for faunation of microbiota in the rumen.

Faunation within the rumen is the first sign of independence of the neonatal calf. Soon after, by about 3 wk of age, calves will begin to graze and ruminate alongside their dam and peers (Reinhardt and Reinhardt, 1982; Vitale et al., 1986), but will not completely wean from milk until between 7 and 14 mo of age (Reinhardt and Reinhardt, 1982). The phenomenon of social facilitation stimulates the calf to join others who are consuming or handling feeds (Galef, 1988), and social learning occurs when calves mimic grazing behavior through observation of others (Galef and Laland, 2005). Cattle graze gramineous plants including grasses, lichens, herbs, and leaves of woody trees; however, cattle select feedstuffs based on availability and so will move to different areas based on grass access, and will browse during dry seasons (Holechek et al., 1982). Given this diverse diet, it is important that young naïve grazers are able to quickly learn which foods are appropriate to consume. Greater feeding efficiency of young calves is achieved through socially acquired acquisition of feeding habits rather than trial and error (Veissier et al., 1998). Accordingly, social learning theory indicates that the most effective social models are the dam and dominant peers (Bandura, 1977). Information may be transferred from experienced to inexperienced foragers within a herd (Mirza and Provenza, 1994). Social learning is thus important in reducing food neophobia, the fear of novel foods, which prevents consumption of nonnutritive and toxic feedstuffs (Galef and Laland, 2005), and social learning is a phenomenon also described in confined raised heifers (Costa et al., 2016b).

In natural and seminatural conditions, it is clear that appropriate development of grazing behavior relies upon learning from social models about where and what to eat. In addition, conventionally raised calves do not experience diet diversity. In grazing systems, rotational forages and multispecies pastures promote diet changes and provide different nutrients to the heifer (Gregorini et al., 2017). It is also apparent that when given a choice of novel feeds, there are individual preferences related to different personalities, where some heifers prefer no novelty and others prefer to spend half of their time with a novel feedstuff or with a novel flavor (Meagher et al., 2017). This evidence suggests that a complex diet is natural for cattle, and some are motivated to experience diet diversity.

Much of the feeding and weaning practices employed in conventional calf raising are in contrast to the natural behavior of the calf. Milk (either whole milk or milk replacer) is often fed by nipple bottle or bucket in 2 or 3 feedings, typically totaling 4 to 6 L daily (USDA, 2016). Feeding to 10% of body weight is approximately half of what a calf would typically drink when raised with its dam, leading to behaviors indicative of hunger such as repeated visits to the milk feeder (De Paula Vieira et al., 2008). This practice of restricted milk feeding is argued to promote earlier consumption of solid feed and rumen development, which facilitates weaning at young ages (often before 2 mo of age; USDA, 2016; as reviewed by Kertz et al., 2017). However, there is growing interest in feeding higher amounts of milk to achieve increased weight gains before weaning; with appropriate gradual weaning methods to encourage early solid feed intake, such as an initial early milk reduction (e.g., (Rosenberger et al., 2017) or weaning calves based on their ability to consume solid feed (de Passillé and Rushen, 2016), calves can successfully be raised on a higher plane of nutrition. Best practices such as feeding high amounts of milk with a nipple bottle have been cited by producers as requiring added labor and thus added cost to the operation (Medrano-Galarza et al., 2017); this is likely why milk feeding remains restricted in many countries. Consequently, bucket feeding is often used because they are fast and easy to clean (Medrano-Galarza et al., 2017); however, this practice is associated with higher nonnutritive oral behaviors such as sucking on fixtures (Horvath and Miller-Cushon, 2017), likely due to the calf's inability to satisfy its natural motivation to suckle from a teat (Jensen, 2003). Costa et al. (2016a) suggested that such abnormal oral behaviors can be rectified when limited milk allowances, bucket feeding, and abrupt weaning methods are corrected.

Summary

In summary, under natural or seminatural conditions, calves remain hidden for the first few days of life, but join the herd thereafter and rely on the dam until weaning around 7 mo. By a few weeks of age, and as the calf grows, she forms social bonds with others and learns a complex array of feeds to consume and how to graze through social facilitation and learning from her peers and dam. Calves raised on conventional methods, on the other hand, are housed in isolation in a physically limited space until weaning around 2 mo of age. In these 2 mo, calves are offered a uniform diet, and approximately fed half of their ad libitum milk intake. It follows that such contrasting practices to natural settings would affect the behavior, performance, and health of calves in the short and long term. This will be the focus of the remainder of this review.

SHORT- AND LONG-TERM EFFECTS OF CONVENTIONAL RAISING UNDER RESTRICTED ENVIRONMENTAL CONDITIONS

Given the differences in maternal, social, physical, and nutritional environments of the young dairy calf during conventional raising when compared to natural systems, it would seem important to explore the potential effects of such environmental restrictions on the calf in the short- and long-term. To date, few studies have directly compared outcomes associated with raising calves in natural or seminatural environments (such as with the dam, other adults, and other calves). However, there is growing evidence suggestive of potential detrimental effects of artificial raising under restricted compared to less restrictive environments on later behavior, performance, and health of the growing heifer (in the short term) and the adult dairy cow (in the long term).

Restricted Maternal Environment

Several studies have investigated the potential impact of cow–calf separation on calf weight gains, behavior, and sleep patterns. Calves that remained with the dam for 2 wk had improved weight gains, which were maintained for at least 2 wk after separation (Flower and Weary, 2001), but there is less consensus when calves remained with the dam for shorter durations of 4 d (Weary and Chua, 2000; Valníčková et al., 2015). One study found improved weight gains in calves that were housed with the dam but were prevented from suckling compared to calves with no contact with the dam (Krohn et al., 1999), suggesting that there may be some benefits to early housing with the dam apart from nutritional dependence. A short duration with the dam before separation at 4 d of age did, however, result in increased frequency of social play in the weeks after separation compared to just 1 d with the dam (Stěhulová et al., 2008), and differences in spontaneous play were seen at 12 wk of age (Valníčková et al., 2015). Others suggest that the stress of separation is reduced (e.g., fewer vocalizations) when calves are raised with the dam but are not nutritionally dependent on her (Johnsen et al., 2018), and when providing fence-line separation (Johnsen et al., 2015). These factors suggest dams can remain with dairy calves (as reviewed by Johnsen et al., 2016), but that the stress calves experience at removal may be reduced if calves receive milk from other sources.

Calves raised with their dams also show some indication of reduced fear of novel situations, such as isolation in a novel environment (Wagner et al., 2015), exposure to novel food (Costa et al., 2014), and more appropriate social behavior when introduced to an unfamiliar calf (Wagner et al., 2013) including less physiological responses when confronted with an unfamiliar peer (Buchli et al., 2017). These effects were seen several weeks (Costa et al., 2014), several months (Buchli et al., 2017), and 2 yr (Wagner et al., 2015) after separation. However, other studies have shown no difference in behaviors when presented with a novel object (Buchli et al., 2017) or novel environment (Wagner et al., 2012). Social behavior at the time heifers integrated with the milking herd at 2 yr of age was also affected by level of maternal care; Wagner et al. (2012) found that calves provided access to the dam for 12 wk demonstrated more submissive postures than calves separated at birth, perhaps because these calves were able to learn the social hierarchy of the herd and appropriate social behaviors from an early age. Sleep patterns may also be impacted; Hänninen et al. (2008) found that calves that were separated from their dam had shorter and more fragmented sleeping bouts compared to calves that remained with their dams (Hänninen et al., 2008); sleep was only measured during the first few days of life, so it remains to be seen if such patterns persist after separation.

