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Dam-rearing of dairy calves in automatic milking systems

Evaluation of behaviour, growth, fertility
and first-lactation milk yield

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Abstract

Cow-calf contact (CCC) systems offer behavioural and nutritional opportunities for dairy calves that are often restricted or altogether lacking in artificial rearing systems. However, research thus far has focused heavily on the short-term effects of providing CCC, and rarely on contact periods longer than 3 months. The aim of this thesis was to assess the behavioural development and productive performance of dam-reared dairy calves, from birth to the end of their first lactation. Calves were reared in 1 of 5 experimental trials; calves (12–26 per trial) had 3–6 months of full contact with their dams, after which they were weaned, separated, and managed with other youngstock on the research farm. To allow for comparisons of growth, fertility, and first-lactation milk yield, dam-reared heifers were matched on a 1:1 basis to farm-managed, artificially-reared heifers. During the preweaning rearing period, calves housed in a calf-driven system performed fewer but longer suckling bouts as they aged, while this change in suckling behaviours was not observed in calves housed with cow-driven CCC. Allosuckling (i.e., suckling on cows other than the dam) behaviour increased with age for all calves when housed indoors, and was more prevalent with cow-driven CCC. Additionally, dam-reared heifers grew at high rates (1.1–1.4 kg/d) during the contact period. In response to fenceline weaning at both 4 and 6 months of age, calves vocalised, reduced their lying time, increased their locomotor activity, and demonstrated growth checks. These responses were slightly stronger for 4-month-old calves but were overall not associated with time spent in close proximity to dams prior to weaning. Fertility-based measures appeared similar between dam-reared and artificially-reared animals, both prior to first calving and during the first lactation. Dam-reared animals produced less milk and had a poorer persistency during their first lactation; however, milk yield varied between individuals, which may be linked to differences in dam-calf contact management during rearing. This thesis provides evidence that extended periods (i.e., 3–6 months) of dam-calf contact facilitate high growth and expression of motivated suckling behaviours in calves prior to weaning, but may negatively influence long-term productive performance.

Keywords: cow-calf contact, dam rearing, calf management, heifer development, suckling, dam-calf bond, weaning distress, milk yield, fertility, dairy cattle

Mjölkraskalvar som hålls tillsammans med kor i automatiska mjölkningssystem

Utvärdering av beteende, tillväxt, fertilitet samt mjölmängd i första laktationen

Sammanfattning

Mjolkproduktion där ko och kalv har kontakt med varandra (CCC) erbjuder beteendemässiga och näringsmässiga möjligheter för kalvarna som ofta är begränsade eller helt saknas i artificiella uppfödningssystem. Hittills har forskningen dock i hög grad fokuserat på kortsiktiga effekter av CCC och sällan utvärderat kontaktperioder längre än 3 månader. Syftet med denna avhandling var att utvärdera hur CCC kalvar utvecklas från födseln till slutet av deras första laktation. Kalvarna hölls med korna i fem separata försöksomgångar med 3–6 månaders kontakt som antingen styrdes av korna (4 omgångar) eller kalvarna (1 omgång). För jämförelser av tillväxt, fertilitet och mjölmängd under den första laktationen matchades CCC kvigor 1:1 med artificiellt uppfödda kvigor i samma besättning. Under mjolkperioden diade kalvarna i det kalvstyrd systemet färre gånger per dygn, men längre tid per gång med ökande ålder, detta mönster sågs inte hos kalvarna i det kostyrda systemet. Andelen korsdiande (att dia annan ko än sin moder) ökade med åldern för alla kalvar och var överlag vanligare i det kodrivna systemet. I tillägg hade kvigkalvarna uppfödda i CCC system hög tillväxt (1,1–1,4 kg/dag) under perioden de gick med kor. Vid avvänjning reagerade kalvarna med fler vokalisationer, minskad liggtid, ökad rörelse och avstannad tillväxt, både när avvänjningen gjordes vid 4 och 6 månaders ålder. Dessa reaktioner var något starkare hos kalvar som avvandades vid 4 månader, däremot var de inte relaterade till hur nära kalvarna uppehöll sig sina mödrar innan avvänjningen. Utvärderade fertilitetsmått var likartade mellan djur som fötts upp i CCC och artificiellt, både före första kalvningen och under den första laktationen. De djur som fötts upp i CCC system producerade mindre mjölk och hade sämre uthållighet i sin första laktation, det var dock stor variation i mjölmängd mellan CCC individer. Denna avhandling ger belägg för att längre perioder (3–6 månader) av kontakt mellan kalvar och deras mödrar ger förutsättningar för hög tillväxt och uttryck av sugbeteende hos kalvar före avvänjning, men kan påverka den långsiktiga produktionen negativt.

Nyckelord: ko och kalv, uppfödning av kalvar, kalvskötsel, utveckling av kvigor, digivning, anknytning, avvänjningsstress, fertilitet, mjölmängd, mjölkkor

Dedication

To Kiah.



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List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I. Wegner, C.S., Chan, C.W., Rönnegård, L., Agenäs, S., Lidfors, L. and Eriksson, H.K. (2025). Suckling and allosuckling behavior of dairy calves in indoor dam-rearing systems. *Frontiers in Veterinary Science*, 12, 1617158.
- II. Wegner, C.S., Rönnegård, L., Agenäs, S. and Eriksson, H.K. (2025). Behavioural responses of dairy cows and calves to fenceline weaning after 4 or 6 months of full cow-calf contact. *Animal*, 19 (6), 101525.
- III. Wegner, C.S., Eriksson, H.K., Edvardsson Rasmussen, A., Agenäs, S., Rönnegård, L. and Ferneborg, S. Effects of extended dam-calf contact on growth, first-lactation milk yield, and reproductive performance in dairy heifers—A retrospective cohort study. (manuscript)

Papers I and II are published open access.

The contribution of Claire Wegner to the papers included in this thesis was as follows:

- I. Planned, performed, and supervised data collection in both studies, and analysed the data. Wrote the first draft of the manuscript, produced all figures and tables, and prepared and uploaded data to an online repository.
- II. Contributed to planning and developing data collection protocols for the weaning study, and had the main responsibility for coordinating and running the larger on-farm trial. Conducted a formal analysis of the data, interpreted the data, created figures and tables, and wrote the first draft of the manuscript. Prepared and uploaded data to an online repository.
- III. Planned the study, collected data from the research farm database, and performed a formal analysis of the data. Interpreted the data, wrote the first draft of the manuscript (apart from the discussion on reproductive performance), and produced all figures and tables.

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Abbreviations

ADG	Average daily gain
AR	Artificially-reared
BW	Body weight
CCC	Cow-calf contact
DR	Dam-reared
ECM	Energy-corrected milk
EMM	Estimated marginal mean
IQR	Inter-quartile range
SD	Standard deviation
SE	Standard error
SH	Swedish Holstein
SR	Swedish Red

1. Introduction

Over the past 35 years, the dairy sector has undergone considerable development in response to technological advancements, environmental and economic pressures, and shifting societal perspectives on animal welfare. Perhaps most obvious is the global shift towards fewer, but larger, farms (Barkema et al. 2015). In Sweden, for example, there has been a nearly 90% reduction in the number of individual dairy farms since 1990, while the average herd size has more than quadrupled (Karlsson et al. 2023). Notable farm-level changes include a transition towards loose-housing systems (Barkema et al. 2015; Karlsson et al. 2023), and an uptake in automatic milking systems following their commercial introduction in 1992 (de Koning 2011). On an animal level, social housing is increasingly recommended for calves over individual housing [e.g., by the European Food Safety Authority (EFSA; 2023) and the Canadian Code of Practice (NFACC 2023)].

Alongside changes on farms, public attitudes towards farm animal welfare are also shifting (Alonso et al. 2020). Many citizens—including both those affiliated and unaffiliated with the dairy sector—express disapproval of contentious practices such as early cow-calf separation (North America: Ventura et al. (2013), Sirovica et al. (2022); Germany: Busch et al. (2017); Brazil: Hötzel et al. (2017)). The practice of separating the calf from the dam shortly after birth and thereafter rearing the calf individually (as opposed to in groups) is still widely implemented across the US (70% of farms; USDA 2016) and Europe (78% [median] of farms across 14 countries; Marcé et al. 2010). Arguments for this practice include a reduced risk of disease transmission, the ability to ensure adequate colostrum intake in newborn calves (Ventura et al. 2013; Sumner & von Keyserlingk 2018), and the aim of avoiding later separation distress by limiting the development of a strong dam-calf bond (Sirovica et al. 2022). Nevertheless, there is a growing global interest in allowing dairy calves to be reared by their dams.

Systems wherein dairy calves are managed alongside adult cattle—so-called cow-calf contact (CCC) systems (Sirovnik et al. 2020)—offer behavioural (e.g., suckling) and social (e.g., maternal-filial bonding, group housing) opportunities that are often lacking for artificially-reared calves. Although research on CCC systems has expanded substantially in recent years (Aytemiz Danyer et al. 2024), critical knowledge gaps must be addressed before these systems can be successfully implemented on a larger

scale. This thesis will investigate approaches to rearing dairy calves with their dams in freestall housing systems that use automatic milking, considering differences in pen design and type of dam-calf contact. The physical and behavioural development of the calves will be examined from birth, through a dam-calf contact period of 3 to 6 months, to the end of their first lactation. Furthermore, the productive performance of heifers and primiparous cows, including fertility-based measures and milk yield, will be assessed in relation to providing early-life dam-calf contact. In altogether doing so, this thesis aims to guide recommendations for further developing dam-rearing systems that are practical for producers while still supporting high standards of welfare for calves.

2. Background

2.1 Cow-calf contact systems

To put it simply, “CCC system” is an umbrella term to describe any dairy system where cows and calves are housed together, including both foster cow systems and dam-calf contact (i.e., dam-rearing) systems. Terminology for describing CCC systems was developed by Sirovnik et al. (2020) to foster clear and unambiguous dialogue among stakeholders. At minimum, CCC systems should be characterised by the type of physical contact they permit, the duration of daily CCC, and whether it is the cow or calf that has primary control over the amount of physical contact (see Figure 1). Additional distinctions can be made to include the type of cow traffic in the pen (free, pre-milking, or post-milking) and whether there are shared resources available within contact areas—barn areas wherein physical CCC is possible.

Despite agreement on terminology, no official definition for what constitutes a CCC system—and thus differentiates it from artificial rearing systems—exists, neither in literature nor through industrial guidelines. There is currently a wide range of contact periods used when defining CCC systems, particularly within qualitative or survey-based studies, where some research questions have required a distinction. For example, Neave et al. (2022) categorised New Zealand farmers as practising CCC if dam-calf contact was permitted for at least 48 hours, likely due to the rarity of this practice regionally at the time. Alternatively, to eliminate producers that only

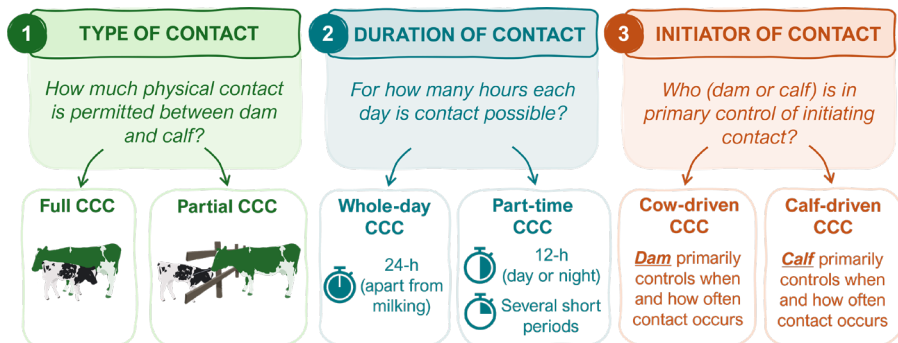


Figure 1. Terminology used to describe cow-calf contact (CCC) systems based on the type, duration, and primary initiator of contact, as adapted from Sirovnik et al. (2020).

practised CCC during the colostrum-feeding period, Eriksson et al. (2022) required a minimum of 7 days of contact for inclusion in their survey of European CCC practices. Others still have defined CCC as farms keeping cows and calves together for at least 2 weeks (Vaarst et al. 2020; Hansen et al. 2023). It remains unclear what length of contact sufficiently benefits both cow and calf to offset the stress of separation (Sirovnik et al. 2020), although for calves, the benefits of CCC are likely to increase with the contact duration (EFSA 2023).

Recently, efforts have been made to identify and describe existing CCC systems in Europe (Eriksson et al. 2022; Bertelsen & Vaarst 2023; Johanssen et al. 2023; Rell et al. 2024) and North America (Durrenwachter et al. 2025), revealing a wide range of management solutions with clear regional differences. According to Eriksson et al. (2022), who surveyed 104 farms practising CCC across 6 European countries, this can be viewed as an indication that CCC is feasible across a variety of management systems. In general, CCC farms tend to have smaller herd sizes compared to farms primarily practising artificial rearing (Eriksson et al. 2022; Hansen et al. 2023), although there is some evidence of cow-calf rearing on larger farms (i.e., 450–600 adult cows; Eriksson et al. 2022; Vaarst & Christiansen 2023).

Further insights can be drawn from those directly responsible for the successful implementation of CCC: the farmers. Concerns for farm economy (e.g., labour increases, loss of saleable milk) and calf welfare (e.g., poor colostrum intake, stress of separation after prolonged CCC) are often expressed by farmers who currently practice artificial rearing, with many further viewing their current barn setups as unsuitable for facilitating cow-calf (Neave et al. 2022; Hansen et al. 2023) or dam-calf (Bertelsen & Vaarst 2023) contact. In contrast, current CCC practitioners identified many of the same factors as drivers for implementing CCC, citing a reduced workload (Neave et al. 2022; Bertelsen & Vaarst 2023) and improvements for calf welfare (Eriksson et al. 2022; Hautzinger et al. 2025). Nonetheless, the issue of separation stress is often echoed among CCC farmers (Vaarst et al. 2020; Eriksson et al. 2022; Hansen et al. 2023; Johanssen et al. 2023; Hautzinger et al. 2025). In a sample of Norwegian farmers who had discontinued the practice and returned to artificial rearing, separation stress was reported as the primary reason by 54% of the total 213 respondents (Hansen et al. 2023). While it would be valuable to further dissect the individual experiences of these producers, continued research is needed to develop weaning and

separation methods that minimise stress for the cow, calf, and farmer (see Section 2.2.2). Ultimately, understanding how farmers perceive both the barriers and benefits of CCC systems is crucial for developing support tools that are context-specific, relevant, and practical for implementation.

Given the novelty of the research field, these insights from farmers' varied experiences may provide a foundation for future experimental studies. It is important to note that some of the experiences described by farmers relate to CCC systems that utilise foster cows, either as a sole rearing method or in combination with dam-rearing (Eriksson et al. 2022; Bertelsen & Vaarst 2023). While foster-cow systems may provide a feasible means of achieving CCC, it remains a topic that requires further research and discussion (see Whalin et al. 2025). To remain aligned with the scope of this thesis, the following sections will focus largely on dam-calf contact systems.

2.2 Development of dam-reared calves

The early life of a dairy heifer reared in a dam-calf contact system can effectively be broken down into three distinct phases: the milk-feeding (i.e., preweaning) phase, the weaning and separation phase, and the postweaning phase. While the length of each phase may differ vastly across farms and regions (Eriksson et al. 2022), there remain commonalities in the early-life experiences and development—both social and physical—of dam-reared heifers.

2.2.1 Milk-feeding phase

During the milk-feeding phase, calves in dam-calf contact systems have access to behavioural and nutritional opportunities beyond those offered to artificially-reared calves. To begin, dam-reared calves have the possibility to develop a unique social bond, known as a dam-calf (or maternal-filial) bond, and to perform highly motivated behaviours such as suckling. Additionally, calves in these systems are often not subject to the same degree of feed restriction as in other conventional rearing systems (e.g., whole milk or milk replacer fed at 10% of body weight; Urie et al. 2018; Mahendran et al. 2022), which may translate to increases in growth and physical development (as reviewed by Meagher et al. 2019). In Europe, the length of the milk-feeding phase on CCC farms may be inferred based on reports of median weaning age (12 weeks in non-organic CCC systems, 17 weeks in organic), although

this estimate includes periods of artificial milk-feeding, as well as foster cow and hybrid (i.e., mix of foster cow and dam-rearing) systems (Eriksson et al. 2022).

