Myth: "Calves forgive and forget" – early socialization and housing effects on performance, health, behavior and cognition^a

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Abstract

Early-life social contact in dairy calves has been associated with effects on performance, health, behavior, and cognition. Here we will first describe the negative impact of social isolation in mammals, especially dairy calves, followed by a summary of the opportunities and benefits of providing social partners in early life. Finally, we will discuss what we know about how to successfully raise calves in groups from birth, with emphasis on the benefits and challenges associated with group housing. We conclude with solutions to common pitfalls for producers that are already using group housing or those interested in transitioning. Pair or group housing of dairy calves can provide positive outcomes and can be done successfully when attention is given to group size, cleanliness, proper nutrition, and management.

Key words: dairy calves, housing, socialization

Résumé

Le contact social tôt dans la vie chez les veaux laitiers influence la performance, la santé, le comportement et la cognition. Nous allons décrire en premier l'impact négatif de l'isolement social chez les mammifères et plus particulièrement chez les veaux laitiers et nous enchainerons avec un survol des opportunités et des bénéfices de promouvoir le contact social tôt dans la vie. Finalement, nous allons discuter de la possibilité d'élever avantageusement des veaux en groupe à partir de la naissance et mettre l'accent sur les bénéfices et les défis associés à l'élevage en groupe. Nous concluons avec des solutions aux écueils les plus fréquents auxquels font face les producteurs qui utilisent déjà l'élevage en groupe ou qui pensent s'y convertir. L'élevage en paire ou en groupe chez les veaux laitiers peut avoir des retombées positives et peut se faire avantageusement en se souciant de la taille du groupe, de la propreté, de la bonne alimentation et de la gestion.

Introduction

Most farmed mammals such as sheep, pigs, horses, and beef cattle are housed with their dam during the milkfeeding period, and the young normally also have contact with conspecifics of a similar age. Dairy cattle production is the exception; standard practice in the North American dairy industry is to separate the calf and dam immediately after birth and raise calves in individual pens during the milkfeeding period. This occurs on as many as 75% of farms in the USA,⁷¹ 88% in Canada,⁷³ and 70% in Brazil.³⁰ This limited maternal and social contact is in contrast to the evolutionary nature of cattle.

Under natural or semi-natural conditions the calf will remain close to its dam during the first few days, but after the second week of life, the calf will begin to interact with other calves in the herd and even begin to graze and ruminate beginning at around 3 weeks of age; several months later, calves will begin to graze regularly with the herd.^{62,76} During this progression from maternal dependence to independence, the young calf relies on social interactions to learn how to become a proficient forager.⁶⁰ This type of social learning or 'learning from others' is thought to be especially important in the development of feeding behaviors by transmitting information about suitable food items from experienced to inexperienced. This also occurs in our systems of intensivelyraised dairy replacement animals; in recent studies, naïve heifers that were introduced to pasture with experienced cows began to graze sooner than heifers who had no social model to learn from,¹² and calves that were raised in a social group were quicker to sample and consumed more novel foods compared with those housed alone.¹⁰

Young ruminants naturally form social relationships even in the first weeks of life, and will rely on social information from the dam and other calves that will influence their behavioral development. Thus many questions arise regarding how early-life social isolation of calves under standard commercial farm conditions affects the development of social and feeding behaviors. Here, we will summarize the literature describing the positive effects of early-life social contact in dairy calves, followed by a discussion on how to raise calves in groups successfully. We describe the benefits and challenges associated with group housing of dairy calves with a focus on performance, health, and behavioral issues, and conclude with practical solutions for implementing group housing on commercial farms. Interested readers are invited to read an in-depth discussion on this topic in the recent review in the Journal of Dairy Science.⁹

The impact of social isolation on dairy calves

Before we discuss the evidence related to individual housing of dairy calves, it is necessary to highlight the early work on isolation of other social mammals to understand why we might predict abnormal development and behavioral problems in calves. Perhaps the most famous of studies on the social deprivation of young animals is that of Dr. Harry Harlow from the University of Wisconsin, who, in 1965, demonstrated the profound effects of early-life maternal separation and conspecific isolation of monkeys on brain and behavior development, resulting in significant disruptions in social behavior, hyperactivity, and increased sensitivity to stressors.²⁷ Since then, hundreds of papers have found similar effects of social deprivation in a variety of other species including rats, mice, voles, and pigs, among others.^{25,38,65,85} These effects are known to carry over into adulthood such as impaired maternal care, increased aggression, and impaired social recognition.^{40,46,47,70,74,75} Even partial maternal separation has been associated with long-term changes in emotionality, cognitive functioning, and stress coping mechanisms in nonhuman primates.²¹ This evidence provides a consensus on the profound effects of partial or total isolation in mammals.

Although little work has focused on social isolation of farm animals, the few studies available report similar results to those in the primate and rodent literature. For example, piglets weaned at younger ages were slower to habituate to their new environment, interacted less with other pigs, and spent less time feeding than pigs weaned at an older age.^{13,85} Lambs separated from the dam showed reduced frequency of vocalization, were slower to initiate movements, and displayed an increased cortisol response during an openfield test compared with animals raised in a complex social environment^{52,55} (reviewed by Napolitano et al⁵⁴). Overall, the early work in primates and rodents, and more recently in farm animals, demonstrates that early social interaction with the mother or conspecifics is critical for normal development in social species.