Evidence from studies in rodents that were separated immediately at birth showed significant detrimental effects on the functioning of the prefrontal and mesolimbic regions of the brain, and thus long-term brain metabolism (Spivey et al., 2011), which in turn affected decision-making behavioral restraint, and behavioral inhibition of artificially raised mice (Lovic et al., 2011). This evidence may explain the finding that dam-raised calves performed much better during a reversal-learning task, requiring the calf to relearn a previously acquired discrimination task, while the majority of separated and individually housed calves were never able to successfully relearn the task (Meagher et al., 2017). However, pair-raised calves also reverse learn better and habituated quicker to a repeated novel object test when compared to calves raised individually (Gaillard et al., 2014). This suggests social structure likely plays a component in decision-making and behavioral flexibility in dairy cattle. Adaptive learning is important for dairy cattle, given the numerous environmental changes in the production system, such as changes in diet, regrouping, stocking density at the feed bunk or lying stalls, and introduction to the milking parlor. It is known that individuals differ greatly in how they cope with these changes (e.g., reviewed by Neave et al., 2018); it is possible that behavioral flexibility may be compromised due to a lack of early maternal care, but this requires further investigation.

Further indication of brain functioning modifications due to maternal separation comes from evidence of altered neural maternal activation when mice are separated from the dam immediately rather than at typical weaning age (Foscolo et al., 2017). These alterations were evident even when mice were temporarily separated from the dam for 4.5 h per day (Aguggia et al., 2013). This suggests that mice who do not receive appropriate maternal care have immediate changes to the brain that affect mothering ability later in life. Indeed, mice that were separated early from their dam provided poor maternal care to their young as adults; interestingly this effect could be mediated by human stroking to mimic maternal grooming after separation (Lovic et al., 2011). Similarly, calves with a foster dam showed more pronounced maternal behavior as adults compared to with no dam (Le Neindre (1989a, 1989b), suggesting that lack of maternal care may have carryover effects to provision of maternal care as adult cows.

Temporarily separated mice also showed changes in gene expression impacting the oxytocinergic system (Aguggia et al., 2013); oxytocin production is important for the dairy cow as it plays roles in social communication and attachment (Telgmann et al., 2003), maternal care including milk letdown (Negrão and Marnet, 2002), reproduction (Fuchs et al., 1992), and coping with novel environmental situations (Sutherland and Tops, 2014). A consequence of a disrupted oxytocinergic system immediately after birth is insecure attachment (Notzon et al., 2016), where the young are dependent upon the mother and are unable to explore novel peers or situations without the mother's presence (Bowlby, 1984). In racehorses, separation from the dam for as little as an hour leads to permanent insecure attachment including less play and increased social aggressiveness regardless of age (Henry et al., 2009). In domesticated species, oxytocin may be involved in the expression of social behavior and a potential indicator of positive emotional states (Rault et al., 2017); thus, there is a need to explore the possible permanent disruption of the oxytocinergic system due to maternal separation in cattle.

In mice, early maternal separation alters the immune response to host microbiota (Riba et al., 2014), suggesting similar effects may be seen during cow–calf separation but there are limited reports of health associated with calves kept with their dam. One study reported calves never incurred diarrhea or BRD over the 2-yr period (Grøndahl et al., 2007), but interpretations are limited as there was no control to disentangle excellent farm management from a real effect of cow–calf raising. Another study showed that calf diarrhea prevalence was higher in calves raised with the dam compared to calves raised in groups with an automated feeder (Roth et al., 2009). Future research should determine if the immune response in calves is compromised as a result of early cow–calf separation.

Taken together, this evidence indicates that when calves are separated immediately at or soon after birth, there are negative effects on weight gain, play and sleeping patterns, and fearfulness and behavioral flexibility when faced with novel situations. These effects may be explained by research in rodents suggesting that maternal separation can cause lasting effects on brain functioning and development of the oxytocinergic system regulating behavioral inhibition, decision-making, and appropriate social behaviors. The majority of research to date has focused on the short-term effects of maternal separation, which calls for further research to investigate the potential long-term implications. Future research should identify if the impact of cow–calf separation is due to nutritional dependency, social contact, or both, and how each of these factors independently contribute to longer term social and cognitive impairments at maturity. It would also be of interest to determine if calves are permanently affected by isolation in the preweaning period, and if calves raised in groups perform and behave similarly to calves in dam-raised conditions; for instance, calves with maternal contact may be better able to cope with changes in their environment as a result of stressful management practices such as diet changes, regrouping, and introduction to the milking parlor. Incorporating longer-term dam-rearing of calves in dairy production systems is already taking place around the world (Johnsen et al., 2016). Further research is needed to determine the feasibility of incorporating cow–calf pairs in dairy farming, and the benefits of doing so.

Restricted Social and Physical Environment

The removal of the calf from the dam involves both maternal separation and social separation from the herd that current research in dairy cattle has yet to disentangle. Consequently, much of the evidence associated with cow–calf separation that we have presented thus far involves a component of both maternal and social attachment; it is possible that some of these negative effects may be minimized in artificially raised calves if they are housed with other social companions. For example, Meagher et al. (2017) found that pair-housed calves performed similarly to dam-raised calves when learning a reversal task, and calves in these housing systems learned much quicker than individually raised calves. The effects of individual compared to pair or group housing of calves on behavior, cognition, and performance were recently reviewed in detail by Costa et al. (2016b). We highlight key findings from this review, complemented with the most recent evidence since the review.

The vast majority of studies comparing individual with social housing (either paired or grouped) show some type of improvement associated with social housing, with some studies showing neutral effects, and notably no study reporting negative effects (see Costa et al., 2016b); this suggests that even a minimum level of social companionship may alleviate some of the detrimental effects of isolation. Pair- or group-housed calves have been shown to be less fearful or reactive when faced with novel situations, such as a novel environment (De Paula Vieira et al., 2012), new feeding equipment (De Paula Vieira et al., 2010), unfamiliar calves (Jensen and Larsen, 2014), unfamiliar feeds (Costa et al., 2014), and during restraint (Duve et al., 2012). Specifically, greater reactivity of conventional calves to these novel factors includes greater latency to approach, longer contact with novel peers, and increased activity when faced with a novel environment. At the time of mixing with other calves after weaning, those that were previously socially housed were also more socially competent, engaging in less aggressive behavior, and achieved higher social ranks than individually housed calves (Veissier et al., 1994). These effects may be related to poor behavioral flexibility of individually housed calves in response to novelty; indeed, individually housed calves showed impaired cognitive performance on a reversal-learning task, reflecting impaired flexibility (Gaillard et al., 2014).

Several recent studies support previous findings that pair-housed calves have improved feed intake and growth over individually housed calves, especially when paired as soon as possible after birth (e.g., Costa et al., 2015; Jensen et al., 2015). At a commercial facility, calves raised in paired hutches ate twice as much of a novel food and ate more solid feed, but had similar weight gains to those raised in a single hutch (Whalin et al., 2018). However, Jersey calves that were paired in a single hutch with an outdoor run did show improved growth (Pempek et al., 2016). Pair-housed calves also showed greater feeding time during weaning (Overvest et al., 2018) and fewer vocalizations in response to milk removal after weaning (De Paula Vieira et al., 2010; Bolt et al., 2017), and were quicker to resume feeding after mixing into a larger group pen (De Paula Vieira et al., 2010). These positive effects of providing a social partner are hypothesized to be due to the benefits of social facilitation encouraging early and greater feed intake, and social buffering of the negative impact of weaning.