Dam-calf bond

The dam-calf bond, like other strong social bonds, is resilient to short-term separations and is expressed through affiliative behaviours, such as a preference for close proximity and allogrooming (Newberry & Swanson 2001). This bond is established within hours of birth, presumably facilitated by maternal licking, and continues to strengthen over the following days (von Keyserlingk & Weary 2007; Lidfors 2022). To date, work within dam-calf contact systems has explored factors affecting the strength of the dam-calf bond; more specifically, whether bond strength is influenced by the daily duration (full vs part-time; Bertelsen & Jensen 2023a; Jensen et al. 2024a) or extent (permission vs restriction of suckling; Johnsen et al. 2015; Wenker et al. 2020) of physical CCC.

Despite its function in reinforcing the dam-calf bond, exploration of spatial proximity in the context of dam-calf attachment is limited. Studies of indoor-housed beef (Stěhulová et al. 2013) and free-ranging Raramuri Criollo (Nyamuryekung'e et al. 2020) cattle have shown that dam-calf pairs spend progressively less time in close proximity (i.e., within 1–2 m) over the calf's first month of life. A similar pattern was observed for free-ranging Maremma dam-calf pairs up to an age of two months; however, in this study, a wider definition of what constitutes “close” proximity was used (≤ 15 m; Vitale et al. 1986). Interestingly, Wenker et al. (2021) only observed a decrease in dam-calf proximity for indoor-housed dairy cattle with part-time CCC, while no such patterns were evident in pairs with full CCC. However, the authors only reported the time spent in close proximity when the dam was standing, whereas the other studies did not discriminate based on cow or calf posture (Vitale et al. 1986; Stěhulová et al. 2013; Nyamuryekung'e et al. 2020). Beyond two months of age, time spent in close proximity appears largely independent of calf age (beef, age 2–5 months; Kour et al. 2021b).

Suckling behaviour

Suckling, referring to the calf's ingestion of milk from an udder (Sirovnik et al. 2020), is a highly motivated behaviour that functions primarily to provide nutrition for the calf. Our knowledge of this behaviour is based largely on non-dairy breeds (see review by Lidfors 2022), since management practices

in dairy production have historically restricted opportunities for study. Understanding how suckling behaviour of dairy calves manifests under different CCC conditions is essential for developing nuanced approaches to dam-rearing.

Logically, one might begin by exploring calf behaviour in relation to daily contact time. Dairy calves in loose-housing systems with whole-day CCC have been observed to perform between 7 and 13 suckling bouts per day (Bertelsen & Jensen 2023a), which aligns with reports for free-ranging beef calves (Kour et al. 2021a). In a 24-hour period, the total amount of time dairy calves spend suckling can range from 32 to 44 minutes (Fröberg & Lidfors 2009; Bertelsen & Jensen 2023a; Jensen et al. 2024b). Reducing the available time for dam-calf contact does not always result in a corresponding reduction in suckling time. Several studies have compared the behaviour of calves housed with either whole-day or half-day contact and found no visible differences in the total duration (Jensen et al. 2024b) or frequency of suckling per day (Bertelsen & Jensen 2023a). Even after restricting some calves from half-day contact to a mere 2 hours of daily contact time, Jensen et al. (2024b) found that their total suckling time remained the same. Thus, in these cases, calves appear capable of adapting their feeding patterns in response to the available contact time. In systems where contact is restricted to short (i.e., 15–30 minutes) periods before or after milking, a practice used by over one-third of European CCC producers (Eriksson et al. 2022), calves perform on average three bouts per day, together totalling 24–29 minutes of suckling (Margerison et al. 2003; Fröberg et al. 2008; Roth et al. 2009). However, while the expression of suckling behaviours is clearly altered under this degree of contact restriction, calves performed very few non-nutritive oral behaviours (Margerison et al. 2003; Fröberg et al. 2008), suggesting that their motivation to suckle may still be satisfied.

The age of the calf can also influence suckling behaviour. Observations over the first two months of life reveal that dairy calves change their behaviour to perform fewer (Fröberg & Lidfors 2009; Bertelsen & Jensen 2023a), but longer (Lidfors et al. 2010; Johanssen et al. 2024), suckling bouts per day, perhaps in response to a growth in stomach capacity. However, longitudinal studies are scarce, and those available have only followed calves up to 9 weeks of age. It is unknown how suckling behaviour develops up to ages that reflect current milk-feeding practices within CCC systems (i.e., 12–17 weeks; Eriksson et al. 2022).

One aspect of suckling that has often been observed but rarely discussed in literature is the performance of the behaviour on cows other than the dam—known as allosuckling. Several theories have been presented as to why this behaviour occurs from a biological perspective, some of which can be applied to cattle. One, allosuckling may improve the immunological competence of the calf, as suckling from several cows allows the calf to obtain a larger diversity of antibodies (Roulin & Heeb 1999). Second, this behaviour may be compensatory; for example, in response to a low birth weight (Víchová & Bartoš 2005). Third, allosuckling may simply serve to provide adequate nutrition (as reviewed by Mota-Rojas et al. 2021), contributing to the calf's growth, survival, and overall fitness. Allosuckling has also been interpreted as an indicator of a modified dam-calf bond; for example, when calves are born into group-housed settings, a substantial proportion direct teat-seeking or suckling towards alien cows (Edwards 1983; Illmann & Špinka 1993). However, despite reports of allosuckling occurring across a variety of dam-calf contact systems (Le Neindre 1989; Fröberg & Lidfors 2009; Johnsen et al. 2015; 2021a), only two studies have explored system-level differences—specifically, whole-day versus half-day contact—in relation to the behaviour (Bertelsen & Jensen 2023a; Jensen et al. 2024b). Factors pertaining to the individual calf, such as age, or to the management system itself, including whether contact is cow- or calf-driven, remain largely unexamined.

Calf growth

During the milk-feeding phase, average daily gain (ADG) is one of the most commonly reported indicators of calf physical development. While a high growth rate is often associated with dam-calf contact systems, including by farmers currently practising CCC (Eriksson et al. 2022; Hansen et al. 2023; Hautzinger et al. 2025), it is not necessarily an effect of the added contact *per se* (as discussed by Johnsen et al. 2016). High growth rates during the milk-feeding phase have also been achieved through feeding artificially-reared calves *ad libitum* whole milk (0.9 kg/d; Bertelsen & Jensen 2023b) or milk replacer (1.2 kg/d; Miller-Cushon et al. 2013). Regardless, calves reared with full, whole-day CCC have been reported to grow at rates ranging from 0.9 kg/d to 1.4 kg/d (Roth et al. 2009; Fröberg et al. 2011; Johnsen et al. 2021b; Bertelsen & Jensen 2023b; Zipp & Knierim 2024; van Zyl et al. 2025). While the range of ADG observed for calves in half-day CCC systems is slightly narrower (0.9–1.0 kg/d), studies comparing calf growth between

the two contact durations report no difference (Nicolao et al. 2022; Bertelsen & Jensen 2023b; Zipp & Knierim 2024). This suggests that the variation in calf growth observed across studies may be attributable to other differences in calf management.

In more restricted suckling systems, calf growth appears to depend on the timing of dam-calf contact relative to milking. Restricting contact to within 2 hours after milking has generally not been associated with positive effects on calf growth, with calves performing equally (0.5 kg/d; Fröberg et al. 2008) or worse (0.4 kg/d; Nicolao et al. 2022) compared to artificially-reared controls. This is likely due to a low availability of milk; Holstein-cross calves consumed on average only 1.1 kg of milk per day when contact was restricted to two 15-minute periods post-milking, despite spending a large proportion of this time suckling (Margerison et al. 2003). Conversely, providing dam-calf contact before milking has been shown in at least one study to result in good growth (0.7 kg/d, compared to 0.6 kg/d for control calves offered 8 kg milk/day; Nicolao et al. 2022). To even further solidify the relationship between weight gain and milk intake, calves with access to partial dam-calf contact (i.e., no suckling permitted) do not always demonstrate the growth gains typically observed with CCC (also reviewed by Meagher et al. 2019). For example, Wenker et al. (2022b) observed that calves fed identical milk diets (7.5–10.5 L/d)—but differed in whether or not they had partial CCC—grew at comparable rates, while calves with full CCC grew an average 0.3 kg more per day. Ultimately, calf growth during the milk-feeding period is closely linked to milk intake; systems that restrict milk availability in some capacity (e.g., through restricting the daily contact duration) can expect lower growth rates compared to systems that do not.

2.2.2 Weaning and separation

In CCC systems, the processes of weaning and separation from the dam are often discussed in tandem, as both represent major stressors for calves and typically occur relatively close in time. These events not only impact calf welfare but are also a key concern for farmers, who frequently cite separation distress as a major challenge in maintaining CCC systems (Eriksson et al. 2022; Hansen et al. 2023; Hautzinger et al. 2025). Consequently, much of the existing research has focused on **how** these procedures are carried out, with particular attention to methods that may mitigate stress and growth checks—such as gradually reducing daily contact time to limit milk intake,

thereby more closely mimicking the gradual weaning process observed under semi-natural conditions (as reviewed by Whalin et al. 2021, 2025).

Abrupt, two-step, and gradual weaning and separation strategies

Under abrupt weaning, calves experience the sudden and simultaneous loss of milk and maternal contact, often eliciting strong behavioural responses (Bertelsen & Jensen 2023b; Neave et al. 2024a) and short-term depressions in growth (Roth et al. 2009; Fröberg et al. 2011). As such, efforts have been made to develop methods that separate weaning and separation events temporally, either through two-stage (e.g., nose flaps or fenceline separation) or gradual approaches (e.g., daily or weekly reductions in CCC). Indeed, compared to abruptly weaned calves, fenceline separation has been demonstrated to result in fewer high-pitched vocalisations and lower activity levels (Bertelsen & Jensen 2023b).

The use of nose flaps, which induces weaning while permitting continued physical dam-calf contact, is suggestively less effective in reducing weaning stress compared to fenceline separation (Wenker et al. 2022a) or a gradual reduction in dam-calf contact time over 3 weeks (1 week each of 12-h, 3.5-h, and fenceline contact; Vogt et al. 2024). Considering that nose flaps have also been shown to cause nasal tissue damage in dairy (Wenker et al. 2022a; Vogt et al. 2024) and beef (Lambertz et al. 2015a; Valente et al. 2022) calves, their suitability as a weaning method warrants reconsideration.

Interestingly, Neave et al. (2024a) found no difference in behavioural responses for calves weaned abruptly or following a three-step reduction in contact time over 2 weeks (50% of 23 h/d for 1 week, then 25% for 1 week, followed by total separation). Observations of suckling behaviour in the same study indicate that reduced contact time did not necessarily limit milk intake (Jensen et al. 2024b), suggesting that calves with step-wise reduction in contact time may in practice have experienced an abrupt cessation of milk feeding. In general, findings regarding gradual weaning and separation methods are conflicting. The study by Vogt et al. (2024) reported high vocalisations for calves weaned gradually over 3 weeks—higher, even, than nose-flap-weaned calves—yet relatively minor reductions in ADG. Recently, van Zyl et al. (2025) tested a novel gradual method whereby the implementation of fenceline contact did not coincide with weaning. Calves were allowed to suckle through the fence with access time gradually reduced over 10 days, after which they were weaned but remained on fenceline contact for one week. They found that calves were able to maintain a high

ADG during the 4 weeks after weaning (1.0–1.1 kg/d); however, behavioural stress indicators were not recorded. Gradual reduction of contact time combined with supplemental milk feeding has also been investigated, where calves underwent a three-step reduction in contact time (24 to 12 h/d, 12 to 6 h/d, 6 to 0 h/d) over either a 4-week or 10-day period prior to weaning (Johnsen et al. 2024; Sørby et al. 2024b). Calves separated over a shorter period emitted more high-pitched vocalisations upon the initial reduction in contact and showed more severe growth checks at the final reduction step, suggesting that a temporally more gradual separation method may be preferred. However, variation in calf responses may further depend on supplemental milk intake (Johnsen et al. 2021b); calves that consumed greater volumes of milk (>1.5 L/d) from an automatic milk feeder were observed to vocalise less and grow at higher rates throughout either separation process (Johnsen et al. 2024; Sørby et al. 2024b).

Considerations of daily contact duration

It has been hypothesised that calves with half-day CCC (i.e., 10–12 h/d) during the milk-feeding phase may be better prepared, nutritionally and socially, for weaning and separation (Neave et al. 2024a). However, empirical evidence suggests that calves with both half-day and whole-day contact respond equally strongly to these events (Bertelsen & Jensen 2023b; McPherson et al. 2025), although the timing of high-pitched vocalisations may differ slightly post-separation (Neave et al. 2024a). Additionally, calves reared with both contact durations experience growth checks of similar magnitudes postweaning (Bertelsen & Jensen 2023b; Zipp & Knierim 2024; McPherson et al. 2025).

Weaning and separating calves based on age

Studies examining age-related differences in calf responses consistently report that separating dam-calf pairs at later ages (i.e., 4–14 days) induces greater distress than when the pair is parted within the first day after birth (Lidfors 1996; Weary & Chua 2000; Flower & Weary 2001). Yet, no work to date has explicitly investigated the responses of dam-reared dairy calves when weaned from milk at different ages. While beef cattle studies (e.g., Lambertz et al. 2015b; Stěhulová et al. 2017) have explored weaning ages extending to those observed under semi-natural conditions (7–14 months; Reinhardt & Reinhardt 1981), the sustained high milk production of dairy

breeds complicates direct comparison between systems. This area requires further research to inform management decisions on optimal weaning age.

2.2.3 Long-term development

Knowledge is scarce regarding the physical and behavioural development of dam-reared calves beyond weaning, likely due to the high costs associated with longitudinal research. Several studies have examined calf growth beyond the milk-feeding phase, though most have focused on relatively short time frames. Wenker et al. (2022b) and Sørby et al. (2024a) reported no differences in 6-month body weight among calves reared with varying dam-calf contact, which ranged in both type (full, partial, or none) and duration (0–67 d). However, in both these studies, non-suckling calves were often offered high volumes of whole milk (Wenker et al. (2022b): 7.5–9 L/d; Sørby et al. (2024a): *ad libitum* for 72% of artificially-reared calves). In contrast, Sinnott et al. (2024) observed a numerically greater body weight at 6 months for calves with 8 weeks of full CCC, although differences in skeletal growth compared with artificially-reared calves had disappeared by 4 months.

Given the limited research on long-term development, it may be relevant to expand our definition of CCC to once more include foster cow systems. Not including studies where contact was limited to the colostrum feeding period (Krohn et al. 1999; Valníčková et al. 2020), only two studies have reported findings related to the later productive performance of calves reared with extended CCC. When comparing primiparous cows that had been dam- or artificially-reared, Zipp & Knierim (2020) reported no differences in age at first calving or milk yield during the first 100 days of lactation. However, as acknowledged by the authors, this study lacked statistical power due to the small sample size (5–9 cows per rearing treatment). Nonetheless, this contrasts with earlier work that compared foster calves reared with restricted CCC (15 minutes suckling, permitted 3 times daily) or artificially (≤ 3 L milk replacer, bucket-fed once daily) for 6 weeks (Bar-Peled et al. 1997). The authors reported a greater performance for CCC-reared individuals, including higher growth rates from birth to conception, a lower age at both conception and first calving, and a tendency for greater uncorrected milk yield during the first 300 days of lactation. Given the limited time for CCC, these findings are likely explained by the quality (i.e., whole milk vs milk replacer) and quantity of liquid feed offered to foster calves.

Furthermore, there may be long-term benefits for the social development of CCC-reared calves. Wagner et al. (2012) observed that dam-reared heifers displayed more submissive behaviours than artificially-reared heifers when introduced to the cow herd prior to calving, which the authors interpreted as evidence of more appropriate social behaviour. Additionally, Le Neindre (1989) reported a greater expression of maternal care—as indicated by calf-directed licking and nursing—by primiparous cows that were foster-cow-reared for 8 months, compared to those reared conventionally.