Given this evidence and the social nature of dairy cattle, it would seem reasonable to expect similar effects of individual housing in dairy calves. We briefly review this research examining the effects of the early-life rearing environment on social behavior, ability to cope with novelty and stressors, and cognitive development. Where relevant, we highlight examples of our own work in these areas. The long-term effects of early-life isolation are also described.

Social behavior

A number of factors play a role in social behavior development, such as the age of first contact with conspecifics and the level of contact. When given the opportunity, calves will begin social interactions as early as 2 d after birth,¹⁸ and calves will form social bonds from a young age. For instance, calves allowed full social contact with another calf, either from birth or from 3 weeks of age, established a stronger bond compared to calves raised with only visual or auditory

contact with other calves.¹⁷ Calves will also form bonds and preference for partners, and will work harder to gain full social contact with a familiar calf than to have limited social contact across a barrier.^{11,19,29} Most recently, Bolt et al found that calves at 8 weeks of age had stable social relationships and partner preferences for familiar calves.⁵

We can also take advantage of the social behavior of calves to achieve higher performance. In a fascinating study, de Paula Vieira et al tested the hypothesis that an older social companion in the pen could improve solid feed intakes in younger calves.¹⁵ Calves were grouped at 7 d of age in groups of either 3 young calves or 2 young calves plus an older weaned calf. Interestingly, calves housed with an older weaned companion consumed more grain and achieved an additional 0.22 lb (100 g)/day of average daily gain during pre-weaning and an additional 0.66 lb (300 g)/day of average daily gain during post-weaning compared to calves housed without an older social model, demonstrating that older companions can serve as knowledgeable social models for younger naïve animals learning to eat solid feeds. In a followup study,¹⁶ those calves housed with an older companion were less reactive to an unfamiliar calf when compared with calves housed in groups of similar age. Collectively this evidence suggests that full social contact with peers from an early age is important and calves are motivated to perform these behaviors. Moreover, early-life socialization allows for development of appropriate social behaviors that can then translate to effective coping skills when faced with social or non-social stressors, as described in the next section.

Novelty and stressors

Dairy cattle often will remain on our farms for many years, and thus are commonly exposed to novel events during management practices, such as changes in diet, pen location, regrouping with new social partners, and new milking procedures. Each of these events requires the individual to adapt quickly and effectively to environmental change. Several recent lines of evidence from the University of British Columbia suggest that early social contact can reduce behavioral reactivity to novel events. De Paula Vieira et al raised calves either individually or in pairs and tested calves alone in a novel arena, and again with an unfamiliar calf.¹⁶ Individually-raised calves were more reactive when alone, and took longer to interact with the new social companion compared to pair-raised calves, suggesting that isolation can lead to heightened reactivity to environmental and social novelty. A follow-up study¹⁵ added a degree of complexity to the social environment by housing calves individually, in pairs, or in a group with access to the dam. When calves were tested alone in a pen containing either a novel object or human handler, those housed in the group with their dam approached the object and human handler quicker than individually raised calves. In a more biologically-relevant novelty test, Costa et al tested the hypothesis that complex social environments may improve the calf's ability to cope with novel feeds that are commonly offered on dairy farms as part of modern dairy cow management.¹⁰ Indeed, calves raised in a group with their dam were less neophobic (the fear of new feeds) compared to individually raised calves: they were quicker to approach and sample from a bucket containing chopped carrots or hay, and consumed more of the novel food during a 30 min test.

The presence of social companions is also known to decrease the impact of stressors during a challenge, termed 'social buffering'.8 In cattle, the presence of conspecifics is known to reduce behavioral reactions to social separation, and calves vocalize less in a novel arena when with familiar calves compared to unfamiliar calves.^{19,59} Furthermore, research from our studies demonstrates some evidence of social buffering during a non-social stressor. On any farm using pasture, dairy heifers face a challenge when first introduced to pasture - they must learn how to graze. Costa et al investigated whether the presence of an experienced grazing companion would aid in the development of grazing behaviors.¹² Groups of 3 naïve heifers were introduced to pasture with either 3 experienced cows or 3 other naïve heifers; those heifers that had the benefit of experienced companions began to graze sooner and displayed fewer stomps and vocalizations compared to heifers with naïve companions, indicating the presence of an experienced companion when first learning to graze may improve the ability of heifers to adapt to this challenge.

This evidence is among a series of studies showing that socially reared calves are less reactive to environmental novelty, and a social companion can provide benefits during social and non-social stressors. The possibilities are endless for using the social environment as a positive element when animals are confronted with novelty. Social buffering of stressors on dairies is likely occurring to some degree already, but reinforcing elements include ensuring animals are known to each other, minimizing competition for resources, and especially housing an animal in the group that is experienced with the transition or novelty.