Beyond the social benefits of pair housing, this practice is typically accompanied by an increase in physical space, which may explain the reduced lying time (i.e., more alert and active) during weaning in pair housed compared to individually housed calves (Chua et al., 2002; Overvest et al., 2018). Other studies found no differences in lying time over 5 wk during winter and summer months but found that paired calves offered two outdoor hutches chose to lie together in a single hutch (Wormsbecher et al., 2017). Pair housed and individually housed calves in this study were reported to make similar use of the indoor and outdoor space (Wormsbecher et al., 2017).

Together this evidence indicates that social housing for calves following maternal separation offers behavioral, cognitive, and performance benefits. However, these studies only followed calves until at most a few weeks after weaning; no study to our knowledge has investigated the longer term effects of early social housing into adulthood. We predict that the improved growth, reduced fear when faced with novel situations, and behavioral flexibility in the first weeks of life will have a lasting impact on the growing heifer and adult cow. Future research should determine the effects of various levels of social contact during early life (e.g., dam with calf and cows, group housing with only peers, or individual housing) on later social and cognitive skills, especially in relation to adaptation to novel situations. Moving forward, the emphasis in research should focus on the long-term benefits of peer social housing and its effects throughout the life of cattle.

Restricted Diet

There is growing evidence of the short- and long-term impacts of an early restricted diet on performance, including growth, production, and reproduction. Limit-feeding calves (4 to 6 L/d of milk) are known to result in poor weight gains before weaning compared to calves fed a higher plane of nutrition (e.g., Khan et al., 2011; Rosenberger et al., 2017), but authors argue that limit feeding milk is more feed efficient due to compensatory postweaning growth by 4 mo of age (Dennis et al., 2018). In a recent meta-analysis, Gelsinger et al. (2016) found that when preweaning average daily gain was between 300 and 500 g/d (typical for calves fed less than 6 L/d), there was minimal effects on future first-lactation milk yield, but increasing effects were found when average daily gain increased from 500 to 900 g/d (typical for calves fed up to 12 L/d). Similar reports with large sample sizes also found that preweaning growth is an important consideration for future milk yield (Soberon et al., 2012; Van De Stroet et al., 2016); for instance, for every 100 g increase in preweaning average daily gain, heifers produced about 110 kg more milk during their first lactation (Soberon et al., 2012). Furthermore, a study that followed calves from birth through multiple lactations found that dry matter intake (DMI) at weaning positively affected first lactation milk production (Heinrichs and Heinrichs, 2011): every 1-kg increase in DMI translated to an additional 290 kg of milk yield in first lactation. One reason for higher lactation yields early in life could be related to parenchymal growth in the mammary tissue, which would result in a larger tissue mass capable of producing milk. Calves fed an accelerated milk program (28% crude protein 25% fat vs. 20% crude protein 20% fat) had 5-fold higher parenchymal mammary development when given exogenous estrogen (Geiger et al., 2016). However, others found that feeding higher amounts of milk or targeting higher growth offered no advantage in first lactation milk yield (Raeth-Knight et al., 2009; Kiezebrink et al., 2015), or studies lacked power to detect differences (Davis Rincker et al., 2011; Korst et al., 2017). These studies suggest that differences in first lactation yields are multifaceted, but evidence to date suggests that even small improvements in early growth and increased weaning DMI may be beneficial much later in life, and potential long-term outcomes may offset the investment of feeding a higher plane of nutrition to calves (Davis Rincker et al., 2011).

Other benefits of feeding a higher plane of nutrition may include improved reproductive outcomes. Davis Rincker et al. (2011) found that calves fed a higher plane of nutrition reached puberty earlier and at lower weights, which translated to earlier conception and calving. There is also some limited evidence of positive effects of enhanced early feeding on fertility at first artificial insemination and age at pregnancy (Terré et al., 2009). Similar findings were found in bull calves that reached puberty earlier and with larger testicles (Dance et al., 2015). These studies, among others (e.g., Raeth-Knight et al., 2009), suggest that nutritional modulation during early life can also have effects on reproductive development.

The feeding and weaning practices of artificially raised calves affect rumen development and microflora colonization. Separation from the dam followed by artificial milk feeding is thought to severely limit the early establishment of a complex microbiota environment, which is required for the development of important ciliate protozoa (Newbold et al., 2015; Yáñez-Ruiz et al., 2015). When calves transition from milk onto a solid feed diet, there is a significant shift in ruminal development and diversity of microbiota. Recent studies showed that calves weaned at earlier ages (6 compared to 8 wk of age) had more rapid and severe changes in the gastrointestinal microbiome at the time of weaning (Meale et al., 2017), and reduced microbial fermentation indicating premature rumen development (Eckert et al., 2015) when weaned early. This is thought to be related to the rapid increase in grain consumption when milk is removed at an early age (Meale et al., 2017). In addition, feeding restricted amounts of milk (<6 L/d) is known to affect the size of the rumen and rumen papillae development (Khan et al., 2011). However, Steele et al. (2014) noted that increased size does not necessarily mean increased surface area to improve efficiency. Overall, feeding and weaning practices that are more similar to the natural environment of the calf suggest that traditional practices (i.e., limited milk allowances, early weaning ages) may have important developmental and functional consequences for the rumen of the calf. However, there are no studies to date investigating how alterations to rumen morphology, physiology, or microbiome in early life affect the functioning and efficiency of the adult ruminant.

One of the most commonly observed abnormal behaviors associated with artificial raising of calves is cross-sucking. Cross-sucking occurs when a calf sucks on a body part of another calf; this behavior is often thought to be a problem related to social housing but is in fact related to restricted milk and teat access. For example, restricting milk in dairy calves to less than 6 L/d reduces the time to finish the milk meal; calves are known to redirect oral behavior in the form of cross-sucking peers (de Passillé et al., 1997; Jung and Lidfors, 2001). When calves are fed high milk allowances from a teat rather than a bucket, cross-sucking is significantly reduced because calves are able to satisfy their natural motivation to suckle (De Passillé et al., 2010). A longer duration of access to an artificial teat was negatively correlated with cross-sucking events in Simmental cattle (Größbacher et al., 2018), whereas milk flow rate and portion size had no effect on cross-sucking (Nielsen et al., 2018). Cross-sucking behavior as a heifer is known to carry into adulthood (Keil et al., 2001), so adjustments to milk-feeding practices to offer increased volume and teat access is especially important to correct this behavior from an early age.

Feeding high milk allowances may also improve health and immune capacity during and after the milk-feeding period. For example, calves fed a higher plane of nutrition had improved immune responses to an oral *Cryptosporidium parvum* challenge (Ollivett et al., 2012) and higher postweaning innate immune response in Jersey calves (Ballou, 2012). However, another study that fed calves to target low vs. high growth rates found no differences in immune capability (Foote et al., 2007). This evidence suggests that plane of nutrition may play a role in immune development in calves. However, regardless of the mechanism of improved immunity, future research is needed to disentangle the interaction between environmental factors and nutritional level on immunity of dairy calves.

Overall, there is growing information that suggests that a restricted milk diet in early life may have important consequences for calves. Conventional feeding practices of calves appear to affect growth, rumen development, and health in the short term, and milk production and reproductive ability in the long term, although there is disagreement in the literature regarding these effects. Future research should investigate possible additional long-term effects of early nutritional restriction such as impaired feeding behavior, abnormal rumen functioning or efficiency, or increased susceptibility to disease. High milk allowances in combination with a true gradual weaning program, such as a step-down weaning, has multiple short- and long-term benefits for the animal. We encourage incorporation of these practices on farms, especially those that use automated feeding systems; while there may be a potential increase in labor for farms that feed manually, we suggest the short- and long-term benefits may outweigh this initial economic cost.