To reiterate, knowledge of how early-life CCC influences calf behaviour and productive performance beyond weaning and separation is severely lacking. An understanding of how different CCC management choices may affect, for example, the reproductive performance and milk yield of cows in the long term is essential for helping producers make informed on-farm decisions.

2.3 Welfare in dam-calf contact systems

Animal welfare can be conceptualised in various ways, but most frameworks converge on three interrelated dimensions: affective state (how the animal is feeling), biological functioning (whether the animal is healthy and functioning well), and natural living (the ability of the animal to live a reasonably natural life) (Fraser et al. 1997; von Keyserlingk et al. 2009). The Three Spheres model acknowledges these as core areas of welfare concern that can, and do, overlap (Figure 2; Fraser et al. 1997). At first glance, dam-calf contact systems appear to address all three concerns: calves are reared in a social environment that reflects more natural herd dynamics (Whalin et al. 2021), grow at high rates (see 2.2.1), and often perform behaviours that may be indicative of a positive affective state, such as play (Boissy et al. 2007; Waiblinger et al. 2020). However, these apparent benefits do not preclude the need for objective welfare assessment, as welfare outcomes may still vary depending on management practices and farm conditions. One recent study attempted to assess animal welfare at a farm level, using the Welfare Quality® protocol to compare indicators of calf and heifer welfare between farms practising CCC (≥ 12 weeks of suckling on dams or foster cows) versus early separation (< 24 h contact; Rademann et al. 2025). Briefly, this protocol uses mainly animal-based indicators to assess welfare across four principal areas—good feeding, good housing, good health, and

appropriate behaviour—and assigns a welfare classification (excellent, enhanced, acceptable, or not classified) based on area-level scores (Blokhuys et al. 2013). Rademann et al. (2025) reported an overall higher level of welfare on CCC farms, with proportionally more farms receiving an overall classification as “excellent”, and contact-reared animals scored higher than artificially-reared animals in both the housing and behaviour categories. This study was the first of its kind and highlighted the need for welfare assessment tools that are adapted to include CCC systems. Moreover, welfare will also differ between farms that practice dam-rearing. For example, half-day CCC compared to whole-day CCC has been shown to elicit a more negative emotional state in cows, based on findings from judgement bias and attentional scope tests (Neave et al. 2023; 2024b). In calves, Sinnott et al. (2024) reported a numerically greater frequency of abnormal oral behaviours for those with night-time versus whole-day contact. Together, these studies suggest that aspects of CCC systems, such as the duration of daily contact, have the potential to influence welfare, at least from the perspective of affective state. Comprehensive evaluations of calf (and cow) welfare across different systems—ideally encompassing all three spheres—will prove essential for developing approaches to dam-rearing that promote a high quality of life.

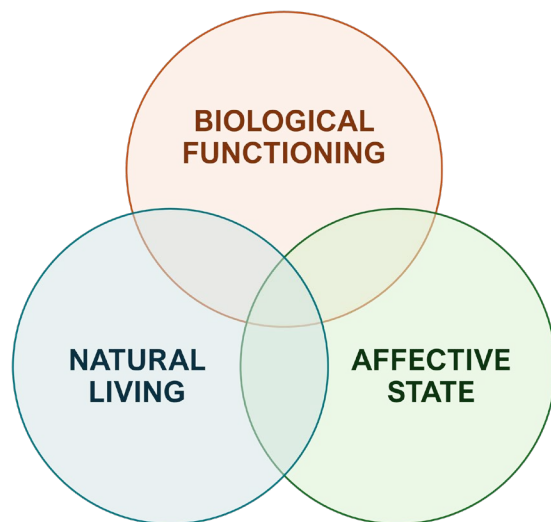


Figure 2. A visual representation of the Three Spheres model of animal welfare, based on Fraser et al. (1997) and redrawn from von Keyserlingk et al. (2009).

3. Aims

The main aim of the thesis was to evaluate the behaviour, growth, fertility, and milk yield of dam-reared dairy calves, from birth through to the end of their first lactation. Dairy calves were reared with dam-calf contact in one of five experimental trials, all of which contained freestall housing and automatic milking, but varied in the type of CCC permitted (i.e., cow-driven vs calf-driven) and both age at and method of weaning and separation.

Specific objectives were:

- To investigate calf suckling behaviour in a cow-driven and a calf-driven CCC system during the first 3 months of life (**Paper I**).
- To assess the frequency of allosuckling in a cow-driven and a calf-driven CCC system and investigate associations of the behaviour with calf age and other calf-level factors (**Paper I**).
- To evaluate changes in ADG and behavioural responses to fenceline weaning after 4 or 6 months of full CCC (**Paper II**).
- To examine the spatial relationship between dam-calf pairs prior to weaning and assess for potential effects on postweaning responses (**Paper II**).
- To estimate pre- and postweaning calf growth in varying dam-rearing systems and compare it to that of artificially-reared calves (**Paper II, Paper III**).
- To describe the fertility of dam-reared versus artificially-reared heifers through to the end of their first lactation (**Paper III**).
- To assess the milk yield of dam-reared versus artificially-reared primiparous cows during the first lactation (**Paper III**).

4. Materials and methods

4.1 Experimental farm and trials

All the experimental trials included in this thesis were performed at the Swedish University of Agricultural Sciences' Swedish Livestock Research Centre in Uppsala between August 2019 and June 2025. The research farm housed both Swedish Holstein (SH) and Swedish Red (SR) dairy cattle of high-producing genetic lines and operated with three primary objectives: research, education, and commercial milk production. At any point in time, there were approximately 240–250 lactating cows in the herd. Under normal (i.e., non-experimental) conditions, purebred heifer calves were reared on the farm as replacement heifers, while bull and beef-on-dairy calves were kept for 2 weeks and then sold to nearby farms to be raised for meat production.

Calves and their dams were enrolled into each trial, referred hereafter as a “batch”, over a 4–6-week period (see Figure 3 for a temporal overview). Enrolment criteria across all batches were that, prior to calving, the dam had no history of *S. aureus* mastitis and was not severely lame; the former was to adhere to the farm's biosecurity protocols, while the latter was to reduce the risk of dams leaving the herd during trial periods. Moreover, while in the individual calving pens, dams could not show aggression towards humans or their own calves; no dams were excluded on this basis. Additional criteria for batches 4 and 5 were that only heifer calves were included. Due to the additional recruitment of control cows in batches 1, 3, and 5 for health outcomes outside the scope of this thesis, dam breed and parity were balanced between the dam-rearing and control groups. A summary of the dams and calves recruited in each of the batches can be viewed in Table 1. A total of six dam-calf pairs were excluded from their respective batches (see Supplementary Table 1 in the Appendix for a detailed breakdown).

Within batches 1 and 3, control calves (born to enrolled control cows) were additionally kept. General management and feeding of these calves followed the artificial rearing protocols of the farm as closely as possible, although control calves in batch 3 were housed in groups (rather than individually) from birth and fed 3 L of whole milk, three times per day (compared to 3 L twice daily, as for farm-managed calves).

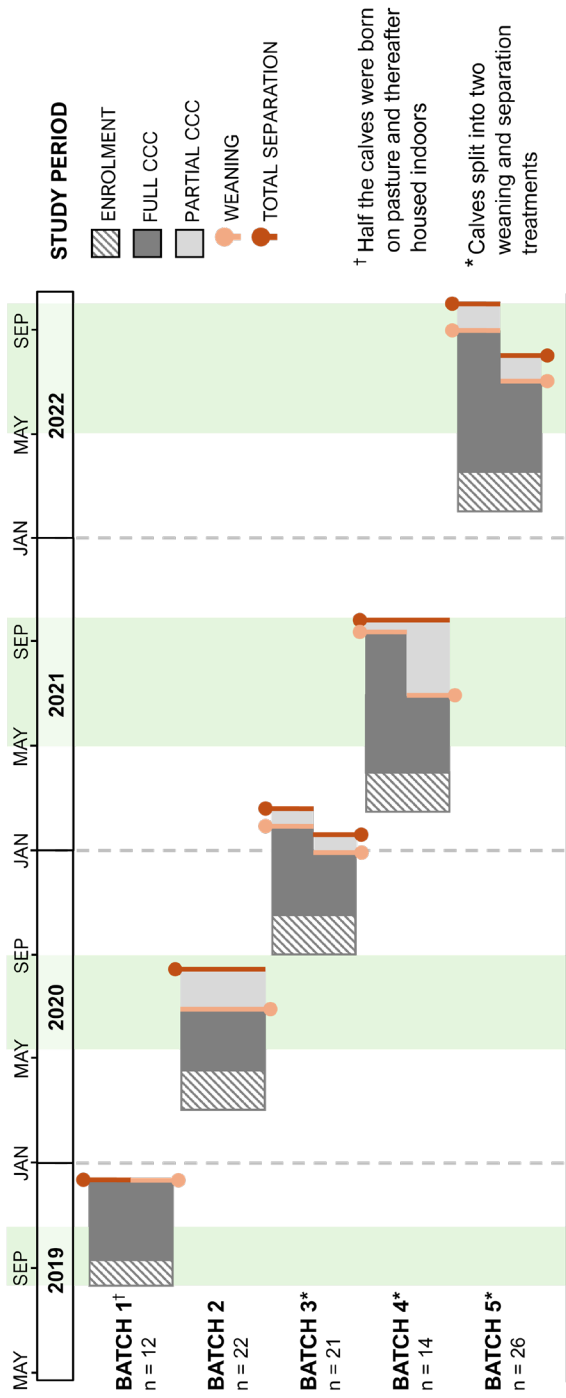


Figure 3. Overview of the experimental batches included in the thesis, from the beginning of enrolment (i.e., when calves were born) to the total separation of calves from their dams. Green shading represents time periods where calves were housed on (batches 1, 2, and 4) or had free access to (batch 5) pasture.

Table 1. An overview of the parity of dams, and both the sex and breed of calves, enrolled in each of the experimental batches as dam-calf contact pairs. Data shows the number of individuals per category of parity, sex, or breed.

		Batch 1	Batch 2	Batch 3	Batch 4	Batch 5
Dam parity	1	5	12	12	5	11
	2	3	4	5	6	5
	3	2	4	2	1	4
	4	2	2	2	2	5 ¹
Calf sex	Male	5	4	7	0	0
	Female	7	18	14	14	26
Calf breed²	SR	6	12	13	7	16
	SH	5	10	8	7	10
	Beef cross	1	0	0	0	0

¹One dam was enrolled with her twin calves.

²Breed: SR = Swedish Red, SH = Swedish Holstein.

The following sections include a general overview of the distinct periods across all the batches: the bonding period, milk-feeding phase, weaning and separation, and the postweaning period.

4.1.1 Bonding period

In batch 1, all dam-reared calves were born in straw-bedded shelters (11.5 m²) located outdoors on pasture. For the remaining four batches, calves were born indoors in individual calving boxes (12.6 m²), bedded with wood shavings. After calving, the quality of the dam's colostrum was measured by barn staff, and if the Brix was lower than 22%, the calf was bottle-fed colostrum from another cow. In batch 3, nine of the 19 dam-reared calves were bottle-fed high-quality colostrum within 6 h of being born as part of an unrelated research outcome.

In batch 1, dams remained with their calves in the individual calving shelters until the dam had been milked at least 6 times, which was done by bringing the dam in from pasture and walking her through the milking unit. During the following batches, dam-calf pairs remained together in the individual calving box until the dam had been milked at least 4 (batch 2) or 6 (batches 3–5) times using a portable milking machine; the time in the calving box corresponded to a median of 3 days (batches 2–5). After this

point, dams and their calves were moved to an experimental pen in the lactating cow barn, apart from batch 1, where 6 dam-calf pairs remained outdoors on pasture (with dam access to the indoor pen for milking) until the calves were an average (standard deviation [SD]) 47 (8) days old.

4.1.2 Milk-feeding phase

From the time calves entered the experimental pen to the point of weaning, they had access to full CCC, meaning there were no restrictions on the type of physical contact permitted. In terms of the duration of contact permitted, calves in batches 2–5 were reared with whole-day CCC through to weaning. In batch 1, calves had whole-day CCC until all calves were an average of 59 (8) days old, after which point full CCC was only available for 12 h daily until weaning.

In all batches, calves had access to a calf creep: a separate, deep-bedded area that was only accessible to calves (Figure 4). Hay, water, silage, minerals (batch 4, 5 only), and concentrate were available to calves in this area. When calves were moved outdoors to pasture in batches 2 and 4, they had access to an outdoor creep with a shelter, containing a dry lying area and the same type of food resources as the indoor creep.

Both dams and calves also had access to a contact area, wherein full CCC was possible, containing shared lying stalls and concentrate feeding stations for dams. In batch 5, shared resources also included two water troughs, a small feeding table, and a mechanical cow brush; however, cow concentrate feeding stations were closed and additional concentrate was instead offered in the milking unit, as an incentive for cows to enter the unit. As dams in batches 1–4 could leave the contact area for other parts of the pen, they were the primary initiators of CCC; these batches are therefore referred to as cow-driven. In contrast, the contact area in batch 5 contained nearly the entire pen, meaning the calves could seek out their dams at any time apart from milking. This batch was therefore operating with calf-driven CCC. Outside the contact area, dams in batches 1–4 had access to additional lying stalls and a feed alley, wherein they could obtain water and feed (a partial-mixed ration). The pen used for these batches contained an automatic selection gate, which was used both to control the direction of cow traffic through the pen, and to limit access to the contact area only to experimental cows with calves. In the pen used for batch 5, cow traffic was free, meaning dams could move freely between the different parts of the pen.

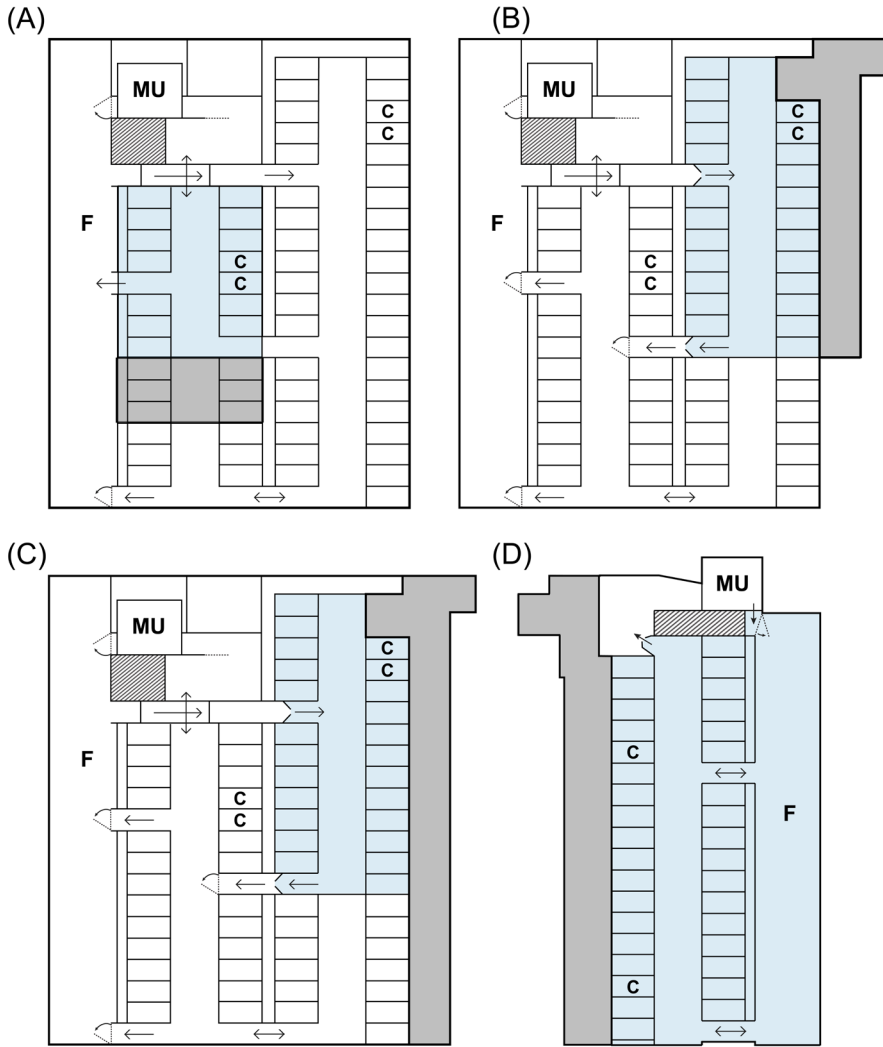


Figure 4. The indoor experimental pen layout used in (A) batch 1, (B) batch 2, (C) batches 3 and 4, and (D) batch 5. The calf creep is shown in grey, and the contact area – where full cow-calf contact between dams and calves was possible – is shown in blue. White areas were only accessible to cows, including non-experimental animals in figures A–C. Arrows indicate the direction of cow traffic. MU = milking unit; C = concentrate station; F = feeding alley. Figures C and D are modified from **Paper 1**.