Cognitive development

Social isolation early in life is also known to impair cognitive functioning. Socially isolated rodents showed deficits in reversal learning, a method often used to assess behavioral flexibility in animals.³⁷ Behavioral flexibility is fundamental for animals to re-learn a task that was previously learned, such as the pathway to the milking parlor, where to find food, or eating a new diet. These are just a few among many transitions that dairy cattle must cope with during their lives on the farm. The Animal Welfare Program at the University of British Columbia was the first lab to apply this method of reversal-learning in dairy calves. Gaillard et al trained calves that were raised individually or in pairs to discriminate between the left arm of a Y-maze containing a white square associated with a positive event (milk bottle) and the right arm containing a black square associated with a negative event (removal of milk).²³ After calves learned this task, the rewarded side of the Y-maze was switched with the

unrewarded side, thus requiring the calves to re-learn the task but this time in reverse. Individually housed calves made more mistakes during the reversal-learning phase compared to pair-housed calves, indicating impaired behavioral flexibility. One study that we set up as a follow up used a color discrimination training task where calves learned to touch a red computer screen to access a reward and to not touch a white screen to avoid a punishment.⁵¹ Calves that were housed with social companions from an early age, either with their dam and other cows and calves, or simply pair-housed, performed better during reversal-learning than did individually raised calves. What is especially fascinating in both Gaillard et al²⁴ and Meagher et al⁵¹ is that all calves regardless of housing condition learned the initial task at a similar rate, yet most individually housed calves never learned the reversal task even when provided twice as many sessions as required by the average socially housed calf. Similar studies in rodents indicate that this cognitive deficit is associated with decreased brain development and plasticity that are essential for success in the reversal task (e.g. Schrijver and Würbel et al;⁶³ Fowler et al;²² Schrijver et al;⁶⁴ Lipkind et al⁴⁵). These cognitive deficiencies may have repercussions later in life when exposure to a variable environment requires behavioral flexibility to adapt to new conditions.

Long-term effects

While there is limited work on the long-term effects of early-life social isolation, likely due to the time required and the challenges associated with maintaining adequate controls, there is some evidence suggesting that negative effects may persist to adulthood. For example, calves reared with a foster cow showed more maternal behavior and more locomotion and exploration during isolation tests years later.^{42,43} Another study reported that dam-reared calves had a smoother transition into the lactating herd, suggesting that social housing of calves may enhance social skills useful later in life.⁷⁹ In a complementary study, cows that had experienced 12 weeks of contact with the dam showed greater behavioral activity during an isolation test in comparison with cows that had been individually raised.78 These studies provide early evidence that the rearing environment may have an impact on behavior later in life. It remains to be understood whether the detrimental effects of social isolation can be reversed through enriched environments or other means.

In conclusion, rearing dairy calves individually impacts social behavior, ability to cope with novelty and stressors, and cognitive development. It is critical to raise a calf that can effectively and successfully cope with the many management practices on a typical commercial farm. Dairy farms can begin to achieve this by designing group housing systems for newborn and milk-fed calves that will meet their physical, behavioral, and psychological needs. However, to rear calves in groups, an understanding of the practical benefits and constraints of social housing is essential. We address these issues in the following section.

How to Group-House Dairy Calves: Challenges and Solutions

One of the most commonly cited reasons for moving to group housing is reduced labor, but a growing body of work has shown other benefits of group housing, including improved feed intake and weight gain. However, concerns still remain regarding the impact of social housing on disease transmission and behavioral issues, such as cross-sucking and competition. We summarize the literature on these issues, highlighting some of our own work in this area, and describe how farms can successfully manage group housing to avoid common pitfalls while still maximizing the benefits of social housing.

Benefit: feed intake and weight gain

Group housing of calves is associated with increased weight gain compared with individual housing, which is likely due to an increase in dry matter intake especially when calves are offered high milk allowances. Contact with the dam or other older animals within the first few weeks of life is known to stimulate young ungulates to start sampling solid feed at a younger age.^{39,56} It is thought that the presence of a social companion aids in learning first how to access and manipulate feed, but also stimulates attention toward feed while others are feeding, resulting in increased feed intake, especially in the pre-weaning phase. Many farmers describe this observation when transitioning to pair or group housing. This phenomenon is known for decades in cattle. An early study in the 70s showed that social housing increased concentrate intake during the pre-weaning period, resulting in higher weight gains after weaning.⁸³ Similar results have been reported more recently, such as increased solid feed consumption,³⁵ earlier onset of rumination,^{2,3} and increased DMI and weight gains as early as 41 d of age⁴ in group-housed compared to individually-housed calves.