CONCLUSION

In conclusion, calves raised in conventional systems experience limited social and nutritional availability and diversity in comparison to natural or seminatural environments. Evidence to date suggests that these limitations have consequences in the short and long term. Short-term effects of conventional systems include increased reactivity toward novel social companions, feedstuffs, and environments, and signs of hunger associated with limited milk intake and poor growth during the preweaning period. Some long-term effects of conventional raising include lower social submissiveness, increased reactivity toward a novel environment, and production differences such as milk yield and reproductive performance. We encourage future research to examine potential long-term effects of complex social environments and nutritional abundance in early life on future behavioral responses to stressful management changes involving novelty, social and feeding behavior development, rumen functionality, and health.

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LITERATURE CITED

Aguggia, J.P., M.M. Suárez, and M.A. Rivarola. 2013. Early maternal separation: neurobehavioral consequences in mother rats. Behav. Brain Res. 248:25–31. doi:10.1016/j.bbr.2013.03.040

Allan, C.J., G.N. Hinch, and P.J. Holst. 1991. Behaviour of parturient australian bush goats. II. Spatial relationships and activity patterns. Appl. Anim. Behav. Sci. 32:65–74. doi:10.1016/S0168-1591(05)80164–9

Ballou, M.A. 2012. Immune responses of Holstein and Jersey calves during the preweaning and immediate postweaned periods when fed varying planes of milk replacer. J. Dairy Sci. 95:7319–7330. doi:10.3168/jds.2012-5970

Bandura, A. 1977. Social learning theory. Englewood Cliffs (NJ): Prentice Hall.

Becker, E.R., and T. Hsiung. 1929. The method by which ruminants acquire their fauna of infusoria, and remarks concerning experiments on the host-specificity of these protozoa. Proc Natl Acad Sci USA. 15:684–690.

Bolt, S.L., N.K. Boyland, D.T. Mlynski, R. James, and D.P. Croft. 2017. Pair housing of dairy calves and age at pairing: effects on weaning stress, health, production and social networks. PLos One. 12:e0166926. doi:10.1371/journal.pone.0166926

Bornstein, M.H. 1989. Sensitive periods in development: structural characteristics and causal interpretations. Psychol. Bull. 105:179–197. doi:10.1037/0033-2909.105.2.179

Bouissou, M., A. Boissy, P. Le Neindre, and I. Veissier. 2001. The social behaviour of cattle. In: Keeling, J. and H. Gonyou, editors. Social behaviour in farm, animals. New York (NY): CABI Publishing.

Bowlby, J. 1984. Violence in the family as a disorder of the attachment and caregiving systems. Am. J. Psychoanal. 44:9–27, 29. doi:10.1007/BF01255416

Bryant, M.P., and N. Small. 1960. Observations on the ruminal microorganisms of isolated and inoculated calves. J. Dairy Sci. 43:654–667. doi:10.3168/jds.S0022-0302(60)90216-2

Buchli, C., A. Raselli, R. Bruckmaier, and E. Hillmann. 2017. Contact with cows during the young age increases social competence and lowers the cardiac stress reaction in dairy calves. Appl. Anim. Behav. Sci. 187:1–7. doi:10.1016/J.APPLANIM.2016.12.002

Chapman, C.E., P.S. Erickson, J.D. Quigley, T.M. Hill, H.G. Bateman, F.X. Suarez-Mena, and R.L. Schlotterbeck. 2016. Effect of milk replacer program on calf performance and digestion of nutrients with age of the dairy calf. J. Dairy Sci. 99:2740–2747. doi:10.3168/JDS.2015–10372

Cho, Y.I., and K.J. Yoon. 2014. An overview of calf diarrhea - infectious etiology, diagnosis, and intervention. J. Vet. Sci. 15(1):1–17. doi:10.4142/jvs.2014.15.1.1

Chua, B., E. Coenen, D.J. van, and D.M. Weary. 2002. Effects of pair versus individual housing on the behavior and performance of dairy calves. J. Dairy Sci. 85:360–364. doi:10.3168/JDS.S0022-0302(02)74082–4

Cortese, V.S. 2009. Neonatal immunology. Vet. Clin. North Am. Food Anim. Pract. 25:221–227. doi:10.1016/j.cvfa.2008.10.003

Costa, J.H.C., W.G. Costa, D.M. Weary, L.C.P. Machado Filho, and M.A.G. Von Keyserlingk. 2016a. Dairy heifers benefit from the presence of an experienced companion when learning how to graze. J. Dairy Sci. 99:562–568. doi:10.3168/jds.2015–9387

Costa, J.H., R.R. Daros, M.A. von Keyserlingk, and D.M. Weary. 2014. Complex social housing reduces food neophobia in dairy calves. J. Dairy Sci. 97:7804–7810. doi:10.3168/jds.2014-8392

Costa, J.H.C., M.A.G. von Keyserlingk, and D.M. Weary. 2016b. Invited review: effects of group housing of dairy calves on behavior, cognition, performance, and health. J. Dairy Sci. 99:2453–2467. doi:10.3168/jds.2015-10144

Costa, J.H., R.K. Meagher, M.A. von Keyserlingk, and D.M. Weary. 2015. Early pair housing increases solid feed intake and weight gains in dairy calves. J. Dairy Sci. 98:6381–6386. doi:10.3168/jds.2015-9395

Dance, A., J. Thundathil, R. Wilde, P. Blondin, and J. Kastelic. 2015. Enhanced early-life nutrition promotes hormone production and reproductive development in Holstein bulls. J. Dairy Sci. 98:987–998. doi:10.3168/jds.2014-8564

Daros, R.R., J.H. Costa, M.A. von Keyserlingk, M.J. Hötzel, and D.M. Weary. 2014. Separation from the dam causes negative judgement bias in dairy calves. PLos One 9:e98429. doi:10.1371/journal.pone.0098429

Davis Rincker, L.E., M.J. Vandehaar, C.A. Wolf, J.S. Liesman, L.T. Chapin, and M.S. Weber Nielsen. 2011. Effect of intensified feeding of heifer calves on growth, pubertal age, calving age, milk yield, and economics. J. Dairy Sci. 94:3554–3567. doi:10.3168/jds.2010-3923

De Passillé, A.M., T.F. Borderas, and J. Rushen. 2011. Weaning age of calves fed a high milk allowance by automated feeders: effects on feed, water, and energy intake, behavioral signs of hunger, and weight gains. J. Dairy Sci. 94:1401–1408. doi:10.3168/jds.2010-3441

De Passillé, A.M.B., and J. Rushen. 2006. Calves' behaviour during nursing is affected by feeding motivation and milk availability. Appl. Anim. Behav. Sci. 101:264–275. doi:10.1016/j.applanim.2006.02.007

De Passillé, A.M., and J. Rushen. 2016. Using automated feeders to wean calves fed large amounts of milk according to their ability to eat solid feed. J. Dairy Sci. 99:3578–3583. doi:10.3168/jds.2015–10259

De Passillé, A.M., J. Rushen, and M. Janzen. 1997. Some aspects of milk that elicit non-nutritive sucking in the calf. Appl. Anim. Behav. Sci. 53:167–173. doi:10.1016/S0168-1591(96)01161-6