Both pens contained a single milking unit, either a DeLaval VMS™ Classic (batches 1–4) or a DeLaval VMS™ V300 (batch 5), which dams could visit for milking if it had been at least 6–8 hours since their previous milking.

4.1.3 Weaning and separation

Both the age and method of weaning and separation varied between the different batches, but in all cases, total separation was achieved by moving the calves to another part of the barn or farm. In batch 1, all but three calves were abruptly weaned and simultaneously separated 8 weeks after the implementation of 12-h contact, at an average calf age of 16 (1.3) weeks. One heifer calf was weaned and separated 1 week earlier, due to the dam contracting *S. aureus* mastitis and needing to be moved out of the pen. Additionally, two bull calves were weaned at 11 (0.4) weeks of age due to reproductive behaviours in one of the animals.

In batch 2, all calves were weaned simultaneously using a combination of nose flaps followed by fenceline separation. Nose flaps were inserted at an average calf age of 15 (1.4) weeks. Exactly 2 weeks later, they were removed, and calves were allowed only fenceline contact for an additional 4 weeks. At 21 (1.4) weeks, calves were permanently separated by moving the cows to a distant pasture.

Calves in batch 3 were assigned to one of two different weaning and separation treatments: nose flaps for 2 weeks followed by total separation (two-stage), or nose flaps for 1 week followed by fenceline contact for 1 week and then total separation (three-stage). Additionally, the treatments were staggered; the two-stage calves were removed from the pen prior to weaning of the three-stage calves. Across both treatments, weaning was performed at an average age of 16 (1.0) weeks.

For batches 4 and 5, calves were assigned treatments that differed in weaning age: 4 or 6 months. In batch 4, the weaning method differed slightly between treatments as well. Calves were either weaned via nose flaps at 17 (2.4) weeks old (nose flaps removed after 4 days) and thereafter housed with fenceline contact for an additional 12 weeks, or fenceline weaned at 28 (2.0) weeks and permanently separated 1 week later. In batch 5, calves were fenceline weaned at either 18 (1.9) or 26 (1.4) weeks of age, housed with fenceline contact for 4 weeks, and then permanently separated.

4.1.4 Postweaning period

Following total separation, male calves and beef-mix heifers left the herd. Meanwhile, purebred heifers joined the general population of youngstock and were reared following the research farm's management protocols. Heifers were group-housed together with artificially-reared heifers of similar ages and weights—first in small rooms with deep-bedded lying areas, then in freestall pens within the youngstock barn. When heifers were at least 14 months old and weighed a minimum of 350 kg, they were artificially inseminated upon observations of estrus. Upon calving, individuals were housed and milked with other lactating cows in one of five freestall pens, each containing a single milking unit.

4.2 Data collection

The data collected during the thesis stemmed from a range of sources, including video recordings, live observations, animal-mounted sensors, and the research farm's database (Table 2).

4.2.1 Behavioural data

Calf behaviours were observed during the suckling period of two batches—one with cow-driven CCC and the other with calf-driven CCC (**Paper I**)—as well as directly before and after weaning at 4 or 6 months of age (**Paper II**). For all behavioural observations, cows were marked with unique symbols using animal-safe paint, and calves wore coloured collars. During live observation sessions, binoculars were used, and a 10-minute acclimation period always preceded each observation period.

Table 2. General description of the data used in each of the papers included in this thesis, including the batches to which the data pertains, the source of the data, and the average calf ages corresponding to the period of data collection.

Paper	Batch(es)	Data source(s)	Calf age range
I	3, 5	Video recordings	3–15 weeks
II	5	Live observations, sensors, farm database	Birth–1 year
III	1–5	Farm database	Birth–3 years

Suckling and allosuckling behaviour

Video recordings from ceiling-mounted fisheye cameras (Samsung SNF-8010VM) were used to observe suckling and allosuckling behaviours of calves in batches 3 (cow-driven CCC) and 5 (calf-driven CCC). Three trained observers used continuous recording and behaviour sampling to register all suckling bouts during 24-h periods at average calf ages of 3, 6, 9, 12 (both batches), and 15 (cow-driven batch only) weeks. During each suckling bout, the ID of both the focal calf and cow was recorded to differentiate between bouts of suckling on the dam and allosuckling. Additionally, it was recorded if there were other calves suckling on the focal cow at the start of an event. For allosuckling events recorded in the cow-driven batch, it was noted if the focal calf's dam was physically present within the contact area at the start of the event.

Behaviour around weaning

Pre- and postweaning calf behaviours in batch 5 were recorded using both live observations and sensors. All calves were equipped with leg-mounted accelerometers (IceQube, Peacock Technology [previously IceRobotics]; discontinued) that automatically recorded lying time and step count in 15-minute intervals. Direct observations were performed during three consecutive days in the week prior to each weaning event by two trained observers – one each with a view of either the indoor or outdoor area. The observers used scan sampling with 10-minute intervals to record each calf's proximity to their dam during four 2-hour observation periods, resulting in a

Definition: Suckling bout

The definition of a suckling bout used in **Paper I** is based on that of Fröberg and Lidfors (2009), with criteria for separation of behavioural bouts based on Jensen (2011) and Špinka and Illmann (1992). The following is an excerpt from **Paper I**:

“The calf [is] near (<10 cm) or touching the udder with its mouth for ≥ 1 min and visibly, rhythmically sucking through. Contact between the mouth and udder [may] be broken for periods of <1 min, and suckling bouts [occurring] within 10 min on the same cow [are] considered part of the same event.”

total of 48 scans per calf and day. Proximity was scored as being “close” (within 4 m of dam indoors, within 8 m outdoors) or not. Suckling bouts were additionally recorded using one-zero sampling during each interval, with no differentiation made between suckling on the dam and allosuckling.

Direct observations were also performed by one (of four possible) observer on day 1, 2, 3, 5, 8, and 11 after each weaning event, when weaned calves were housed outdoors with fenceline contact with dams. Whether calves performed feed-seeking behaviours (i.e., actively picking at or consuming hay, grass, silage or minerals) or were out of sight was recorded using an identical scan sampling protocol as during the preweaning observations (i.e., 10-minute intervals, for 8 hours per day). Furthermore, one-zero sampling was performed in 5-minute intervals to record calf vocalisations; this behaviour was recorded on a per-calf basis.

4.2.2 Performance data and matching controls

To evaluate the performance of heifers from birth to the end of their first lactation (**Paper III**), production-based measures were primarily collected from the farm’s database, where information related to body weight (BW), body condition of lactating cows, fertility, and milk yield was routinely recorded. This data was only extracted for the 61 heifers that both survived until their first calving (see Supplementary Table 2 for a list of heifers that exited the farm prior to calving) and were not included as dams in later CCC trials ($n = 5$).

As control (i.e., artificially-reared) heifers were not recruited for all batches, a propensity score matching procedure was performed to select individuals suitable for comparison with dam-reared heifers (Rosenbaum & Rubin 1983; Stuart 2010). During matching, dam parity, calving year, calving season, and dam breed were considered as the covariates that needed to be balanced (Figure 5). The group-housed artificially-reared heifers were pooled with farm-managed artificially-reared heifers, resulting in a total of 221 artificially-reared heifers that reached their first calving and were therefore available for matching. Each dam-reared heifer was ultimately matched to an artificially-reared heifer with the most similar propensity score (i.e., the heifer most similar in terms of dam parity, dam calving year and season, and dam breed). Performance data was therefore additionally extracted for the 61 matched artificially-reared heifers.

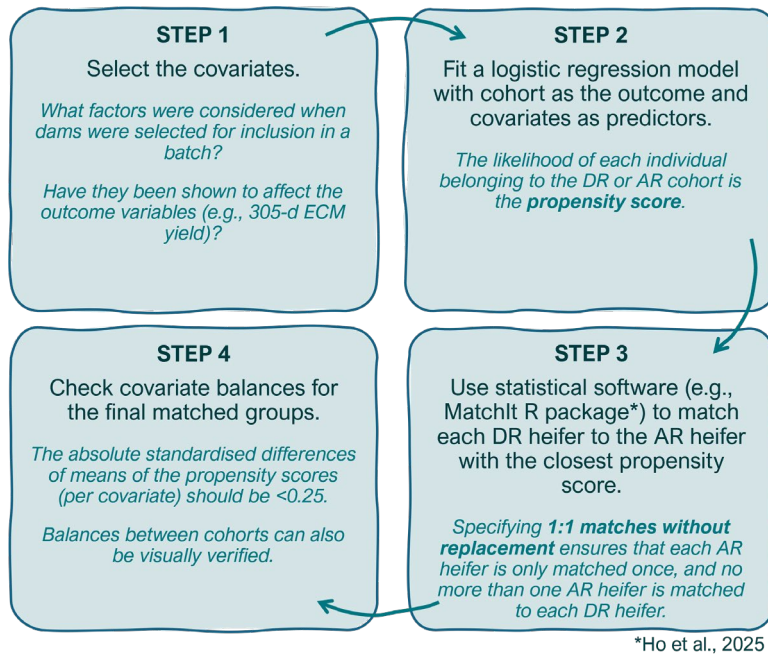


Figure 5. Flowchart outlining the steps taken to match artificially-reared (AR) heifers to dam-reared (DR) heifers using propensity scores (Stuart 2010).

Body weight and condition

All young stock on the farm were weighed at birth, weaning, and thereafter approximately once per month. Additional BW data was collected for heifers in batches 1–5, including weekly or biweekly measurements directly before and after weaning. During lactation, body condition was estimated daily on a continuous scale of 1–5 via a camera (DeLaval BCS) that scored cows from above as they exited the milking robot.

Fertility and milk yield measures

Insemination data during both the rearing period and the first lactation was extracted from the farm’s database, including the number of inseminations (and their dates) and any positive pregnancy results. During lactation, milk yield from individual milking sessions was collected, as well as milk composition (fat, protein, and lactose) from monthly samples.

4.3 Data handling and statistical analyses

All analyses were performed using R (version 4.4.2). Normally distributed raw data is presented as mean (SD), skewed data as median (Q1–Q3), and model estimates as estimated marginal means (EMM) $\pm$ standard error (SE). For all models relating to suckling or allosuckling behaviour, behavioural changes after weaning, or daily energy-corrected milk (ECM) yield, animal ID was included as a random effect (intercept) to account for repeated measures.

Linear mixed effects models were used to test the effects of calf age, breed, and sex (cow-driven system only, as no bull calves were included in the calf-driven system) on the daily number of suckling bouts (no. bouts/d), total time spent suckling (min/d), and suckling bout duration (min/d) in either a cow-driven or calf-driven CCC system (models 1 & 2; **Paper I**). To explore possible associations of calf age, sex (cow-driven only), birth weight, and the presence of other suckling calves (1/0) with the probability of allosuckling (binomial; 1/0), we fit two mixed-effects logistic regression models—one for each system type (models 3 & 4; **Paper I**). Results are presented separately per system type due to the differences in pen setup and management between batches 3 and 5.

Prior to modelling calf responses to fenceline weaning, activity data from the accelerometers was cleaned and summed per calf-day. Data from the 6 days immediately preceding weaning was then averaged to create a baseline for step count (steps/d) and lying time (min/d) for each calf. Postweaning activity measures were calculated as the daily difference in behaviour from the respective baseline. As behavioural responses did not appear linear with time, linear mixed effects models were fitted with day postweaning (day 1–11) as a quadratic function, and treatment (weaning at 4 or 6 months), dam-calf proximity (3-day average % time spent in close proximity preweaning), dam parity (primi- vs multiparous), and treatment $\times$ time as additional fixed effects (models 5 & 6; **Paper II**). To evaluate time spent feed-seeking after weaning (min/h), a similar linear mixed effects model was fit, with treatment, time (as a quadratic function), treatment $\times$ time, and dam-calf proximity as fixed effects (model 7; **Paper II**). Postweaning vocalisation occurrence was calculated as the percentage of sampling intervals in which the behaviour occurred and is reported descriptively (**Paper II**).

Considering that the effects of feeding high planes of nutrition on preweaning growth are well-established, confirmatory analysis using a linear

regression model was performed to test for differences in preweaning (birth–weaning) ADG between dam-reared heifers and artificially-reared matched heifers (model 8; **Paper III**). Additionally, linear regression was used to explore differences in preweaning management for postweaning (weaning–1st insemination) ADG, given that few studies have evaluated the growth of dam-reared heifers beyond a few weeks or months postweaning (model 9; **Paper III**). Both models included dam parity, birth season, and breed, as well as significant two-way interactions. ADG for the 2-week period following weaning was calculated to assess potential growth checks and is reported descriptively.

Exploratory analyses were used to estimate the effect of preweaning management (dam- or artificial-rearing) on milk yield outcomes, including 305-d ECM yield (kg), average daily ECM yield (kg/day), and lactation persistency (change in ECM between 100 and 250 days in milk; kg/day). Backwards elimination was used to construct linear fixed-effects (305-d ECM yield; model 10) and mixed-effects (daily ECM yield; model 11) regression models, keeping only variables (of those known to influence milk yield) with $P \leq 0.1$ in the final models (**Paper III**). For 305-d ECM yield, the final model included preweaning management, breed, milking frequency, age at first calving, and calving year. The final model for daily ECM yield contained preweaning management, breed, lactation stage (early, peak, mid, or late), milking frequency, and season. Finally, linear regression was performed to explore potential differences in lactation persistency, with preweaning management and breed included as fixed effects (model 12).

Measures relating to fertility were handled and reported descriptively (**Paper III**). For handling of all measures, inseminations occurring within 1 day were counted only once. Prior to the first lactation, the number of inseminations, first service conception rate, and age at first calving were calculated for each heifer. During the first lactation, the number of inseminations was calculated only for primiparous cows that were inseminated at least once. Additionally, the calving-to-first-service interval and number of days open were calculated for each dam-reared or artificially-reared primiparous cow.

5. Main results

5.1 Behaviour and growth during the milk-feeding phase

5.1.1 Suckling and allosuckling behaviour

Between 3 and 15 weeks of age, bull and heifer calves reared in a cow-driven CCC system did not change their suckling behaviours, spending an average 42 (17.0) minutes ($P = 0.30$) suckling across 4 (1.5) bouts per day, with individual suckling bouts averaging 11 (4.9) minutes in length (Figure 6A).

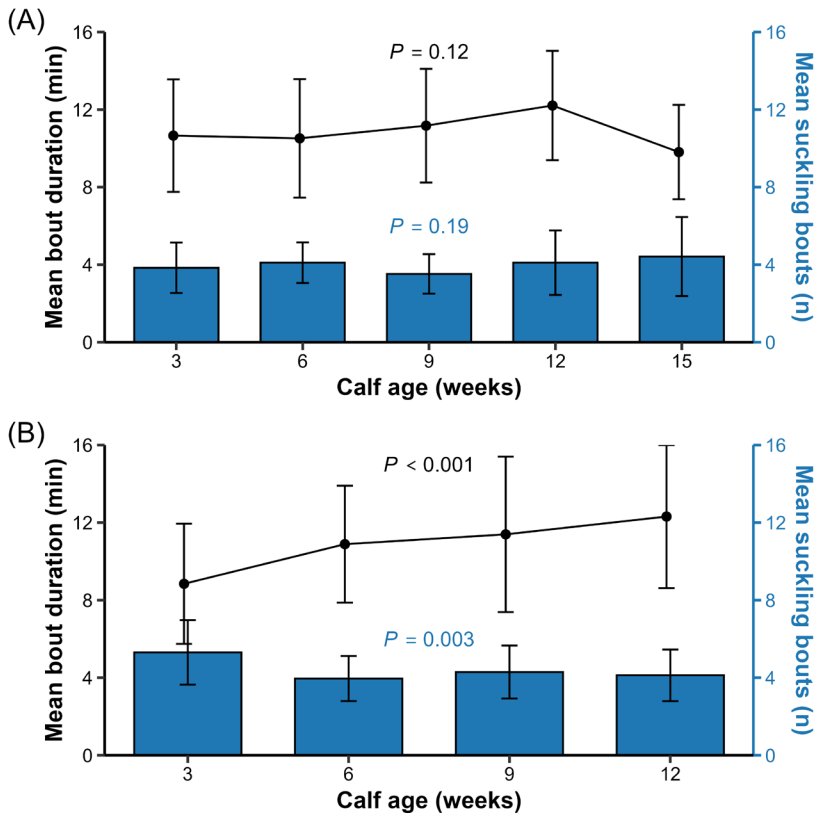


Figure 6. The mean suckling bout duration (minutes/bout; lines) and number of daily suckling bouts (bouts/day; bars) for calves when housed in systems with either cow-driven (A) or calf-driven (B) cow-calf contact. Data is based on raw values (per calf, per observation age), and P -values indicate the association between either behaviour and calf age. Error bars represent standard deviation.