These benefits can be seen even when calves are simply paired with a single partner. Much of our work has focused on the benefits of pair housing calves as a practical solution for farms that are using individual housing but their facility is not feasible for group housing. One of our recent studies¹¹ set out to determine when calves should be paired to gain the advantages of social rearing. We housed calves either individually, in pairs from birth ('early-paired') or at 6 weeks of age ('late-paired') and provided all calves with ad libitum TMR (the same ration prepared for fresh cows), grain, hay, and water. Milk was provided at 8 L/d for the first 28 days, then 6 L/d until 50 days, and weaning was completed by 55 days of age. When calves were paired at birth, they consumed more grain than did the individually reared and late-paired calves both before and after weaning, consuming on average 2.2 lb (1 kg) more grain per day by 10 weeks of age. This increased solid feed intake translated to better weight gains: early-paired calves achieved an average weight gain of 2 lb (890 g)/d over the 10-week experimental period compared to 1.6 lb (750 g)/d in individual and late-paired calves. Our study complements an earlier study that found calves paired at birth or at 3 weeks of age consumed more solid feed than did individually housed calves.⁶⁹ The results of our study begin to identify the critical period when calves must be grouped to gain the benefits of social rearing. This period appears to be somewhere up to 3 weeks of age, but we recommend pairing or grouping as early as possible to achieve the greatest benefits of increased intake and weight gains.

Challenge: competition and cross-sucking

An obvious advantage of individual housing is that competition, aggression, and cross-sucking are prevented. For calves reared in groups, the majority of aggression occurs around the feeder, especially when fed from a single automatic milk feeder,²⁸ and this aggression intensifies when calves are fed restricted milk allowances and when fewer teats are available.⁷⁷ Several strategies can be employed to reduce competition and aggression during feeding. Ideally, 1 teat per calf should be provided. Barriers between teats that protect the calf's head and shoulders,³⁴ or offering milk in fewer and larger portions³³ can lower competition for access to teats. Aggressive behavior can also be minimized by maintaining stable groups⁵³ with calves of similar age.²⁰

Cross-sucking in group-housed calves is another commonly cited problem (e.g. Lidfors and Isberg⁴⁴), but other studies have reported little to no cross-sucking in groups (e.g. Chua et al,⁷ Mattiello et al⁴⁹), suggesting that the problem can be managed. Cross-sucking often becomes a problem when the ability to engage in natural suckling behaviour is prevented or limited. This can be mitigated by feeding milk through a teat instead of a bucket, allowing calves to access milk for many hours of the day instead of just 1 or 2 feedings, and even providing a dry teat for calves to suckle on (reviewed by Jensen³²). Enhanced milk-feeding programs (i.e. feeding more than 8 L of milk per day) will also help to reduce cross-sucking, since the motivation for this behavior is closely associated with the motivation to drink milk.¹⁴ Overall, research indicates that competition and crosssucking can occur in groups as a result of poor milk-feeding practices. Solutions include providing enough milk and teats for suckling, and maintaining stable social groups of similar ages when possible.

Challenge: disease transmission

One common reason for individually housing young calves is to limit disease transmission. It is believed that individual pens may also facilitate monitoring, resulting in better treatment of disease.⁴¹ The majority of dairy farms are raising their animals individually (75% in the USA).⁷¹ Furthermore, most of the illnesses affecting calves are enteric and respiratory diseases that can be spread between calves through fecal-oral and nose-nose contact, which should be minimized by individual housing.^{48,50,66} In theory, these diseases should be mostly eliminated over the years of individual

housing of dairy calves. A look at calf mortality rates around the world suggests that maintaining good health can still be challenging on many farms. Korea reported a mortality rate of 10.7% during the first year of life,³¹ 14.5% mortality rate from birth to first calving in the UK,⁶ and 4.4% and 3.2% for calves aged 3 days to 1 month old and 1- to 6-months old in France, respectively.⁶¹ Yearly mortality of heifers in the United States has been reported to be 6.9% and 7.8% on calf ranches and dairy farms, respectively.^{71,80}

Despite the standard of individual housing, there is little evidence of improved calf health in this system. Some studies have indeed reported more health problems in group-reared calves (e.g. Webster et al;84 Gulliksen et al24), but other empirical studies have found no advantage of individual housing when compared with small groups (e.g. Waltner-Toews;^{81,82} Perez et al;⁵⁸ Johnson et al³⁶). Diarrhea and respiratory illness, the most common diseases in young calves, are not consistently associated with group housing (e.g. Hanekamp; Hänninen et al²⁶). However, we caution that many management practices can influence the risk of disease transmission and should be considered in any comparison between systems, such as the amount of milk fed and bedding management. For example, 1 study reported that chronic and acute respiratory diseases and diarrhea occurred more frequently in grouphoused veal calves, but this comparison was confounded by differences in milk feeding methods between grouped (computer-controlled) and individual (bucket-fed twice per day) calves (Maatje et al48).

Two key practices that can help to minimize disease spread are group size and method of grouping. When it comes to group size, bigger is not better. Groups of less than 8 calves are easiest to manage successfully, and reportedly have reduced respiratory illness and severe diarrhea compared to larger groups (e.g. Svensson and Liberg;⁶⁷ Svensson et al⁶⁸). Groups of 2, 4 or 8 made no difference in terms of disease incidence.¹ Higher morbidity and mortality in large groups of calves may be due to difficulty in detecting, examining and treating sick calves, resulting in delayed treatments.^{66,72} An 'all-in-all-out' grouping system should be used whenever possible to minimize the spread of disease between groups. This form of management helps to prevent the spread of infections between groups of animals raised in the same unit by allowing for cleaning and disinfection between groups. For example, Pedersen et al showed that dynamic groups in which new calves were continuously introduced and removed had lower daily gains and a higher incidence of disease than did stable groups (using an all-in-all-out system).⁵⁷ Clean milk feeding equipment and bedding are also essential to maintaining good health, as well as early identification and treatment of sick animals. We suggest that controlling these variables can be an effective method of minimizing health problems, and calves can maintain good health in groups if housing is properly managed. Farms that are experiencing problems to keep their calves healthy should first manage these factors before transitioning to social housing. With

proper colostrum management, identification and treatment of sick animals, clean bedding, a good ventilation system and proper nutrition, group housing with minimal incidence of disease can be achieved.