De Passillé, A.M., B. Sweeney, and J. Rushen. 2010. Cross-sucking and gradual weaning of dairy calves. Appl. Anim. Behav. Sci. 124:11–15. doi:10.1016/J.APPLANIM.2010.01.007

De Paula Vieira, A., V. Guesdon, A.M. de Passillé, M.A.G. von Keyserlingk, and D. M. Weary. 2008. Behavioural indicators of hunger in dairy calves. Appl. Anim. Behav. Sci. 109:180–189. doi:10.1016/j.applanim.2007.03.006

De Paula Vieira, A., M.A. von Keyserlingk, and D.M. Weary. 2010. Effects of pair versus single housing on performance and behavior of dairy calves before and after weaning from milk. J. Dairy Sci. 93:3079–3085. doi:10.3168/jds.2009-2516

De Paula Vieira, A., A.M. de Passillé, and D.M. Weary. 2012. Effects of the early social environment on behavioral responses of dairy calves to novel events. J. Dairy Sci. 95:5149–5155. doi:10.3168/jds.2011-5073

Dennis, T.S., F.X. Suarez-Mena, T.M. Hill, J.D. Quigley, R.L. Schlotterbeck, R.N. Klopp, G.J. Lascano, and L. Hulbert. 2018. Effects of gradual and later weaning ages when feeding high milk replacer rates on growth, textured starter digestibility, and behavior in Holstein calves from 0 to 4 months of age. J. Dairy Sci. 101:9863–9875. doi:10.3168/jds.2018–15319

Duve, L.R., and M.B. Jensen. 2011. The level of social contact affects social behaviour in pre-weaned dairy calves. Appl. Anim. Behav. Sci. 135:34–43. doi:10.1016/j.applanim.2011.08.014

Duve, L.R., D.M. Weary, U. Halekoh, and M.B. Jensen. 2012. The effects of social contact and milk allowance on responses to handling, play, and social behavior in young dairy calves. J. Dairy Sci. 95:6571–6581. doi:10.3168/jds.2011-5170

Eckert, E., H.E. Brown, K.E. Leslie, T.J. DeVries, and M.A. Steele. 2015. Weaning age affects growth, feed intake, gastrointestinal development, and behavior in Holstein calves fed an elevated plane of nutrition during the preweaning stage. J. Dairy Sci. 98:6315–6326. doi:10.3168/jds.2014-9062

Flower, F.C., and D.M. Weary. 2001. Effects of early separation on the dairy cow and calf: 2. Separation at 1 day and 2 weeks after birth. Appl. Anim. Behav. Sci. 70:275–284. doi: 10.1016/S0168-1591(00)00164-7

Foote, M.R., B.J. Nonnecke, D.C. Beitz, and W.R. Waters. 2007. High growth rate fails to enhance adaptive immune responses of neonatal calves and is associated with reduced lymphocyte viability1. J. Dairy Sci. 90:404–417. doi:10.3168/jds.S0022-0302(07)72641–3

Fóscolo, D.R.C., F.S.M. Machado, and C.C. Coimbra. 2017. Duality of early life maternal separation effects on offspring initial development and maternal neuronal activation. FASEB J. 31(suppl 1):723.723-723.723. doi:10.1096/fasebj.31.1_supplement.723.3

Fröberg, S., and L. Lidfors. 2009. Behaviour of dairy calves suckling the dam in a barn with automatic milking or being fed milk substitute from an automatic feeder in a group pen. Appl. Anim. Behav. Sci. 117:150–158. doi:10.1016/j.applanim.2008.12.015

Fuchs, A.R., H. Helmer, O. Behrens, H.C. Liu, L. Antonian, S.M. Chang, and M.J. Fields. 1992. Oxytocin and bovine parturition: a steep rise in endometrial oxytocin receptors precedes onset of labor. Biol. Reprod. 47:937–944.

Gaillard, C., R.K. Meagher, M.A. von Keyserlingk, and D.M. Weary. 2014. Social housing improves dairy calves' performance in two cognitive tests. PLos One. 9:e90205. doi:10.1371/journal.pone.0090205

Galef, B.J. 1988. Communication of information concerning distant diets in a social, central-place foraging species: Rattus norvegicus. In: Erlbaum editor. Social Learning: Psychological and Biological Perspectives. Hillsdale, NJ, USA. pp. 119–139.

Galef, B.G., and K.N. Laland. 2005. Social learning in animals: empirical studies and theoretical models. Biosci. 55:489. doi:10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2

Geiger, A.J., C.L.M. Parsons, and R.M. Akers. 2016. Feeding a higher plane of nutrition and providing exogenous estrogen increases mammary gland development in Holstein heifer calves. J. Dairy Sci. 99:7642–7653. doi:10.3168/jds.2016-11283

Gelsinger, S.L., A.J. Heinrichs, and C.M. Jones. 2016. A meta-analysis of the effects of preweaned calf nutrition and growth on first-lactation performance. J. Dairy Sci. 99:6206–6214. doi:10.3168/jds.2015-10744

Gregorini, P., J.J. Villalba, P. Chilibroste, and F.D. Provenza. 2017. Grazing management: setting the table, designing the menu and influencing the diner. Anim. Prod. Sci. 57:1248–1268. doi:10.1071/AN16637

Griffin, D., M.M. Chengappa, J. Kuszak, and D.S. McVey. 2010. Bacterial pathogens of the bovine respiratory disease complex. Vet. Clin. North Am. Food Anim. Pract. 26:381–394. doi:10.1016/j.cvfa.2010.04.004

Größbacher, V., C. Winckler, and C. Leeb. 2018. On-farm factors associated with cross-sucking in group-housed organic Simmental dairy calves. Appl. Anim. Behav. Sci. 206:18–24. doi:10.1016/j.applanim.2018.05.030

Grøndahl, A.M., E.M. Skancke, C.M. Mejdell, and J.H. Jansen. 2007. Growth rate, health and welfare in a dairy herd with natural suckling until 6–8 weeks of age: a case report. Acta Vet. Scand. 49:16. doi:10.1186/1751-0147-49-16

Hammon, H.M., J. Steinhoff-Wagner, U. Schönhusen, C.C. Metges, and J.W. Blum. 2012. Energy metabolism in the newborn farm animal with emphasis on the calf: endocrine changes and responses to milk-born and systemic hormones. Domest. Anim. Endocrinol. 43:171–185. doi:10.1016/j.domaniend.2012.02.005

Hänninen, L., H. Hepola, S. Raussi, and H. Saloniemi. 2008. Effect of colostrum feeding method and presence of dam on the sleep, rest and sucking behaviour of newborn calves. Appl. Anim. Behav. Sci. 112:213–222. doi:10.1016/J.APPLANIM.2007.09.003

Hegland, R.B., M.R. Lambert, N.L. Jacobson, and L.C. Payne. 1957. Effect of dietary and managemental factors on reflex closure of the esophageal groove in the dairy calf. J. Dairy Sci. 40:1107–1113. doi:10.3168/jds.S0022-0302(57)94602–7

Heinrichs, A.J., and B.S. Heinrichs. 2011. A prospective study of calf factors affecting first-lactation and lifetime milk production and age of cows when removed from the herd. J. Dairy Sci. 94:336–341. doi:10.3168/jds.2010-3170

Henry, S., M.A. Richard-Yris, S. Tordjman, and M. Hausberger. 2009. Neonatal handling affects durably bonding and social development (Neonatal Handling). PLos One. 4:e5216. doi:10.1371/journal.pone.0005216