In contrast, heifers reared with calf-driven CCC tended to increase their total time spent suckling ($P = 0.06$), performing fewer—but longer—suckling bouts as they aged (Figure 6B). Importantly, in both systems, bouts of allosuckling were an estimated 3 (calf-driven) to 4 (cow-driven) minutes shorter compared to suckling bouts that involved the dam ($P < 0.001$).

Allosuckling was more frequently observed in the cow-driven as opposed to the calf-driven system (36% vs 14% of all observed suckling bouts; Supplementary Figure 1). In both CCC systems, the odds of allosuckling increased with increasing calf age (cow-driven: $P = 0.01$, calf-driven: $P = 0.003$). Of the remaining calf-level factors tested, only the presence of other suckling calves was found to be associated with allosuckling ($P < 0.001$); calf birth weight (cow-driven: $P = 0.27$, calf-driven: $P = 0.68$) and calf sex (cow-driven: $P = 0.36$) were not associated with the behaviour.

5.1.2 Dam-calf proximity

During the week prior to weaning at 4 or 6 months of age, calves spent a median 27% (Q1–Q3: 22–42%) and 39% (34–47%) of their time in close proximity to their dams, respectively (Figure 7).

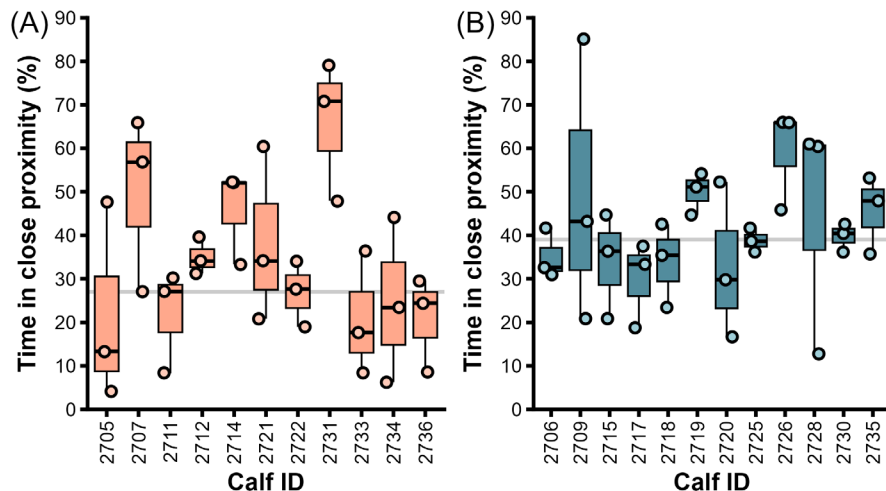


Figure 7. The percent of observed time spent by dam-calf pairs in close proximity—defined as being within 4 (indoors) or 8 m (outdoors)—during 3 consecutive days in the week before fenceline weaning at 4 (A) or 6 (B) months of age. Box boundaries show interquartile range (IQR), whiskers show 1.5x the IQR, the midlines indicate median values, grey lines the overall median time in close proximity, and dots the daily values.

5.1.3 Calf growth

Across calves in all batches, including bull calves, the average birth weight was 39 (5.8) kg. Of the heifers who survived to first calving, the growth rate between birth and weaning was 1.3 (0.17) kg/d—higher compared to artificially-reared matched controls (0.9 [0.07] kg/d). Although significant interactions were found for preweaning management (dam vs artificial rearing) with birth season ($P < 0.001$) and dam parity ($P = 0.01$), growth rate was always higher for dam-reared heifers. Within batches, preweaning ADG for heifers with dam-calf contact ranged from 1.1–1.4 kg/d (Table 3).

Table 3. Average daily gain (ADG; kg/d) of heifers reared in different experimental batches during periods before and after weaning. Data is shown as mean, with standard deviation in brackets, and n refers to the number of individuals per batch for which ADG was calculated. For batch 1, the body weight on the day closest to weaning was used for calculations of preweaning and postweaning ADG.

Batch	n	Birth–weaning	Weaning–2 weeks postweaning ¹	Weaning–first insemination
1	6	1.2 (0.07)	—	0.8 (0.08)
2	9	1.3 (0.11)	0.2 (0.42)	0.8 (0.09)
3	9	1.1 (0.18)	0.7 (0.34)	0.8 (0.08)
4	13	1.3 (0.18)	0.6 (0.38)	0.9 (0.09)
5	24	1.4 (0.14)	0.1 (0.49)	0.8 (0.09)

¹Value not calculated for batch 1, since weighing was not performed on the exact date of weaning.

5.2 Calf responses to weaning

5.2.1 Behavioural responses

Following fenceline weaning after 4 or 6 months of whole-day CCC in the calf-driven system, heifer calves of both treatments responded similarly, although the behavioural responses were slightly more pronounced in 4-month-old calves. There was a significant interaction of treatment with time postweaning for differences (compared to preweaning baseline) both in lying time ($P < 0.001$) and step count ($P = 0.048$). On day 1 postweaning, 4- and 6-month-old calves increased their daily step count by an estimated 5892 ± 1313.5 and 3904 ± 1168.4 steps, respectively. The calves weaned at 6 months returned to baseline levels for this activity by 4 days postweaning,

whereas it took younger calves an additional day. Both groups of calves also decreased their lying time immediately after weaning (4 months: -5.6 ± 0.77 h/d, 6 months: -3.6 ± 0.87 h/d), but neither returned to baseline for this behaviour during the 11 days postweaning.

All calves vocalised on the first day following weaning (4 months: mean [SD] 40 [10.3]% intervals/h, 6 months: 43 [11.2]% intervals/h) and thereafter decreased this behaviour over the following days. However, on day 2, 4-month-old calves were observed to vocalize in approximately 8% more 5-minute sampling intervals per hour compared to the 6-month-old calves. Large variation among calves was evident for this behaviour (Figure 8).

Feed-seeking behaviour during the 11 days after weaning did not differ between the two weaning ages ($P = 0.24$), although there was a quadratic increase with time ($P < 0.001$). Furthermore, proximity to the dam prior to weaning was not associated with any of the postweaning behaviours, including the difference in lying time ($P = 0.37$) and step count ($P = 0.37$), as well as feed-seeking behaviour ($P = 0.12$).

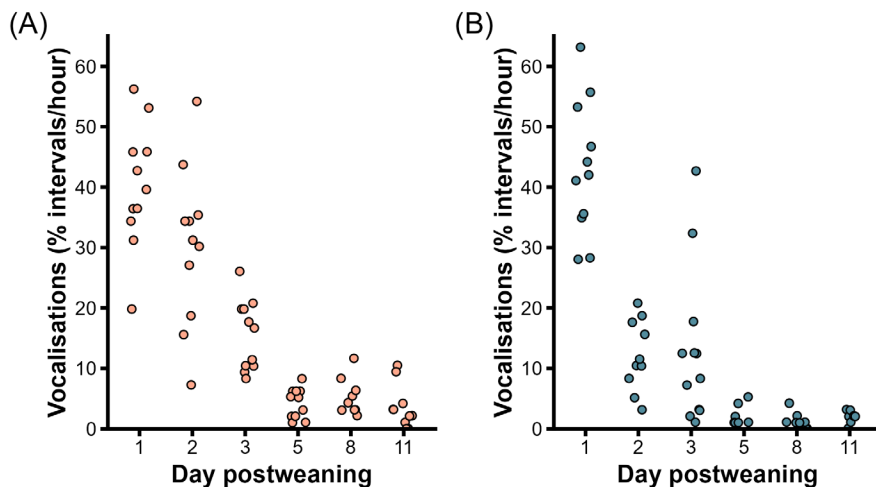


Figure 8. Vocalisation responses of calves following fenceline weaning after either 4 (A) or 6 (B) months of full, whole-day dam-calf contact. Dots represent the average percent of 5-minute intervals per hour, based on 8 hours of observations per day, during which each calf vocalised at least once.

5.2.2 Physical responses

Growth checks were evident for dam-reared heifers following weaning, although there were some numerical differences between batches (see Table 3). During the 2 weeks immediately after weaning, the average ADG for dam-reared heifers was 0.4 (0.49) kg/d. Meanwhile, artificially-reared matched heifers grew at an average rate of 1.1 (0.31) kg/d during this period, although postweaning BW measures were only available for one-third of these calves. Within batch 5, growth checks were also apparent within both weaning treatments (Figure 9). Heifers weaned at 6 months appeared to resume gaining BW after 3 weeks, which was somewhat earlier than for 4-month-old heifers.

Following weaning, heifers reared with dam-calf contact continued to grow, on average, at slightly lower rates until first insemination compared to artificially-reared controls (0.8 [0.09] vs 0.9 [0.07] kg/d; $P = 0.005$; see Table 3 for ADG per batch); yet, at first insemination, dam-reared heifers maintained a numerically greater average BW (480 [47.7] vs 432 [40.6] kg).

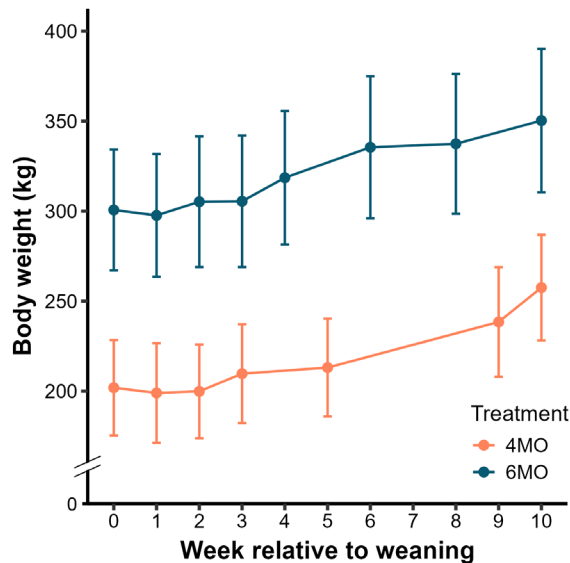


Figure 9. Body weight of calves weaned via fenceline separation after either 4 ($n = 11$) or 6 ($n = 12$) months of dam-calf contact, relative to the week of weaning (week 0). Error bars represent standard deviation.

5.3 Fertility

Comparing dam-reared heifers to artificially-reared matched heifers, similar values were observed prior to first calving in the age at first insemination (median: 14.7 vs 14.9 months), first service conception rate (57% vs 62%), and age at first calving (median: 24 months for both groups). Numerically, proportionally more dam-reared heifers required at least 3 inseminations to conceive for the first time (23% vs 13%). During the first lactation, the calving-to-first-service interval (mean: 106 days for both groups) and number of days open (median: 118 vs 117 days) were similar for dam-reared and artificially-reared primiparous cows, but the former required a numerically somewhat greater number of inseminations (mean: 1.9 vs 1.6).

5.4 First-lactation milk yield

Primiparous cows that were reared with dam-calf contact in early life produced an estimated 498 kg less ECM during their first 305 days of lactation compared to artificially-reared matched cows (95% confidence interval [CI]: -987 to -8 kg). Moreover, dam-reared individuals also produced less ECM per day (-1.9 kg/d; 95% CI: -3.6 to -0.1 kg/d) and demonstrated a poorer persistency during lactation (-0.019 kg/d; 95% CI: -0.035 to -0.004 kg/d).

Descriptive comparisons of 305-d ECM by quartile revealed similar values for the 25% highest-yielding individuals (mean [SD]; dam-reared: 10789 [694.0] kg, artificially-reared: 10870 [707.9] kg). However, differences in 305-d yield increased as the quartile interval decreased, with a 1413 kg difference in average 305-d ECM between the 25% lowest-yielding groups. When looking at the breakdown of quartile intervals per experimental batch, it was evident that the majority of dam-reared primiparous cows in the bottom two quartile intervals were reared in the same batch (Table 4). Furthermore, heifers from batch 5 had, on average, a lower first-lactation ECM yield compared to those reared in other batches (Figure 10A); no such pattern was evident for persistency (Figure 10B).

Table 4. Number of dam-reared primiparous cows in each experimental batch, as shown per quartile interval for 305-d energy-corrected milk (ECM) yield.

Batch	Quartile interval			
	<Q1	Q1–Q2	Q2–Q3	≥Q3
1	1	2	0	2
2	1	2	2	3
3	1	1	3	4
4	1	1	5	4
5	9	7	3	1

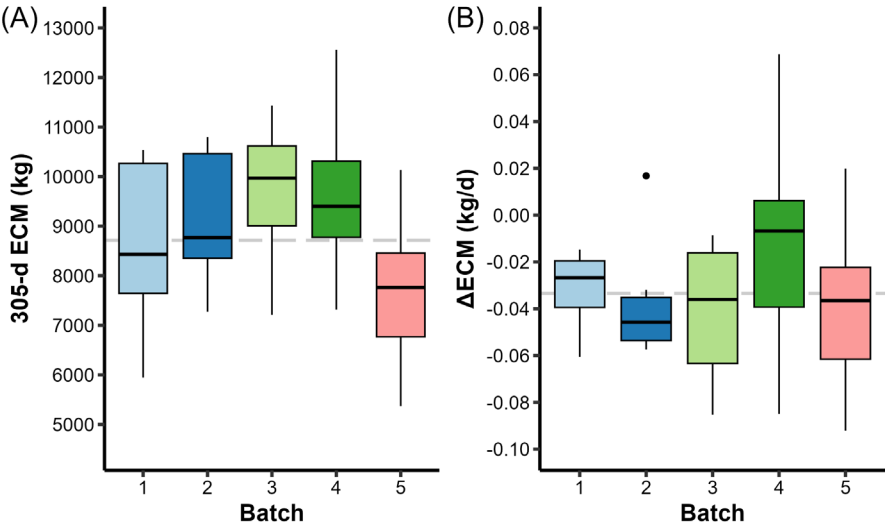


Figure 10. Boxplots showing the first-lactation 305-d energy-corrected milk (ECM) yield (**A**) and lactation persistency (**B**; change in daily ECM yield) of dam-reared primiparous cows per experimental batch (n per batch: batch 1 = 5; batch 2 = 8; batch 3 = 9; batch 4 = 11; batch 5 = 20). Dashed horizontal lines indicate the average value across all dam-reared primiparous cows. Box boundaries show interquartile range (IQR), whiskers extend to the most extreme value no more than 1.5 times the IQR, midlines indicate median values, and points beyond the whiskers denote outliers.

6. General discussion

The work presented in this thesis addressed key questions concerning both the behavioural and short- and long-term productive performance of dairy calves with up to six months of dam-calf contact, when reared in automatic milking systems. In investigating these questions, several overarching themes emerged, including the potential role of CCC management in shaping calf behaviour and performance, the influence of calf age on weaning responses, and the practical implications of extended dam-calf contact—both for calves and farmers. Collectively, the findings from this thesis contribute to the ongoing discussion on how dams and calves can be managed together in ways that support both welfare and productivity, as well as provide inspiration and direction for future research.

6.1 Calf behaviour and productive performance under different CCC management systems

The practical implementation of dam-calf contact often depends on existing barn infrastructure (Bertelsen & Vaarst 2023), and variation in how contact is organised (e.g., daily duration, initiator of contact) may influence the behaviour and performance of calves in dam-rearing systems. While the study design presented in this thesis did not allow for statistical comparisons between cow-driven and calf-driven CCC systems, descriptive comparisons may still provide valuable insights.