In summary, group housing faces many benefits but also some challenges. When socially housed, calves have the advantage of learning from their pen-mates where to find and how to eat solid feed, leading to increased solid feed intakes before and after weaning. This benefit is especially clear when calves are fed higher volumes of milk. Many of the problems associated with group housing, such as illness and competition among calves, are reduced when using small and stable groups. In much of our work we have kept calves in the smallest group possible – a pair! We recommend that producers interested in trying group housing on their farm start with pairs or triplets, using animals that are most similar in age. A simple solution for some farms is to remove the partitions between individual pens or hutches to create pairs.

Conclusions

The detrimental effects of social isolation are now recognized in a range of species, and we have highlighted newer work on dairy calves showing that individually-raised calves have deficient social skills, difficulties to cope with novel situations, and poor learning abilities. Social housing for calves improves solid feed intake pre-weaning, and helps improve overall weight gain during the transition from milk to solid feed. The challenges associated with group housing include disease transmission, competition at the feeder and cross-sucking, but we have presented research suggesting that calves can be grouped in good health with minimal abnormal behaviors if housing is properly managed. Grouping calves early will have returns: the long-term effects of earlylife social rearing are beginning to show that adults can have improved production and reduced behavioral reactivity later in life. We encourage producers to test out group housing by starting with pairs of calves that are similar in age, and if this works well, groups can be expanded to 3 or 4. We predict that producers will see the benefits within weeks of transitioning to group housing.

Endnote

^aThis is a summarized version of the recent invited review by Costa et al. *J Dairy Sci* 2016; 99:2453-2467.

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References

1. Abdelfattah EM, Schutz MM, Lay DC, Marchant-Forde JN, Eicher SD. Effect of group size on behavior, health, production, and welfare of veal calves. *J Anim Sci* 2013; 91:5455-5465.

2. Babu LK, Pandey HN, Sahoo A. Effect of individual versus group rearing and feeding of different levels of milk and skim milk on nutrient utilization in crossbred calves. Asian-australas. *J Anim Sci* 2003; 16:1455-1459.

3. Babu LK, Pandey HN, Sahoo A. Effect of individual versus group rearing on ethological and physiological response of cross-bred calves. *Appl Anim Behav Sci* 2004; 87:177-191.

4. Bernal-Rigoli JC, Allen JD, Marchello JA, Cuneo SP, Garcia SR, Xie G, Hall LW, Burrows CD, Duff GC. Effects of housing and feeding systems on performance of neonatal Holstein bull calves. *J Anim Sci* 2012; 90:2818-2825.

5. Bolt SL, Boyland NK, Mlynski DT, James R, Croft DP. Pair housing of dairy calves and age at pairing: effects on weaning stress, health, production and social networks. *PloS one* 2017; 12, e0166926.

6. Brickell JS, McGowan MM, Pfeiffer DU, Wathes DC. Mortality in Holstein-Friesian calves and replacement heifers, in relation to body weight and IGF-I concentration, on 19 farms in England. *Animal* 2009; 3:1175-1182.

7. Chua B, Coenen E, Van Delen J, Weary DM. Effects of pair versus individual housing on the behavior and performance of dairy calves. *J Dairy Sci* 2002; 85:360-364.

8. Cohen S, Wills TA. Stress, social support, and the buffering hypothesis. *Psychol Bull* 1985; 98:310-357.

9. Costa JHC, von Keyserlingk MAG, Weary DM. Invited review: effects of group housing of dairy calves on behavior, cognition, performance, and health. *J Dairy Sci* 2016; http://dx.doi.org/10.3168/jds.2015-10144

10. Costa JHC, Daros RR, von Keyserlingk MAG, Weary DM. Complex social housing reduces food neophobia in dairy calves. *J Dairy Sci* 2014; 97:7804-7810.

11. Costa JHC, Meagher RK, von Keyserlingk MAG, Weary DM. Early pair housing increases solid feed intake and weight gains in dairy calves. *J Dairy Sci* 2015; 98:6381-6386.

12. Costa JHC, Costa WG, Weary DM, Machado Filho LCP, von Keyserlingk MAG. Dairy heifers benefit from the presence of an experienced companion when learning how to graze. In press. *J Dairy Sci* 2015; Volume: pages?

13. Davis ME, Sears SC, Apple JK, Maxwell CV, Johnson ZB. Effect of weaning age and commingling after the nursery phase of pigs in a wean-to-finish facility on growth, humoral and behavioral indicators of well-being. *J Anim Sci* 2006; 84:743-756.