Hill, T.M., J.D. Quigley, F.X. Suarez-Mena, H.G. Bateman, and R.L. Schlotterbeck. 2016. Effect of milk replacer feeding rate and functional fatty acids on dairy calf performance and digestion of nutrients. J. Dairy Sci. 99:6352–6361. doi:10.3168/jds.2015–10812

Holechek, J.L., M. Vavra, and R.D. Pieper. 1982. Botanical composition determination of range herbivore diets: a review. J. Range Manag. 35:309. doi:10.2307/3898308

Holm, L., M.B. Jensen, and L.L. Jeppesen. 2002. Calves' motivation for access to two different types of social contact measured by operant conditioning. Appl. Anim. Behav. Sci. 79:175–194. doi:10.1016/S0168-1591(02)00137-5

Hötzel, M.J., C. Longo, L.F. Balcão, C.S. Cardoso, and J.H. Costa. 2014. A survey of management practices that influence performance and welfare of dairy calves reared in southern Brazil. PLos One. 9:e114995. doi:10.1371/journal.pone.0114995

Horvath, K.C., and E.K. Miller-Cushon. 2017. The effect of milk-feeding method and hay provision on the development of feeding behavior and non-nutritive oral behavior of dairy calves. J. Dairy Sci. 100:3949–3957. doi:10.3168/jds.2016-12223

Jasper, J., and D.M. Weary. 2002. Effects of ad libitum milk intake on dairy calves. J. Dairy Sci. 85:3054–3058. doi:10.3168/jds.S0022-0302(02)74391-9

Jensen, M.B. 1999. Effects of confinement on rebounds of locomotor behaviour of calves and heifers, and the spatial preferences of calves. Appl. Anim. Behav. Sci. 62:43–56.

Jensen, M.B. 2003. The effects of feeding method, milk allowance and social factors on milk feeding behaviour and cross-sucking in group housed dairy calves. Appl. Anim. Behav. Sci. 80:191–206. doi:10.1016/S0168-1591(02)00216-2

Jensen, M.B. 2011. The early behaviour of cow and calf in an individual calving pen. Appl. Anim. Behav. Sci. 134:92–99. doi:10.1016/j.applanim.2011.06.017

Jensen, M.B., L.R. Duve, and D.M. Weary. 2015. Pair housing and enhanced milk allowance increase play behavior and improve performance in dairy calves. J. Dairy Sci. 98:2568–2575. doi:10.3168/jds.2014–8272

Jensen, M.B., and L.E. Larsen. 2014. Effects of level of social contact on dairy calf behavior and health. J. Dairy Sci. 97:5035–5044. doi:10.3168/jds.2013-7311

Jewell, P.A. 1973. Mountain sheep: a study in behaviour and evolution. Valerius Geist. University of Chicago Press, Chicago (1971), Price£ 6· 55. 627–628.

Johnsen, J., K. Ellingsen, A. Grondahl, K. Boe, L. Lidfors, and C.M. Mejdell. 2015. The effect of physical contact between dairy cows and calves during separation on their post-separation behavioural response. Appl. Anim. Behav. Sci. 166:11–19. doi:10.1016/j.applanim.2015.03.002

Johnsen, J.F., C.M. Mejdell, A. Beaver, A.M. de Passillé, J. Rushen, and D.M. Weary. 2018. Behavioural responses to cow-calf separation: the effect of nutritional dependence. Appl. Anim. Behav. Sci. 201:1–6. doi:10.1016/j.applanim.2017.12.009

Johnsen, J.F., K.A. Zipp, T. Kälber, A.M. de Passillé, U. Knierim, K. Barth, and C. M. Mejdell. 2016. Is rearing calves with the dam a feasible option for dairy farms?—Current and future research. Appl. Anim. Behav. Sci. 181:1–11. doi:10.1016/j.applanim.2015.11.011

Jung, J., and L. Lidfors. 2001. Effects of amount of milk, milk flow and access to a rubber teat on cross-sucking and non-nutritive sucking in dairy calves. Appl. Anim. Behav. Sci. 72:201–213. doi:10.1016/S0168-1591(01)00110-1

Keil, N.M., L. Audigé, and W. Langhans. 2001. Is intersucking in dairy cows the continuation of a habit developed in early life? J. Dairy Sci. 84:140–146. doi:10.3168/jds.S0022-0302(01)74462-1

Kertz, A.F., T.M. Hill, J.D. Quigley III, A.J. Heinrichs, J.G. Linn, and J.K. Drackley. 2017. A 100-year review: calf nutrition and management. J. Dairy Sci. 100:10151–10172. doi:10.3168/jds.2017-13062

Khan, M.A., D.M. Weary, and M.A.G. Von Keyserlingk. 2011. Invited review: effects of milk ration on solid feed intake, weaning, and performance in dairy heifers. J. Dairy Sci. 94:1071–1081. doi:10.3168/jds.2010–3733

Kiezebrink, D.J., A.M. Edwards, T.C. Wright, J.P. Cant, and V.R. Osborne. 2015. Effect of enhanced whole-milk feeding in calves on subsequent first-lactation performance. J. Dairy Sci. 98:349–356. doi:10.3168/jds.2014-7959

Korst, M., C. Koch, J. Kesser, U. Müller, F.J. Romberg, J. Rehage, K. Eder, and H. Sauerwein. 2017. Different milk feeding intensities during the first 4 weeks of rearing in dairy calves: part 1: effects on performance and production from birth over the first lactation. J. Dairy Sci. 100:3096–3108. doi:10.3168/jds.2016-11594

Krohn, C.C., J. Foldager, and L. Mogensen. 1999. Long-term effect of colostrum feeding methods on behaviour in female dairy calves. Acta Agric Scand A Anim Sci. 49:57–64. doi:10.1080/090647099421540

Langbein, J., and M. Raasch. 2000. Investigations on the hiding behaviour of calves at pasture. Arch. Tierz.-Arch. Anim. Breed. 43:203–210.

Le Neindre, P. 1989a. Influence of cattle rearing conditions and breed on social relationships of mother and young. Appl. Anim. Behav. Sci. 23:117–127.

Le Neindre, P. 1989b. Influence of rearing conditions and breed on social behavior and activity of cattle in novel environments. Appl. Anim. Behav. Sci. 23:129–140.

Lidfors, L., and P. Jensen. 1988. Behaviour of free-ranging beef cows and calves. Appl. Anim. Behav. Sci. 20:237–247. doi:10.1016/0168-1591(88)90049-4

Lidfors, L.M., J. Jung, and A.M. de Passillé. 2010. Changes in suckling behaviour of dairy calves nursed by their dam during the first month post partum. Appl. Anim. Behav. Sci. 128:23–29. doi:10.1016/j.applanim.2010.09.002

Lidfors, L.M., D. Moran, J. Jung, P. Jensen, and H. Castren. 1994. Behaviour at calving and choice of calving place in cattle kept in different environments. Appl. Anim. Behav. Sci. 42:11–28. doi:10.1016/0168-1591(94)90003–5

Lopreiato, V., A. Minuti, F.P. Cappelli, M. Vailati-Riboni, D. Britti, E. Trevisi, and V. M. Morittu. 2018. Daily rumination pattern recorded by an automatic rumination-monitoring system in pre-weaned calves fed whole bulk milk and ad libitum calf starter. Livestock Sci. 212:127–130. doi:10.1016/j.livsci.2018.04.010

Lovic, V., D.J. Palombo, and A.S. Fleming. 2011. Impulsive rats are less maternal. Dev. Psychobiol. 53:13–22. doi:10.1002/dev.20481