To begin, the data revealed that calves in a cow-driven system—specifically that of batch 3—maintained a similar pattern of suckling behaviour between 3 and 15 weeks of age, and were frequently observed to allosuckle (36% of all bouts). Meanwhile, calves in a calf-driven system changed their suckling patterns over time, and allosuckled less frequently overall (14% of all bouts). A detailed discussion of the suckling behaviours observed for either system is presented in **Paper I**, but to reiterate, it seems plausible that the differing behavioural patterns may be related to differences in the amount of available time for contact with dams. In the calf-driven system presented for batch 5 in this thesis, calves had nearly 24-h access to their dams, apart from when dams were in the waiting area or milking unit. In cow-driven systems, the time spent by dams in the contact area may be influenced by the availability of resources. For example, the contact area in

batch 3 contained stalls, which we know from previous work performed in the same batch that dams spent approximately 8.9 hours per day lying in (Wegner & Ternman 2023). In cow-driven systems with more barren contact areas (i.e., no resources apart from access to calves), dams have been observed to spend approximately 2–2.5 hours spread across 5–8 individual visits, depending on whether the dam had free access or milking-dependent access (Johnsen et al. 2021a). Additionally, the direction of cow traffic may influence time spent by dams in a contact area; in batch 3, dams were directed towards the contact area upon leaving the feed alley, provided they were not due to be milked. Yet, regardless of potential differences in available contact time for the cow-driven and calf-driven systems presented in this thesis, the average time spent suckling each day and frequency of suckling bouts were numerically similar, and allosuckling increased with increasing calf age regardless of the system type.

During the milk-feeding phase, calf growth was high across all batches of dam-reared calves (1.1–1.4 kg/d)—higher than that of artificially-reared matched calves in our study (0.9 kg/d), and nearly double the average growth rates reported for Holstein calves that are reared artificially in commercial farms across the UK (0.6–0.7 kg/d; Johnson et al. 2018) and North America (0.7 kg/d; Soberon et al. 2012; Urie et al. 2018). The uniformly high growth across both cow-driven and calf-driven batches aligns with previous work showing no difference in preweaning ADG between whole-day and part-day CCC systems (Bertelsen & Jensen 2023b; Sinnott et al. 2024; Zipp & Knierim 2024), further supporting the idea that reduced daily dam-calf contact time does not necessarily limit milk intake (Jensen et al. 2024b).

In the two weeks immediately after weaning, pronounced growth checks were observed in the calf-driven batch as well as in one of the cow-driven batches (batch 2). Despite all calves experiencing an abrupt cessation of milk at weaning—whether through nose flap insertion, fenceline separation, or total separation—considerable variation among the cow-driven batches suggests that additional environmental or management-related factors may have influenced calf growth responses.

Regarding long-term production performance outcomes, 305-d ECM yield appeared lower among primiparous cows reared in the calf-driven system (batch 5), although the data presented in this thesis alone cannot confirm this difference. Given that primiparous cows from batch 4—where weaning was also performed at 4 and 6 months—were primarily in the 50%

highest-yielding quartiles, this points to an effect of dam-calf contact management rather than weaning age. Calves in batch 5 had nearly unrestricted access to their dams—and therefore to milk—for up to 6 months. Meanwhile, calves in batch 4 were kept on pasture from around 3 months of age; this may have limited their access to milk after this point, as dams were no longer forced to enter the contact area several times per day. Feeding high planes of milk for extended periods of time may promote mammary fat deposition at the expense of parenchymal tissue development (Capuco et al. 1995; Sejrsen et al. 2000)—potentially reducing milk production capacity later in life. The long suckling period, combined with unrestricted dam-calf contact, could have contributed to the poor milk yields observed for dam-reared individuals in batch 5. Interestingly, lactation persistency was poorer for all dam-reared individuals, with no clear patterns between batches. Understanding how combinations of dam-rearing management practices—including system type (cow-driven or calf-driven), daily contact duration, and milk-feeding phase length—affect future production will be crucial for refining rearing strategies that optimise both behavioural and performance-based outcomes.

6.2 Considerations of age and method at weaning

In contrast to the growing body of research exploring various methods of weaning and separation, this thesis is the first to investigate how calf age influences the physical and behavioural responses to weaning.

6.2.1 Weaning age

Age-related differences in behaviour were observed during the first few days immediately following fenceline separation; 4-month-old calves showed increased locomotion, decreased lying time, and a numerically greater vocalisation response compared to calves weaned at 6 months of age. Additionally, younger calves took somewhat longer to recover from postweaning growth checks. The 6-month group was approaching the weaning age range reported for semi-feral Zebu calves observed under semi-natural, non-managed conditions (7–14 months; Reinhardt & Reinhardt 1981). However, while behavioural and physical responses appeared reduced in the 6-month-old calves compared to the 4-month group, they were nevertheless evident and not at levels that could be considered low. One

explanation for the observed responses is a lack of nutritional independence at the time of weaning, also in the older calves. Observations of suckling behaviour in **Paper I** suggest that up to 3 months of age, calves in this batch were still largely dependent on dams for nutritional support, as indicated by a high daily suckling time, with half of the calves having been observed to suckle exclusively from their own dam. Furthermore, calves reared in other whole-day CCC systems have been shown to spend little time consuming solid feed prior to weaning (Roth et al. 2009; Fröberg et al. 2011; Vogt et al. 2024); indeed, the calves in **Paper II** spent little time on feed-seeking activities immediately following weaning (mean 8.6 min/h on day 1 postweaning, compared to 24.8 min/h on day 8).

6.2.2 Weaning method

Although not explicitly tested, the method used to wean the calves in the calf-driven system in **Paper II** may also have contributed to the observed response levels. Unlike weaning under semi-natural conditions (Reinhardt & Reinhardt 1981), fenceline weaning involves an abrupt termination of milk access, which may have exaggerated the responses reported for these calves. Interestingly, postweaning growth was not as negatively impacted for calves in batch 4—which also involved 4- and 6-month weaning treatments—despite the use of abrupt weaning methods (nose flaps or fenceline separation), as in batch 5. This alludes to a potential further influence of preweaning management conditions (see 6.1 for discussion) on weaning response, although observation of behavioural responses was not performed for batch 4.

Nonetheless, findings on the effectiveness of various abrupt and gradual weaning methods in alleviating behavioural and physical weaning responses remain inconclusive (as reviewed by Whalin et al. 2025). Variation among calves in behavioural responses, such as vocalisations (as shown here and by Johnsen et al. 2024), highlights the potential value of further exploring individualised weaning protocols, which may be readily implemented in systems using automatic selection gates to manage dam-calf contact.

6.3 Incorporating dam-calf contact in automatic milking systems

With the increasing adoption of automatic milking systems in intensive dairy production, understanding how dam-calf contact can be effectively integrated into such systems is receiving growing attention in both research and practice. Previous work has explored various aspects of calf performance and behaviour, including studies conducted in Sweden (Fröberg & Lidfors 2009; Fröberg et al. 2011) and more recently in Norway (Johnsen et al. 2021a; 2024; Sørby et al. 2024b). However, this thesis presents the first practical solution for combining calf-driven CCC with automatic milking (see Figure 4D for barn layout) under experimental conditions. The following two sections will discuss some practical implications for calves and farmers based on the results presented in this thesis.

6.3.1 Welfare implications for calves

CCC systems are often portrayed as inherently welfare-friendly, yet such assumptions can be misleading; while they offer opportunities for highly motivated behaviours such as suckling and social contact, poor management or hygiene can still lead to negative welfare outcomes. Applying the Three Spheres model of animal welfare (the spheres being natural living, biological functioning, and affective state; Figure 2; Fraser et al. 1997) allows several welfare insights to be identified for dam-reared calves, given the findings presented in this thesis. From the perspective of natural living, calves housed in both cow-driven and calf-driven systems are able to fulfil their motivation to suckle, as evidenced by numerically similar total suckling times and number of daily suckling bouts in the two systems. Additionally, calves in these systems have the opportunity to form social bonds and develop social structures that resemble those observed in semi-natural settings (e.g., Sato et al. 1987), although this thesis only explored proximity in relation to the dam-calf bond.

In terms of biological functioning, the dam-rearing strategies investigated in this thesis appeared to result in reduced milk yield during the first lactation compared to artificially-reared matched primiparous cows. However, without knowing the underlying cause of this reduction, it is difficult to determine whether welfare is, or at any point was, compromised, since variation in milk yield can also be due to welfare-neutral factors (von Keyserlingk et al. 2009). Further assessment of this theme would require

additional measures, such as body condition throughout pre- and postpubertal development.

Finally, although affective states were not directly assessed in this thesis, inferences of calf affect at weaning may be drawn from the behavioural responses observed. In general, weaning and separation are unlikely to elicit anything other than a negative affective state; Daros et al. (2014) demonstrated a more pessimistic judgement bias in dairy calves after, compared to before, dam-calf separation at 6 weeks of age. Possible measures to reduce the intensity of this response have been discussed in section 6.2.

6.3.2 Practical considerations for farmers

Several points can be lifted from this thesis for farmers managing high-yielding herds in automatic milking systems who practice or intend to implement dam-rearing. To start with, cow-driven CCC was associated with a higher frequency of allosuckling, although farmers can expect the occurrence of this behaviour to increase as calves age, regardless of management system. For those concerned with this behaviour, a calf-driven system may offer a more attractive solution. In both the cow- and calf-driven systems, the median number of allosuckling bouts per calf remained zero up to 6 weeks of age, suggesting that allosuckling can be kept at a low level also by reducing the contact period duration. Given that the presence of other suckling calves was positively associated with allosuckling, reducing the number of dam-calf pairs housed together may further decrease allosuckling. However, the relationship between suckling and allosuckling behaviours and group size was not evaluated in this thesis.

As a second point of consideration, fenceline weaning of calves after either 4 or 6 months of whole-day, calf-driven CCC resulted in pronounced behavioural responses and growth checks (but generally not substantial losses in BW) during the weeks thereafter. Considering that these calves also produced the lowest average 305-d ECM yield of all batches as lactating adults, this management strategy may be best avoided, as it does not appear to substantially reduce weaning stress and may additionally compromise later performance. For farmers who value natural living, weaning at an older age did mildly reduce behavioural stress responses. In general, however, it would be recommended to implement more gradual weaning strategies to

encourage some degree of nutritional and/or social independence in the calf prior to weaning.

Thirdly, it may be in the farmers' best economic interest to consider shorter contact periods (i.e., <3 months), as the results in this thesis suggest that extending full dam-calf contact for 3–6 months may negatively impact later milk yield in heifers. Future work investigating the long-term production effects of varying dam-rearing periods in low-yielding dairy or dual-purpose breeds is welcomed.

Finally, several anecdotal observations have been compiled that may be of interest to farmers. Across all batches, calves appeared to learn to navigate the housing system quickly, regardless of whether contact was cow- or calf-driven. In batch 5, where calves had access to the cow feeding area, a subsection of the feeding table was modified to contain an open front, to allow calves to feed alongside their dams. Despite a horizontal bar to prevent calves from escaping, barn staff noted the occurrence of this very event on several occasions. Depending on barn layout, this poses risks for calves, such as entering foreign cow pens, colliding with animals that are being moved, and potentially falling into (temporarily) open manure pits. Headlocks (i.e., for adult cows) may also constitute a risk for calves. On a separate note, the nasal cavities of calves in batches 3 and 4 were documented following the removal of nose flaps; even when worn for the minimum time recommended by the manufacturer (i.e., 4 days), evidence of soft-tissue damage was still apparent 2 weeks later. If nose flaps are to be used, it is essential to provide an open source of water, as not all calves willingly drink from pressure-activated water bowls while wearing the nose flaps. Additionally, mineral licks should be available to calves prior to weaning; up to batch 4, the primary source of selenium available to the calves was through the concentrate. As we have discussed throughout this thesis, it is likely that calves ate very little concentrate during the milk-feeding phase. When one male calf in batch 3 suffered an abrupt muscle degeneration upon weaning and was subsequently euthanised, this was later linked to a suspected selenium deficiency.

6.4 Limitations and future perspectives

While this thesis provides new insight into the behavioural and physical development of calves under different dam-calf contact systems, certain

limitations should be acknowledged. To start with, there were several data measures that were not collected, largely due to practical constraints (e.g., time, resources), that limited our interpretation of certain findings. For example, the collection of individual feed intake data or feed-seeking behaviour in calves prior to weaning in **Paper II** would have allowed for a more nuanced discussion on nutritional dependence in relation to weaning age. Additionally, the collection of measures relating to body condition (e.g., backfat thickness) and growth (e.g., heart girth, hip height, wither height) at regular intervals until, and including, calving would help us better understand the long-term effects of preweaning management on the physical development of the calves. Measurements to assess physical development would be best collected for a randomised controlled trial, rather than the retrospective cohort design utilised in **Paper III**, where artificially-reared controls were matched from the larger population of primiparous cows on the research farm.

This leads me to a second limitation of the thesis: the lack of a true control group for estimating the effect of preweaning management on production performance outcomes. Propensity score matching is a powerful matching technique that has been used, for example, to infer causal effects of vaccine status (using a specific mastitis bacterin) on milk production outcomes in dairy cattle (Sánchez-Castro et al. 2023). Although one-to-one matching based on propensity scores was used in this thesis, the artificially-reared cohort could alternatively have consisted of all other heifers that calved in comparable years and seasons to the dam-reared cows. While this increase in sample size would have increased the statistical power, the overall study would still have remained underpowered for milk production outcomes, and there would be greater imbalances for factors such as breed, which is known to influence 305-d milk yield (see Supplementary Figure 2 for propensity score distribution of unmatched artificially-reared individuals). Ultimately, matching techniques can be particularly useful in contexts such as longitudinal CCC research, where recruiting suitable controls is costly, provided that the candidate pool is large enough to allow for high-quality matches.

Thirdly, one might criticise the lack of physiological stress indicators in **Paper II**. While physiological measures may be used to support behavioural indicators of weaning-related stress, there are several reasons why they were not considered for collection. Many commonly-used physiological indicators

of stress—such as heart rate, cortisol, or changes in body temperature—are confounded with physical activity (Dawkins 2003). As locomotion typically increases after weaning (as reviewed by Enríquez et al. (2011) for beef calves), these measures would have been difficult to interpret. Perhaps of note, fecal cortisol metabolites have previously been collected as a physiological marker of weaning stress in dairy calves, but their interpretation was complicated by confounding effects of dietary composition (i.e., higher fecal cortisol metabolites with milk-based diets; Vogt et al. 2023, 2024). Finally, the sampling process for many physiological measures (e.g., blood cortisol) involves physical handling, which would have risked influencing the calves’ behavioural responses.

Despite these limitations, the findings of this thesis highlight several avenues for future research. While dam-calf proximity did not serve as a good predictor for behavioural weaning responses, this measure was observed to vary greatly among calves—and in some cases, among days within individual calves. Little is currently known about the spatial relationships between cows and calves in different dam-calf contact systems, and discussions of what distance may constitute “close” proximity are largely lacking in this context. Recent advancements in sensor technology (e.g., proximity loggers and ultra-wideband-based positioning systems) may help address these questions.

To build on the earlier discussion of management system differences (see 6.1), controlled trials that permit a direct comparison of cow-driven versus calf-driven CCC are needed. For example, a split-pen design—where either pen half contains either cow-driven or calf-driven contact, but cows share a milking unit—would allow control over differences in both pen and time. Including several replicates, where management treatment is alternated between pen halves, would further control for potential differences between pen halves.