14. de Passillé AM. Sucking motivation and related problems in calves. *Appl Anim Behav Sci* 2001; 72:175-187.

15. de Paula Vieira A, de Passilé AM, Weary DM. Effects of the early social environment on the behavioural responses of dairy calves to novel events. *J Dairy Sci* 2012; 95:5149-5155.

16. de Paula Vieira A, von Keyserlingk MAG, Weary DM. Presence of an older weaned companion influences feeding behavior and improves performance of dairy calves before and after weaning from milk. *J Dairy Sci* 2012; 95:3218-3224.

17. Duve LR, Jensen MB. The level of social contact affects social behaviour in pre-weaned dairy calves. *Appl Anim Behav Sci* 2011; 135:34-43.

18. Duve LR, Jensen MB. Social behavior of young dairy calves housed with limited or full social contact with a peer. *J Dairy Sci* 2012; 95:5936-5945.

19. Færevik G, Jensen MB, Bøe KE. Dairy calves social preferences and the significance of a companion animal during separation from the group. *Appl Anim Behav Sci* 2006; 99:205-221.

20. Færevik G, Jensen MB, Bøe KE. The effect of group composition and age on social behavior and competition in groups of weaned dairy calves. *J Dairy Sci* 2010; 93:4274-4279.

21. Fahlke C, Lorenz JG, Long J, Champoux M, Suomi SJ, Higley JD. Rearing experiences and stress-induced plasma coritsol as early risk factors for excessive alcohol consumption in nonhuman primates. *Alcohol Clin Exp Res* 2000; 24:644-650.

22. Fowler CD, Liu Y, Ouimet C, Wang Z. The effects of social environment on adult neurogenesis in the female prairie vole. *J Neurobiol* 2002; 51:115-128. 23. Gaillard C, Meagher RK, von Keyserlingk MAG, Weary DM. Social housing improves dairy calves' performance in two cognitive tests. *PLoS ONE* 2014; 9.2:e90205.

24. Gulliksen S, Lie K, Loken T, Osteras O. Calf mortality in Norwegian dairy herds. *J Dairy Sci* 2009; 92:2782-2795.

25. Haller J, Harold G, Sandi C, Neumann ID. Effects of adverse early-life events on aggression and anti-social behaviours in animals and humans. *J Neuroendocrinology* 2014; 26:724-738.

26. Hanekamp WJA, Smits AC, Wierenga HK. Open versus closed barn and individual versus group-housing for bull calves destined for beef production. *Livestock Production Science* 1994; 37:261-270.

27. Hänninen L, Hepola H, Rushen J, de Passillé AM, Pursiainen P, Tuure VM, Syrjälä-Qvist L, Pyykkönen M, Saloniemi H. Resting behaviour, growth and diarrhoea incidence rate of young dairy calves housed individually or in groups in warm or cold buildings. *Acta Agric Scand* 2003; Sect. A 53:21-28. 28. Harlow HF, Dodsworth RO, Harlow MK. Total social isolation in monkeys. *Proc Natl Acad Sci U.S.A.* 1965; 54:90-96.

29. Herrmann J, Knierim U. Auswirkungen der Tränketechnik auf das Sozialverhalten zwei bis acht Wochen alter Mastkälber in Gruppenhaltung (Effects of different feeding techniques on the social behaviour from two to eight weeks old veal calves in group housing). *Aktuelle Arbeiten zur artgemässen Tierhaltung* 1999; 382:130-136.

30. Holm L, Jensen MB, Jeppesen LL. Calves' motivation for access to two different types of social contact measured by operant conditioning. *Appl Anim Behav Sci* 2002; 79:175-194.

31. Hötzel MJ, Longo C, Balcão LF, Cardoso CS, Costa JHC. A survey of management practices that influence performance and welfare of dairy calves reared in Southern Brazil. *PloS ONE* 2014; 9:e114995.

32. Hur TY, Jung YH, Choe CY, Cho YI, Kang SJ, Lee HJ, Ki KS, Baek KS, Suh GH. The dairy calf mortality: the causes of calf death during ten years at a large dairy farm in Korea. *Korean J Vet Res* 2013; 53:103-108.

33. Jensen MB. 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* 2003; 80:191-206.

34. Jensen MB. Computer-controlled milk feeding of dairy calves: The effects of number of calves per feeder and number of milk portions on use of feeder and social behavior. *J Dairy Sci* 2004; 87:3428-3438.

35. Jensen MB, de Passillé AM, von Keyserlingk MAG, Rushen J. A barrier can reduce competition over teats in pair-housed milk-fed calves. *J Dairy Sci* 2008; 91:1607-1613.

36. Jensen MB, Duve LR, Weary DM. Pair housing and enhanced milk allowance increase play behavior and improve performance in dairy calves. *J Dairy Sci* 2015; 98:2568-2575.