Marcé, C., R. Guatteo, N. Bareille, and C. Fourichon. 2010. Dairy calf housing systems across Europe and risk for calf infectious diseases. Animal 4:1588–1596. doi:10.1017/S1751731110000650

McGuirk, S.M. 2008. Disease management of dairy calves and heifers. Vet. Clin. North Am. Food Anim. Pract. 24:139–153. doi:10.1016/j.cvfa.2007.10.003

Meagher, R.K., D.M. Weary, and M.A.G. Von Keyserlingk. 2017. Some like it varied: individual differences in preference for feed variety in dairy heifers. Appl. Anim. Behav. Sci. 195:8–14. doi:10.1016/j.applanim.2017.06.006

Meale, S.J., S.C. Li, P. Azevedo, H. Derakhshani, T.J. DeVries, J.C. Plaizier, M.A. Steele, and E. Khafipour. 2017. Weaning age influences the severity of gastrointestinal microbiome shifts in dairy calves. Sci. Rep. 7:198. doi:10.1038/s41598-017-00223-7

Medrano-Galarza, C., S.J. LeBlanc, A. Jones-Bitton, T.J. DeVries, J. Rushen, A.M. de Passillé, and D.B. Haley. 2017. Producer perceptions of manual and automated milk feeding systems for dairy calves in Canada. Can. J. Anim. Sci. 98(2):250–259. doi:10.1139/cjas-2017-0038

Hohenheimer Arbeiten, Reihe: Tierische Produktion (Germany, FR).

Mirza, S.N., and F.D. Provenza. 1994. Socially induced food avoidance in lambs: direct or indirect maternal influence? J. Anim. Sci. 72:899–902.

Neave, H.W., D.M. Weary, and M.A.G. Von Keyserlingk. 2018. Review: individual variability in feeding behaviour of domesticated ruminants. Animal. 12:s419–s430. doi:10.1017/S1751731118001325

Negrão, J.A., and P.-G. Marnet. 2002. Effect of calf suckling on oxytocin, prolactin, growth hormone and milk yield in crossbred Gir x Holstein cows during milking. Reprod Nutr Dev. 42:373. doi:10.1051/rnd:2002032

Neigh, G.N., C.F. Gillespie, and C.B. Nemeroff. 2009. The neurobiological toll of child abuse and neglect. Trauma. Violence Abuse. 10:389–410. doi:10.1177/1524838009339758

Newbold, C.J., G. de la Fuente, A. Belanche, E. Ramos-Morales, and N.R. McEwan. 2015. The role of ciliate protozoa in the rumen. Front. Microbiol. 6:1313. doi:10.3389/fmicb.2015.01313

Nielsen, P.P., M.B. Jensen, U. Halekoh, and L. Lidfors. 2018. Effect of portion size and milk flow on the use of a milk feeder and the development of cross-sucking in dairy calves. Appl. Anim. Behav. Sci. 200:23–28. doi:10.1016/j.applanim.2017.11.012

Notzon, S., K. Domschke, K. Holitschke, C. Ziegler, V. Arolt, P. Pauli, A. Reif, J. Deckert, and P. Zwanzger. 2016. Attachment style and oxytocin receptor gene variation interact in influencing social anxiety. World J. Biol. Psychiatry. 17:76–83. doi:10.3109/15622975.2015.1091502

Ollivett, T.L., D.V. Nydam, T.C. Linden, D.D. Bowman, and M.E. Van Amburgh. 2012. Effect of nutritional plane on health and performance in dairy calves after experimental infection with cryptosporidium parvum. J. Am. Vet. Med. Assoc. 241:1514–1520. doi:10.2460/javma.241.11.1514

Overvest, M.A., R.E. Crossley, E.K. Miller-Cushon, and T.J. DeVries. 2018. Social housing influences the behavior and feed intake of dairy calves during weaning. J. Dairy Sci. 101:8123–8134. doi:10.3168/jds.2018-14465

Parker, K.J., and D. Maestripieri. 2011. Identifying key features of early stressful experiences that produce stress vulnerability and resilience in primates. Neurosci. Biobehav. Rev. 35:1466–1483. doi:10.1016/j.neubiorev.2010.09.003

Pempek, J.A., M.L. Eastridge, S.S. Swartzwelder, K.M. Daniels, and T.T. Yohe. 2016. Housing system may affect behavior and growth performance of jersey heifer calves. J. Dairy Sci. 99:569–578. doi:10.3168/jds.2015-10088

Provenza, F.D., and D.F. Balph. 1987. Diet learning by domestic ruminants: theory, evidence and