Finally, many questions remain regarding the long-term effects of providing dam-calf contact during early life. To start, research is needed to disentangle the effects of feeding high planes of milk nutrition for varying lengths of time from providing dam-calf contact, as the extent to which the latter contributed to the lower milk yield outcomes in **Paper III** remains unclear. To instead touch on the social aspect of dam-calf contact, how does being reared in a freestall system with adult cattle affect the life-long resilience of dairy calves (i.e., their ability to cope with, and recover from,

adverse events)? Additionally, while this thesis to an extent addressed outcomes related to fertility and reproductive performance, this is an area that deserves greater attention. For example, the combined use of accelerometers and video recordings may allow for observations of puberty onset in dam-reared vs artificially-reared heifers managed on the same farm. In this thesis, dam-reared heifers were inseminated according to the research farm's protocols, but it would be interesting to determine if they can conceive and calve at a younger age, and how this may affect their subsequent first lactation milk yield and longevity. Moreover, research should evaluate how prolonged dam-calf contact influences the production potential of male calves (e.g., growth potential, meat quality) and their ability to adapt to a new farm environment. Given that nearly half of the young bulls and steers slaughtered for meat in Sweden are from dairy breeds (Gård & Djurshälsan 2023), it is important to consider how CCC systems could be adapted to include these animals. As a final point, much of the research conducted on CCC systems to date—including that presented in this thesis—has been carried out under controlled experimental conditions (as discussed by Whalin et al. 2025). The generalisability of such findings may therefore be limited, underscoring the need for future herd-level observational studies conducted on commercial farms.

7. Conclusions

The work presented in this thesis increases the current understanding of calf behaviour and productive performance during different life stages in freestall dam-rearing systems with automatic milking—specifically, the pre- and postweaning rearing stages and during the first lactation.

The main conclusions were:

- Calves reared with calf-driven CCC changed their suckling behaviour as they aged to perform fewer but longer suckling bouts. Meanwhile, calves reared with cow-driven CCC showed consistent behaviour across the first 3 months of life.
- Allosuckling was frequently observed, which aligns with previous findings for dairy dam-rearing systems. This behaviour increased with calf age and was more likely to occur when other calves were already engaged in suckling. Furthermore, allosuckling was more often observed with cow-driven as opposed to calf-driven CCC.
- Fenceline weaning calves after 6 months of full CCC, compared to 4 months, may lessen behavioural responses, but does not eliminate them. At both ages, calves showed signs suggesting a lack of nutritional and social independence prior to weaning, including vocalisations, temporary growth checks, increases in step count and feed-seeking activities, and decreases in lying time.
- Time spent in close spatial proximity varied widely between dam-calf pairs and did not appear to be related to calf age. Moreover, time spent in close proximity prior to weaning did not predict behavioural responses of calves after weaning.
- Prior to weaning, both dam- and artificially-reared heifers grew at high rates, although dam-reared heifers gained on average 44% more weight per day compared to artificially-reared heifers.

- Immediately after weaning, dam-reared heifers experienced growth checks, but despite slower subsequent growth, they remained heavier than artificially-reared heifers at first insemination.
- Fertility-based outcomes were numerically similar between dam-reared and artificially-reared individuals, both as heifers and primiparous cows.
- Compared to artificially-reared individuals, primiparous cows reared with 3–6 months of full CCC produced less ECM and demonstrated a poorer persistency during their first lactation.
- There were no numerical differences in 305-d ECM yield amongst the highest-yielding 25% of dam-reared and artificially-reared primiparous cows, while there was nearly a 1500 kg difference between the lowest-yielding 25% cows of each rearing cohort. Notably, the lowest-yielding dam-reared individuals were primarily reared in the same batch, suggesting management differences between dam-rearing systems may influence milk yield.

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Popular science summary

Dairy calves are commonly separated from their mothers soon after birth and fed milk or milk replacer artificially. Cow-calf contact (CCC) systems offer an alternative approach, where calves stay with their mothers or adult cows and drink milk through suckling. These systems allow calves to express natural suckling behaviours and form strong social bonds, and they can often drink larger amounts of milk compared to calves that are raised artificially. In this thesis, dairy calves were kept with their mothers for three to six months, and their behaviour, growth, fertility, and milk yield were studied, both during the time together with the cows and afterwards as they themselves grew into adults.

Five separate experimental trials were run, during which the cow barn was modified to accommodate the calves. This included the installation of gates, to prevent calves from entering areas intended only for cows, and the construction of an exclusive calf area known as a “calf creep”. In two of these trials, calf behaviour was observed, first during the three-to-six months when they were with their mothers, and additionally when they were weaned and integrated into the regular herd. To allow for comparisons of production-based outcomes, each mother-reared calf was matched with an artificially-reared calf from the research farm that was of similar age and background; for these outcomes, female calves from all five trials were used.

During the contact period, calves showed differing patterns of suckling behaviour, depending on how contact was managed. In the “calf-driven” system, where calves decided when to seek their mothers, the calves suckled less frequently but for a longer duration on each occasion as they grew older. In contrast, in the “cow-driven” system, where the mothers most often determined when contact occurred, suckling behaviour remained more consistent. However, in both systems, calves suckled from cows other than their own mothers—a behaviour known as allosuckling—and this became more common as calves aged, especially in the cow-driven system.

It was then tested in one of the experimental trials how the calves reacted when weaned and partly separated from their mothers at either four or six months of age. At both ages, calves vocalised, spent less time lying down, and increased their movement—all signs of distress often seen during weaning. The calves also grew more slowly during the weeks following weaning. Younger calves responded slightly stronger than older calves,

particularly during the first few days after weaning, although neither group seemed prepared for the transition to solid food and reduced mother contact.

Calves raised in CCC systems grew at high rates (1.1–1.4 kg per day) until weaning. This was much higher compared to artificially-reared calves, who grew an average of 0.9 kg per day, likely due to their having greater access to milk. The artificially-reared calves were only offered 6–9 litres of milk per day, while mother-reared calves were not restricted in their milk intake. After weaning, this pattern reversed; artificially-reared calves continued to grow at the same rate, while mother-reared calves grew slightly slower (0.8 kg per day) until their first insemination. In the long term, fertility was similar between mother-reared and artificially-reared animals, both as heifers and during first lactation. As adults, cows that were previously raised by their mothers produced, on average, less milk during their first lactation compared to those reared artificially. However, there was a large variation in milk yield between mother-reared cows. Those with the highest milk yields performed equally well as the highest-producing artificially-reared cows. Yet among the lowest-yielding cows, mother-reared cows produced 1400 kg less milk, on average, compared to artificially-reared cows. Lactation persistency, which is a measure of how quickly the milk production declines during lactation, was also on average poorer for mother-reared cows. Many of the CCC cows with the lowest milk yields appeared to have been raised in the same experimental trial, which suggests that milk production may be influenced by differences in how CCC is managed.

In summary, allowing calves to remain with their mothers for up to six months appears to benefit their early growth, but this early advantage might come at the expense of milk production in later life. Moreover, calves appeared unprepared for the loss of milk and mother contact even at six months of age, which is considerably older than when calves in CCC systems are normally weaned. This thesis provides practical advice for farmers who may be interested in starting with CCC, and acts as a basis for further research, particularly on the long-term effects of mother rearing.

Populärvetenskaplig sammanfattning

Mjölkraskalvar separeras vanligtvis från sina mödrar strax efter födseln och utfodras med mjölk eller mjölkersättning, vi kallar det artificiell uppfödning. System där ko och kalv har kontakt (CCC) erbjuder ett alternativt tillvägagångssätt, där kalvarna i stället går tillsammans med vuxna kor och dricker mjölk genom att dia. Dessa system gör det möjligt för kalvarna att uttrycka naturliga beteenden som att dia och att bilda starka sociala band. De har också ofta ett högre intag av mjölk än kalvar som föds upp artificiellt. I denna avhandling hölls mjölkraskalvar tillsammans med sina mödrar i tre till sex månader. Kalvarnas beteende, tillväxt, fruktsamhet och mjölkproduktion studerades, både under den tid de hölls tillsammans med korna och efter det, när de växte upp till vuxna kor.

Fem separata försöksomgångar genomfördes, under vilka ladugården modifierades för att inhysa kalvarna. Detta innefattade installation av grindar för att förhindra att kalvarna kom in i områden som endast var avsedda för kor, samt att bygga en avdelning i ladugården som bara kalvarna hade tillgång till, en så kallad kalvgömma. I två av försöksomgångarna observerades kalvarnas beteende under den tid de gick tillsammans med korna, och därefter även när de avvandes och blandades med ungdjur som fötts upp artificiellt. För att möjliggöra jämförelser av produktionsbaserade resultat matchades varje CCC kviga med en kviga på samma försöksgård som fötts upp artificiellt och som hade liknande ålder och var av samma ras, i dessa analyser ingick kvigor från alla fem försöksomgångarna

Under kontaktperioden visade kalvarna olika beteendemönster när de diade, beroende på hur CCC perioden var utformad. I det kalvstyrda systemet, där kalvarna själva kunde bestämma när de skulle söka upp sina mödrar, ändrades diandet över tid så att kalvarna successivt diade färre gånger per dygn men längre tid vid varje tillfälle ju äldre de blev. I det kodrivna systemet, där det främst var korna som initierade kontakt, sågs ingen förändring i antal tillfällen och längden på varje tillfälle. I båda systemen diade kalvarna även andra kor än sina egna mödrar—ett beteende som kallas korsdiande—och detta blev vanligare ju äldre kalvarna blev, särskilt i det kodrivna systemet.

I ett av försöken testades sedan hur kalvarna reagerade när de avvandes från mjölk och separerades från sina mödrar vid fyra eller sex månaders ålder. I båda åldrarna vokaliserade kalvarna, låg ner mindre och rörde sig

mer – alla väl kända tecken på stress som ofta ses vid avvänjning. Kalvarna växte också långsammare under veckorna efter avvänjningen. Yngre kalvar reagerade något starkare än äldre kalvar, särskilt under de första dagarna efter avvänjningen, men ingen av grupperna verkade dock vara tillräckligt förberedd på övergången till fast föda och minskad kontakt med modern.

Kalvarna som föddes upp i CCC-system växte betydligt snabbare (1,1-1,4 kg per dag) än de kalvar som föddes upp artificiellt (0,9 kg/dag), troligen på grund av ett högre intag av mjölk. De artificiellt uppfödda kalvarna fick 6–9 liter mjölk per dag, medan CCC-kalvar inte hade någon begränsning i sitt mjölkintag. Efter avvänjningen vändes detta mönster och medan artificiellt uppfödda kalvar fortsatte att växa i samma takt så växte CCC kalvar något långsammare (0.8 kg per dag) fram tills de blev inseminerade. Den övergripande fruktsamheten var likartad mellan CCC-kvigor och kvigor som fötts upp artificiellt, både som kvigor och under den första laktationen.

Djur som fötts i CCC-systemet gav i genomsnitt mindre mjölk under sin första laktation än dem som fötts upp artificiellt. Det var dock stor variation mellan individer, och de CCC kor som hade högst mjölkproduktion gav lika mycket mjölk som dem som fötts upp artificiellt. De CCC-kor som hade lägst mjölmängd gav i stället i genomsnitt 1400 kg mindre mjölk än dem som fötts upp artificiellt. Laktationens uthållighet, som är ett mått på hur snabbt mjölkproduktionen minskar efter att den är som högst, var också i genomsnitt sämre för kor som fötts upp i CCC. Många av CCC korna med den lägsta mjölkavkastningen kom från samma försöksomgång, vilket tyder på att hur CCC-system utformas kan ha betydelse för mjölkproduktionen i första laktation.

Sammanfattningsvis verkar det som om att kalvar som får stanna hos sina mödrar i upp till sex månader gynnas i sin tidiga tillväxt, men denna tidiga fördel kan vara på bekostnad av lägre mjölkproduktion senare i livet. Dessutom verkade kalvarna inte vara förberedda på förlusten av mjölk och kontakt med modern ens vid sex månaders ålder, vilket är betydligt äldre än vad som är vanlig avvänjningsålder i CCC-system på kommersiella gårdar. Denna avhandling ger praktiska råd till jordbrukare som kan vara intresserade av att börja med CCC och bidrar också med underlag för vidare forskning, särskilt gällande de långsiktiga effekterna av att föda upp kvigkalvar i CCC-system.

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Appendix

Supplementary Table 1. Description of the dam-reared calves that were removed from four of the experimental batches.

Calf ID	Batch	Sex ¹	Breed ²	Age ³	Reason for removal
8203	1	M	SH	27	Dam euthanised on account of a broken leg due to splits.
2470	3	F	SR	11	Dam died during treatment of <i>E. coli</i> mastitis.
2472	3	F	SH	30	Euthanised following a trauma.
2552	4	F	SR	56	Died of nutritional muscular degeneration.
2710	5	F	SR	66	Dam died during treatment of <i>E. coli</i> mastitis.
2732	5	F	SH	87	Euthanised due to a congenital impairment of the digestive system.

¹F = female, M = male.

²SH = Swedish Holstein, SR = Swedish Red.

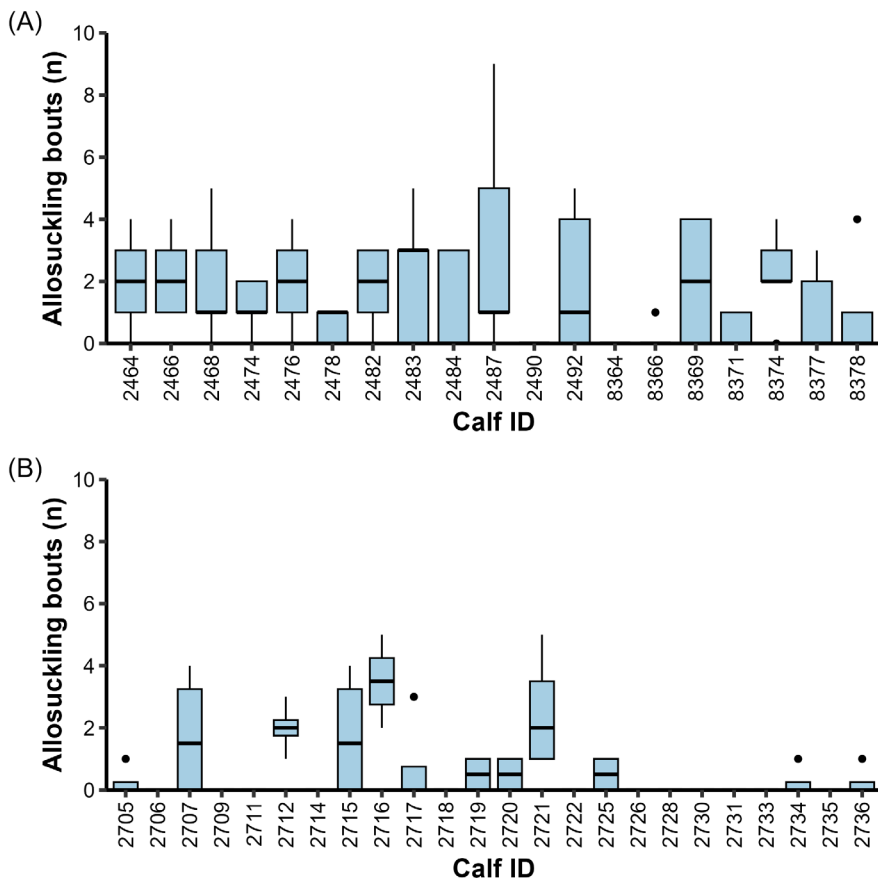
³Age in days at the point of removal from the respective trial.

Supplementary Table 2. Description of the dam-reared heifers that were enrolled in one of five experimental batches but exited the herd prior to first calving.

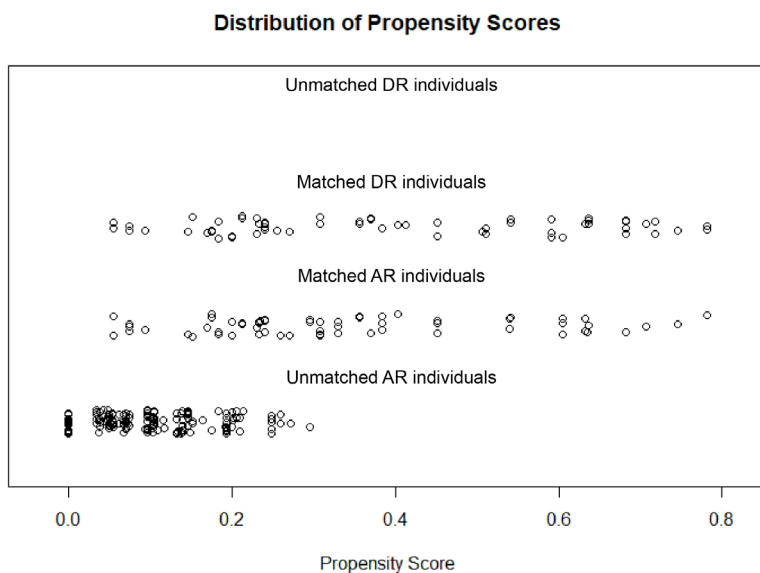
Heifer ID	Batch	Breed ¹	Age ²	Reason for exiting
2260	1	Beef mix	166	Sold live.
2364	2	SH	517	Found dead on pasture.
2366	2	SH	635	Slaughtered due to impaired fertility.
2368	2	SH	511	Found dead on pasture; <i>Clostridium</i> infection suspected at autopsy.
2369	2	SR	628	Slaughtered due to impaired fertility.
2468	3	SR	364	Found dead on pasture; <i>Clostridium</i> infection suspected at autopsy.
2482	3	SR	634	Slaughtered following an abortion at 5.5 months into gestation.
2540	4	SR	782	Slaughtered following a suspected early abortion.