37. Johnson K, Burn CC, Wathes DC. Rates and risk factors for contagious disease and mortality in young dairy heifers. *Anim Sci Rev* 2011; 205:101-113. 38. Jones GH, Marsden CA, Robbins TW. Behavioural rigidity and rule-learning deficits following isolation-rearing in the rat: Neurochemical correlates. *Behav Brain Research* 1991; 43:35-50.

39. Kercmar J, Tobet SA, Majdic G. Social isolation during puberty affects female sexual behavior in mice. *Front Behav Neurosci* 2014; 8:337.

40. Key C, MacIver RM. The effects of maternal influences on sheep: Breed differences in grazing, resting and courtship behaviour. *Appl Anim Behav Sci* 1980; 6:33-48.

41. Kraemer GW, Ebert MH, Schmidt DE, McKinney WT. Strangers in a strange land: a psychobiological study of mother-infant separation in rhesus monkeys. *Child Dev* 1991; 62:548-566.

42. Kung L, Demarco S, Siebenson LN, Joyner E, Haenlein GFW, Morris RM. An evaluation of two management systems for rearing calves fed milk replacer. *J Dairy Sci* 1997; 80:2529-2533.

43. Le Neindre P. Influence of cattle rearing conditions and breed on social relationships of mother and young. *Appl Anim Behav Sci* 1989; 23:117-127. 44. Le Neindre P. Influence of rearing conditions and breed on social behavior and activity of cattle in novel environments. *Appl Anim Behav Sci* 1989; 23:129-140.

45. Lidfors L, Isberg L. Intersucking in dairy cattle—review and questionnaire. *Appl Anim Behav Sci* 2003; 80:207-231.

46. Lipkind D, Nottebohm R, Rado R, Barnea A. Social change affects the survival of new neurons in the forebrain of adult songbirds. *Behav Brain Res* 2002; 133:31-43.

47. Lovic V, Palombo DJ, Fleming AS. Impulsive rats are less maternal. *Dev Psychobiology* 2011; 53:13-22.

48. Lukas M, Bredewold R, Landgraf R, Neumann ID, Veenema AH. Early life stress impairs social recognition due to a blunted response of vasopressin release within the septum of adult male rats. *Psychoneuroendocrinology* 2011; 36:843-853.

49. Maatje K, Verhoeff J, Kremer WDJ, Cruijsen ALM, van den Ingh TSGAM. Automated feeding of milk replacer and health control of group-housed veal calves. *Vet Rec* 1993; 133:266-270.

50. Mattiello S, Canali E, Ferrante V, Caniatti M, Gottardo F, Cozzi G, Andrighetto I, Verga M. The provision of solid feeds to veal calves: II. Behavior, physiology, and abomasal damage. *J Anim Sci* 2002; 80:367-375.

51. McGuirk SM. Disease management of dairy calves and heifers. *Vet Clin North Am Food Anim Pract* 2008; 24:139-153.

52. Meagher RK, Daros RR, Costa JHC, von Keyserlingk MAG, Hötzel M, Weary DM. Individual housing impairs reversal learning and increases fear of novel objects in dairy calves. *PLoS ONE* 2015; 10:e0132828.

53. Moberg GP, Wood VA. Effect of differential rearing on the behavioural and adrenocortical response of lambs to a novel environment. *Appl Anim Ethol* 1982; 8:269-279.

54. Mounier L, Dubroeucq H, Andanson S, Veissier I. Variations in meat pH of beef bulls in relation to conditions of transfer to slaughter and previous history of the animals. *J Anim Sci* 2006; 84:1567-1576.

55. Napolitano F, De Rosa G, Sevi A. Welfare implications of artificial rearing and early weaning in sheep. *Appl Anim Behav Sci* 2008; 110:58-72.

56. Napolitano F, Cifuni GF, Pacelli C, Riviezzi AM, Girolami A. Effect of artificial rearing on lamb welfare and meat quality. *Meat Sci* 2002; 60:307-315. 57. Nolte DL, Provenza FD, Balph DF. The establishment and persistence of food preferences in lambs exposed to selected foods. *J Anim Sci* 1990; 68:998-1002.

58. Pedersen RE, Sørensen JT, Skjøth F, Hindhede J, Rousing Nielsen T. How milk-fed dairy calves perform in stable versus dynamic groups. *Livest Sci* 2009; 121:215-218.

59. Perez E, Noordhuizen JPTM, Van Wuijkhuise LA, Stassen EN. Management factors related to calf morbidity and mortality rates. *Livest Prod Sci* 1990; 25:79-93.

60. Piller CAK, Stookey JM, Watts JM. Effects of mirror-image exposure on heart rate and movement of isolated heifers. *Appl Anim Behav Sci* 1999; 63:93-102.

61. Provenza FD, Balph DF. Diet learning by domestic ruminants: theory, evidence and practical implications. *Appl Anim Behav Sci* 1987; 18:211-232. 62. Raboisson D, Delor F, Cahuzac E, Gendre C, Sans P, Allaire G. Perinatal, neonatal, and rearing period mortality of dairy calves and replacement heifers in France. *J Dairy Sci* 2013; 96:2913-2924.

63. Reinhardt V, Reinhardt A. Natural sucking performance and age of weaning in zebu cattle (Bos indicus). *J Agr Sci* 1981; 96:309-312.