practical implications. Appl. Anim. Behav. Sci. 18:211–232. doi:10.1016/0168-1591(87)90218-8
Provenza, F.D., J.J. Villalba, L.E. Dziba, S.B. Atwood, and R.E. Banner. 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. Small Rumin. Res. 49:257–274. doi:10.1016/S0921-4488(03)00143-3
Raeth-Knight, M., H. Chester-Jones, S. Hayes, J. Linn, R. Larson, D. Ziegler, B. Ziegler, and N. Broadwater. 2009. Impact of conventional or intensive milk replacer programs on Holstein heifer performance through six months of age and during first lactation. J. Dairy Sci. 92:799–809. doi:10.3168/jds.2008-1470
Rault, J.L., M. van den Munkhof, and F.T.A. Buisman-Pijlman. 2017. Oxytocin as an indicator of psychological and social well-being in domesticated animals: a critical review. Front. Psychol. 8:1521. doi:10.3389/fpsyg.2017.01521
Reinhardt, V., and A. Reinhardt. 1982. Mock fighting in cattle. Behaviour. 81:1–12. doi:10.1163/156853982X00490
Reinhardt, C., A. Reinhardt, and V. Reinhardt. 1986. Social behaviour and reproductive performance in semi-wild Scottish Highland cattle. Appl. Anim. Behav. Sci. 15:125–136. doi:10.1016/0168-1591(86)90058-4
Riba, A., C. Lencina, V. Bacquie, C. Harkat, M. Gillet, C. Cartier, M. Baron, C. Sommer, V. Mallet, M. Olier, et al. 2014. Early maternal separation leads to abnormal immune response against commensal microbiota in adult mice. Gastroenterol. 146:S288.
Rørvang, M.V., M.S. Herskin, and M.B. Jensen. 2017. Dairy cows with prolonged calving seek additional isolation. J. Dairy Sci. 100:2967–2975. doi:10.3168/jds.2016-11989
Rørvang, M.V., M.S. Herskin, and M.B. Jensen. 2018a. The motivation-based calving facility: social and cognitive factors influence isolation seeking behaviour of holstein dairy cows at calving. PLos One. 13:e0191128. doi:10.1371/journal.pone.0191128
Rørvang, M.V., B.L. Nielsen, M.S. Herskin, and M.B. Jensen. 2018b. Prepartum maternal behavior of domesticated cattle: a comparison with managed, feral, and wild ungulates. Front. Vet. Sci. 5:45. doi:10.3389/fvets.2018.00045
Rosenberger, K., J.H.C. Costa, H.W. Neave, M.A.G. von Keyserlingk, and D.M. Weary. 2017. The effect of milk allowance on behavior and weight gains in dairy calves. J. Dairy Sci. 100:504–512. doi:10.3168/jds.2016–11195
Roth, B.A., K. Barth, L. Gygax, and E. Hillmann. 2009. Influence of artificial vs. mother-bonded rearing on sucking behaviour, health and weight gain in calves. Appl. Anim. Behav. Sci. 119:143–150. doi:10.1016/j.applanim.2009.03.004
Rushen, J., and A.M. de Passillé. 2014. Locomotor play of veal calves in an arena: Are effects of feed level and spatial restriction mediated by responses to novelty? Appl. Anim. Behav. Sci. 155:34–41. doi:10.1016/j.applanim.2014.03.009
Rushen, J., R. Wright, J.F. Johnsen, C.M. Mejdell, and A.M. de Passillé. 2016. Reduced locomotor play behaviour of dairy calves following separation from the mother reflects their response to reduced energy intake. Appl. Anim. Behavr. Sci. 177:6–11. doi:10.1016/j.applanim.2016.01.023
Soberon, F., E. Raffrenato, R.W. Everett, and M.E. Van Amburgh. 2012. Preweaning milk replacer intake and effects on long-term productivity of dairy calves. J. Dairy Sci. 95:783–793. doi:10.3168/jds.2011-4391
Spinka, M., R.C. Newberry, and M. Bekoff. 2001. Mammalian play: training for the unexpected. Q. Rev. Biol. 76:141–168. doi:10.1086/393866
Spivey, J.M., E. Padilla, J.D. Shumake, and F. Gonzalez-Lima. 2011. Effects of maternal separation, early handling, and gonadal sex on regional metabolic capacity of the preweanling rat brain. Brain Res. 1367:198–206. doi:10.1016/j.brainres.2010.10.038
Staněk, S., V. Zink, O. Doležal, and L. Štolc. 2014. Survey of preweaning dairy calf-rearing practices in Czech dairy herds. J. Dairy Sci. 97:3973–3981. doi:10.3168/jds.2013-7325
Stanton, A.L., D.F. Kelton, S.J. LeBlanc, J. Wormuth, and K.E. Leslie. 2012. The effect of respiratory disease and a preventative antibiotic treatment on growth, survival, age at first calving, and milk production of dairy heifers. J. Dairy Sci. 95:4950–4960. doi:10.3168/jds.2011-5067
Steele, M.A., F. Garcia, M. Lowerison, K. Gordon, J.A. Metcalf, and M. Hurtig. 2014. Technical note: three-dimensional imaging of rumen tissue for morphometric analysis using micro-computed tomography. J. Dairy Sci. 97:7691–7696. doi:10.3168/jds.2014-8374
Stěhulová, I., L. Lidfors, and M. Špinka. 2008. Response of dairy cows and calves to early separation: effect of calf age and visual and auditory contact after separation. Appl. Anim. Behav. Sci. 110:144–165. doi:10.1016/j.applanim.2007.03.028
Sutherland, M.A., and M. Tops. 2014. Possible involvement of oxytocin in modulating the stress response in lactating dairy cows. Front. Psychol. 5:951. doi:10.3389/fpsyg.2014.00951
Terré, M., C. Tejero, and A. Bach. 2009. Long-term effects on heifer performance of an enhanced-growth feeding programme applied during the preweaning period. J. Dairy Res. 76:331–339. doi:10.1017/S0022029909004142
Telgmann, R., R.A. Bathgate, S. Jaeger, G. Tillmann, and R. Ivell. 2003. Transcriptional regulation of the bovine oxytocin receptor gene. Biol. Reprod. 68:1015–1026. doi:10.1095/biolreprod.102.008961
USDA. 2016. Dairy 2014: dairy cattle management practices in the United States. Fort Collins (CO): National Animal Health Monitoring Systems (NAHMS).
Valníčková, B., I. Stěhulová, R. Šárová, and M. Špinka. 2015. The effect of age at separation from the dam and presence of social companions on play behavior and weight gain in dairy calves. J. Dairy Sci. 98:5545–5556. doi:10.3168/JDS.2014–9109
Van De Stroet, D.L., J.A. Calderón Díaz, K.J. Stalder, A.J. Heinrichs, and C.D. Dechow. 2016. Association of calf growth traits with production characteristics in dairy cattle. J. Dairy Sci. 99:8347–8355. doi:10.3168/jds.2015–10738
Van Putten, G., and W.J. Elshof. 1982. Inharmonious behaviour in veal-calves. Hohenheimer Arbeiten, Reihe: Tierische Produktion (Germany, FR). 121: 61–71.
Vasseur, E., F. Borderas, R.I. Cue, D. Lefebvre, D. Pellerin, J. Rushen, K. M. Wade, and A.M. de Passillé. 2010. A survey of dairy calf management practices in Canada that affect animal welfare. J. Dairy Sci. 93:1307–15. doi:10.3168/jds.2009–2429
Veissier, I., A. Boissy, R. Nowak, P. Orgeur, and P. Poindron. 1998. Ontogeny of social awareness in

domestic herbivores. Appl. Anim. Behav. Sci. 57:233–245. doi:10.1016/S0168-1591(98)00099-9

Veissier, I., V. Gesmier, P. Le Neindre, J.Y. Gautier, and G. Bertrand. 1994. The effects of rearing in individual crates on subsequent social behaviour of veal calves. Appl. Anim. Behav. Sci. 41:199–210. doi:10.1016/0168-1591(94)90023-X

Vitale, A.F., M. Tenucci, M. Papini, and S. Lovari. 1986. Social behaviour of the calves of semi-wild Maremma cattle, *Bos primigenius taurus*. Appl. Anim. Behav. Sci. 16:217–231. doi:10.1016/0168-1591(86)90115-2

von Keyserlingk, M.A.G., and D.M. Weary. 2007. Maternal behavior in cattle. Hormones Behav. 52:106–113. doi:10.1016/j.yhbeh.2007.03.015

Wagner, K., K. Barth, R. Palme, A. Futschik, and S. Waiblinger. 2012. Integration into the dairy cow herd: long-term effects of dam contact during the first twelve weeks of life. Appl. Anim. Behav. Sci. 141:117–129. doi:10.1016/j.applanim.2012.08.011

Wagner, K., K. Barth, E. Hillmann, R. Palme, A. Futschik, and S. Waiblinger. 2013. Mother rearing of dairy calves: reactions to isolation and to confrontation with an unfamiliar conspecific in a new environment. Appl. Anim. Behav. Sci. 147:43–54. doi:10.1016/J.APPLANIM.2013.04.010.

Wagner, K., D. Seitner, K. Barth, R. Palme, A. Futschik, and S. Waiblinger. 2015. Effects of dam versus artificial rearing during the first 12 weeks of life on challenge responses of dairy cows. Appl. Anim. Behav. Sci. 164:1–11. doi:10.1016/j.applanim.2014.12.010

Weary, D.M., and B. Chua. 2000. Effects of early separation on the dairy cow and calf. 1. Separation at 6 h, 1 day and 4 days after birth. Appl. Anim. Behav. Sci. 69:177–188. doi:10.1016/S0168-1591(00)00128-3

Whalin, L., D.M. Weary, and M.A.G. von Keyserlingk. 2018. Short communication: pair housing dairy calves in modified calf hutches. J. Dairy Sci. 101:5428–5433. doi:10.3168/jds.2017-14361

Wormsbecher, L., R. Bergeron, D. Haley, A.M. de Passillé, J. Rushen, and E. Vasseur. 2017. A method of outdoor housing dairy calves in pairs using individual calf hutches. J. Dairy Sci. 100:7493–7506. doi:10.3168/jds.2017-12559

Yáñez-Ruiz, D.R., L. Abecia, and C.J. Newbold. 2015. Manipulating rumen microbiome and fermentation through interventions during early life: a review. Front. Microbiol. 6:1133. doi:10.3389/fmicb.2015.01133