64. Schrijver NC, Würbel H. Early social deprivation disrupts attentional, but not affective, shifts in rats. *Behav Neurosci* 2001; 115:437-442.

65. Schrijver NC, Bahr NI, Weiss IC, Würbel H. Dissociable effects of isolation rearing and environmental enrichment on exploration, spatial learning and HPA activity in adult rats. *Pharmacol Biochem Behav* 2002; 73:209-224.

66. Shapiro LE, Insel TR. Infant's response to social separation reflects adult differences in affiliative behavior: A comparative developmental study in prairie and montane voles. *Dev Psychobiol* 1990; 23:375-393.

67. Steenkamer N. Alternative housing systems for veal calves, their effect on welfare and performance and their economic feasibility. In: Signoret JP, ed. *Welfare and husbandry of calves: current topics in veterinary medicine and animal science.* Hingham, MA: Springer, 1982; 226-234 68. Svensson C, Liberg P. The effect of group size on health and growth rate of Swedish dairy calves housed in pens with automatic milk-feeders. *Prev Vet Med* 2006; 73:43-53.

69. Svensson C, Lundborg K, Emanuelson U, Olsson S. Morbidity in Swedish dairy calves from birth to 90 days of age and individual calf-level risk factors for infectious diseases. *Prev Vet Med* 2003; 58:179-197.

70. Tapki I. Effects of individual or combined housing systems on behavioural and growth responses of dairy calves. *Acta Agric Scand* 2007; Sect. A 57:55-60.

71. Toth M, Mikics E, Tulogdi A, Aliczki M, Haller J. Post-weaning social isolation induces abnormal forms of aggression in conjunction with increased glucocorticoid and autonomic stress responses. *Horm Behav* 2011; 60:28-36. 72. USDA. Dairy 2014, "Dairy Cattle Management Practices in the United States, 2014" USDA–APHIS–VS–CEAH–NAHMS. Fort Collins, CO. 2016; #692.0216.

73. van Putten G. Welfare in veal calf units. *Vet Rec* 1982; 111:437-440.

74. Vasseur E, Borderas F, Cue RI, Lefebvre D, Pellerin D, Rushen J, Wade KM, de Passillé AM. A survey of dairy calf management practices in Canada that affect animal welfare. *J Dairy Sci* 2010; 93:1307-1316.

75. Veenema AH, Blume A, Niederle D, Buwalda B, Neumann ID. Effects of early life stress on adult male aggression and hypothalamic vasopressin and serotonin. *Eur J Neurosci* 2006; 24:1711-1720.

76. Veenema AH, Bredewold R, Neumann ID. Opposite effects of maternal separation on intermale and maternal aggression in C57BL/6 mice: link to hypothalamic vasopressin and oxytocin immunoreactivity. *Psychoneuroen*-*docrinology* 2007; 32:437—450.

77. Vitale AF, Tennucci M, Papini M, Lovari S. Social behaviour of the calves of semi-wild aremma cattle, bos primigenius taurus. *Appl Anim Behav Sci* 1986; 16:217-231.

78. von Keyserlingk M AG, Brusius L, Weary DM. Competition for teats and feeding behavior by group-housed dairy calves. *J Dairy Sci* 2004; 87:4190-4194.

79. Wagner K, Seitner D, Barth K, Palme R, Futschik A, Waiblinger S. Effects of mother versus artificial rearing during the first 12 weeks of life on challenge responses of dairy cows. *Appl Anim Behav Sci* 2014; 164:1-11.

80. Wagner K, Seitner D, Barth K, Palme R, Futschik A, Waiblinger S. Integration into the dairy cow herd: Long-term effects of mother contact during the first twelve weeks of life. *Appl Anim Behav Sci* 2012; 141:117-129.

81. Walker WL, Epperson WB, Wittum TE, Lord TK, Rajala-Schultz PJ, Lakritz J. Characteristics of dairy calf ranches: morbidity, mortality, antibiotic use practices, and biosecurity and biocontainment practices. *J Dairy Sci* 2012; 95:2204-2214.

82. Waltner-Toews D, Martin SW, Meek AH. Dairy calf management morbidity and mortality in Ontario Holstein herds. I: The data. *Prev Vet Med* 1986; 4:103-124.

83. Waltner-Toews D, Martin Sw, Meek AH. Dairy calf management, morbidity and mortality in Ontario Holstein herds. III. Association of management with morbidity. *Prev Vet Med* 1986; 4:137-158.

84. Warnick VD, Arave CW, Mickelsen CH. Effects of group, individual, and isolated rearing of calves on weight gain and behavior. *J Dairy Sci* 1977; 60:947-953.

85. Webster AJF, Saville C, Church BM, Gnanasakthy A, Moss R. 1985. Some effects of different rearing systems on health, cleanliness and injury in calves. *Br Vet J* 141:472-483.

86. Worobec EK, Duncan IJH, Widowski TM. The effects of weaning at 7, 14 and 28 days on piglet behaviour. *Appl Anim Behav Sci* 1999; 62:173-182.