¹SH = Swedish Holstein, SR = Swedish Red.

²Age in days at the point of exit (due to sale, slaughter, or death).



Supplementary Figure 1. Boxplots showing the number of allosuckling bouts performed per calf in a system with cow-driven (A) or calf-driven (B) cow-calf contact. Calves were observed between 3 and 12 (4 observation days; calf-driven) or 15 weeks (5 observation days; cow-driven) of age. Box boundaries show interquartile range (IQR), whiskers extend to the most extreme value no more than 1.5 times the IQR, midlines indicate median values, and points beyond the whiskers denote outliers.



Supplementary Figure 2. Plot showing the distribution of propensity scores per category of matched and unmatched dam-reared (DR; $n = 61$) or artificially-reared (AR; $n = 221$) primiparous cows. Propensity scores were based on the following dam factors as covariates: dam parity, calving year, calving season, and dam breed.



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Suckling and allosuckling behavior of dairy calves in indoor dam-rearing systems

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An important element in dairy cow-calf contact (CCC) systems is to ensure sufficient milk intake by calves. However, little is known about possible changes in suckling behavior during suckling periods for calves up to 15 weeks old, and the prevalence of allosuckling is poorly understood in the context of these systems. This research had two aims: first, to explore possible changes in suckling behavior as calves aged when housed in an indoor CCC system, and second, to identify calf-level factors associated with allosuckling. Both aims were independently investigated in two separate studies (cow- and calf-driven contact, respectively) and involved both Swedish Red and Swedish Holstein dams and calves. In the cow-driven study, dam-calf pairs ($n = 19$ male and female calves) had shared access to a separate contact area containing stalls, which dams could leave at any time. In the calf-driven study, calves ($n = 24$ female calves) could access their dams ($n = 23$) in all parts of the pen, except the milking area. Behavior sampling from video was used to record suckling behaviors during a 24-h period at average calf ages of 3, 6, 9, 12 (both studies) and 15 (cow-driven only) weeks. In the cow-driven study, calves behaved consistently across all weeks in terms of suckling bout length and frequency. Calves in the calf-driven study took significantly fewer, but longer, suckling bouts as they aged. The overall frequency of allosuckling observed in the cow-driven study (36%) was higher than that in the calf-driven study (14%). However, the odds of allosuckling increased significantly with increasing calf age in both studies. Calves in the cow-driven study were observed to allosuckle even in the presence of their own dam, and increasingly so as they aged. For both studies, instances of allosuckling were over 140 times more likely when other calves were already engaged in suckling on a cow. We conclude that allosuckling is likely to occur in indoor dam-rearing systems when the animals are housed in automatic milking systems, although the frequency will depend on the age of the calves and the presence of other suckling calves.

KEYWORDS

cross-suckling, calf management, voluntary milking system, dam-rearing, cow-calf contact

1 Introduction

In intensive dairy production systems, calves are most commonly separated from the dam within hours of being born and then reared artificially, leaving them with limited opportunities to exhibit suckling behavior. Calves are highly motivated to suckle and, when prevented from performing this behavior (e.g., feeding via automatic feeders), have been shown to develop non-nutritive oral behaviors (1). From studies performed under semi-natural conditions, it is

known that calves of beef (*Bos taurus*) and Zebu (*Bos indicus*) dairy breeds that are reared by their dams will perform between 9 and 11 suckling bouts within a 24-h period when they are younger than 3 weeks (2, 3), with individual bouts lasting approximately 10–12 min (4, 5). This behavior has been observed to change as calves age, particularly during the first few months, with fewer – but longer – suckling bouts performed (3, 6, 7). Similar patterns of behavioral change have been noted for dam-reared beef calves in confined housing systems (8, 9) and Zebu dairy calves in restricted suckling systems (i.e., 30 min of dam-calf contact twice daily) where cows were also milked (10).

When dairy calves are housed in cow-calf contact (CCC) systems instead of being reared artificially, they will have opportunities to suckle and engage in pre- and post-stimulation behaviors, more closely reflecting the situation under semi-natural conditions and in beef production. Interest toward CCC systems is growing, as evidenced by the recommendations for increased implementation of prolonged (i.e., >24 h) CCC outlined in a recent European report on calf welfare (11). In these systems, dairy calves are housed together with lactating dairy cows, although the type of CCC [i.e., full or partial physical contact; dam or foster cow; (12)] and duration of daily contact permitted can vary greatly between system setups [for variation in European countries, see survey study by Eriksson et al. (13)].

To date, suckling behavior has been described for a variety of CCC systems, including indoor freestall dam-rearing systems (14, 15). There is some evidence to suggest that dairy calves, similar to that which we described earlier for calves under semi-natural conditions, change their behavior to perform fewer (14, 16) – but longer (17) – suckling bouts as they age. However, observations have previously been limited to 9 weeks of age, which is still short of the weaning age range currently reported for European CCC systems (median: 12–17 weeks) (13).

The first aim of our research was to explore how suckling behavior – including suckling bout duration, bout frequency, and the total time per day spent suckling – changed with age for dairy calves housed in indoor CCC systems with either cow- or calf-driven contact with dams. Whether the system was considered cow- or calf-driven depended on which individuals (i.e., dams or calves) could take primary initiative of CCC within the pen [see Sirovnik et al. (12) for detailed definitions]. The ages studied (cow-driven study: 3–15 weeks, calf-driven study: 3–12 weeks) may offer insight into calf behavior during a suckling period that better represents that of current practices, therefore increasing our knowledge base for future management recommendations.

Additionally, while allosuckling (i.e., the act of suckling from an alien cow) has previously been reported for CCC systems with dam-calf contact, observations of the behavior in calves have either been evaluated at only two points in early life (16, 18), or summarized across multiple ages (14). In general, our current understanding of allosuckling in dairy calves is limited, in terms of how it is affected both by calf age and the housing system (e.g., if the calves have access to parts of or the whole pen). Our second aim was therefore to identify potential calf-level factors associated with allosuckling in dairy calves housed in these two different CCC systems. We further wanted to describe the overall frequency of allosuckling in both systems, although any comparisons between systems will be purely descriptive as the study set-up differed in multiple ways. Finally, there are certain

characteristics that may differ between bouts of allosuckling and suckling bouts on the dam. For example, it has been suggested that allosuckling primarily occurs in positions that allow the calf to avoid identification by the cow through smelling or ano-genital licking (19). As such, we also sought to descriptively present calf position and the occurrence of allogrooming during suckling events.

2 Materials and methods

2.1 Animals, housing and management

Both of the studies described below were conducted at the Swedish Livestock Research Centre in Uppsala, Sweden, and operated with full, whole-day CCC, where contact between dams and calves was possible at any point during the day apart from milking sessions. The sample sizes were based on the number of CCC cows recruited for two larger randomized control trials, also including conventionally kept cows not used in the current studies.

2.1.1 Study 1: cow-driven CCC system

A total of 21 dam-calf pairs were enrolled for Study 1 (hereafter referred to as “cow-driven study”), which took place between October 2020 and January 2021. Dam-calf pairs were enrolled over a 6-week period and included both male and female calves. Dams (primiparous: $n = 12$, multiparous: $n = 9$) were only eligible for enrolment if they had no prior history of *S. aureus* mastitis (if multiparous) and were not severely lame [i.e., a gait score of 4 or 5, following Flower and Weary (20)] during the dry period, as per criteria that was established *a priori*. Pairs spent an average (SD) of 3 (0.6) days together in individual calving pens, located in a separate area, before being introduced to group housing in the experimental pen within the cow barn. Two of the 21 dam-calf pairs were removed from the study during the enrolment period – one due to euthanasia of the calf following a trauma (calf age: 30 days), and another after the dam died of *E. coli* mastitis (calf age: 11 days). The remaining calves were an average of 24 (12.6) days old when the study period began. The final number of dam-calf pairs present for observations during the study period – which lasted until an average calf age of 15 weeks – was 19 (Swedish Holstein [SH]: $n = 7$, Swedish Red [SR]: $n = 12$), including 7 male calves and 12 female calves.

Both dams and calves were housed in an indoor freestall pen stocked with 54 (3) cows during the study period that operated with a Feed First™ system (DeLaval International AB, Tumba, Sweden) and automatic milking (see Figure 1A). All cows, including the non-experimental cows, had shared access to two concentrate stations (DeLaval feed station FSC400, DeLaval International AB, Tumba, Sweden), 37 freestalls, a feed alley containing 20 individual feed bins (CRFI, BioControl AS, Rakkestad, Norway) and seven water bowls, and a milking area containing a waiting area and milking unit (DeLaval VMST™ Classic, DeLaval International AB, Tumba, Sweden). Contact between dams and calves was only possible in the contact area, which was an enclosed area within the experimental pen. Only dams with calves (i.e., enrolled in the study) had access to this area, which was controlled by an automatic selection gate (DeLaval Smart Selection Gate SSG, DeLaval International AB, Tumba, Sweden) when cows exited the feed alley. The contact area contained 22 shared freestalls, as well as two additional concentrate feeding stations for

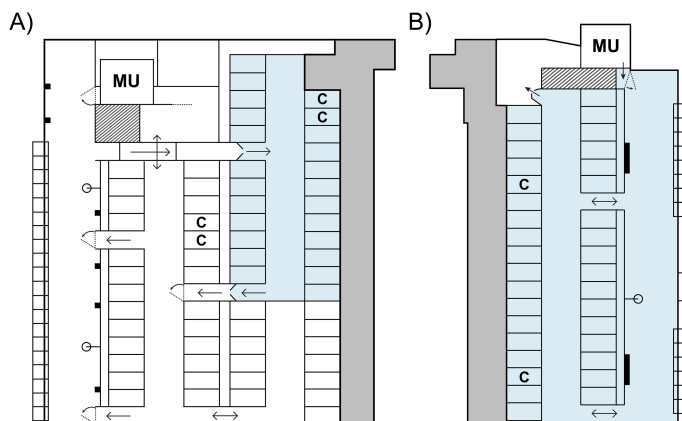


FIGURE 1

Schematic of the experimental pens used in the cow-driven (A) and calf-driven (B) systems, with areas permitting full CCC shown in blue. In the cow-driven system, contact between dam-calf pairs was only possible when cows spent time in the contact area, which they could freely leave. In the calf-driven system, calves could access their dams in almost all areas of the pen. Calves in both systems had additional, exclusive access to a separate calf creep (shown in dark grey), wherein they had access to roughage, concentrate, minerals, and water. All areas shown in white were only accessible to cows; spring-loaded one-way gates prevented calves from entering. MU = milking unit; C = concentrate feeding station. Figures are modified from Wegner and Ternman (21) and Wegner et al. (22).

cows. Dams were directed to the milking area via the selection gate if more than 6 h had passed since their previous milking session. During the study period, cows were milked on average 2.3 (0.58) times per day and delivered 19.5 (9.34) kg of milk daily to the milking unit. As the dams could choose to leave the contact area when motivated to do so, they were the individuals primarily in control over how much dam-calf contact was possible in this study; we therefore refer to this CCC system as cow-driven.

Calves also had exclusive access to a 73.2 m² deep-bedded calf creep containing water, roughage, and concentrate. Movement between the calf creep and contact area was possible through the fronts of the stalls, by walking under the neck and front rails. Spring-loaded one-way gates at both the entrance and exit of the contact area prevented calves from entering other parts of the pen. For more details on housing and management of dams and calves, see Wegner and Ternman (21).

2.1.2 Study 2: calf-driven CCC system

Study 2 (hereafter referred to as “calf-driven study”) was carried out from March to May 2022 and involved an initial 24 dam-calf pairs and 1 dam-calf triad containing twin calves. Dams (primiparous: $n = 11$, multiparous: $n = 14$) and calves were enrolled over a 6-week period according to *a priori*-established enrolment criteria, which stated that the calf was female, and that the dam had no previous history of *S. aureus* mastitis (if multiparous) and was not severely lame during the dry period (following the same criteria as in the cow-driven study). Dam-calf units (SH: $n = 9$, SR: $n = 16$) were housed in individual calving pens for an average of 4 (1.0) days, after which they were introduced to the experimental pen in the cow barn. Calves were an average of 22 (11.4) days old when all pairs had entered the pen and the study period began.

One SR dam-calf pair was removed from the study after the dam was diagnosed with and died of *E. coli* mastitis (calf age: 66 days), while another SH pair was removed due to congenital impaired digestive functioning of the calf (calf age: 87 days). The study period lasted until an average calf age of 12 weeks and ended in mid-May, when dams and calves were granted additional access to an outdoor pasture. A total of 23 dams and 24 calves were available for analyses.

Dams and calves were housed together in an indoor freestall pen with free cow traffic and automatic milking (Figure 1B); no other animals were housed in this pen. Within the pen, CCC was calf-driven, as calves were the primary initiators of contact in this system and could do so in all areas, apart from the calf creep, waiting area, and milking unit (DeLaval VMS™ V300, DeLaval AB International, Tumba, Sweden). Dams could enter the milking unit freely, and either be milked if they had milking permission (which was set at 6 h post-previous milking) or receive a portion of concentrate. On average during the study period, dams were milked 2.8 (0.62) times per day and delivered 18.7 (12.39) kg of milk daily to the milking unit.

Resources shared by both dams and calves included 33 freestalls, two self-filling water troughs, a swinging cow brush (DeLaval SCB, DeLaval International AB, Tumba, Sweden) and a small feeding table containing eight headlock spaces and 1.9 m of open feeding space, where feed was placed in a raised trough to be accessible for calves. Dams had additional access to 14 individual feed bins (CRFI, BioControl AS, Rakkestad, Norway). Meanwhile, calves also had exclusive access to an 80 m² deep-bedded calf creep, which contained *ad libitum* access to water, concentrate and roughage. General pen design and management for this study are described in further detail in Wegner et al. (22).

2.2 Behavioral recordings

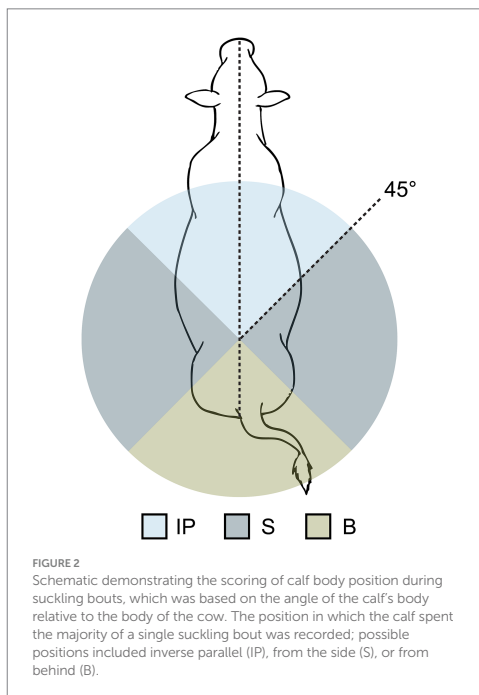
A total of eight (cow-driven study) and six (calf-driven study) fisheye cameras (Samsung SNF-8010VM, Samsung Techwin Co., Ltd., Seoul, South Korea) were installed overhead in all indoor areas. Dams were marked with animal-safe marking spray, while calves were fitted with colored collars to allow the identification of individuals. Behavioral observations were performed by three observers using video data at 24-h periods corresponding to average calf ages of 3, 6, 9, 12 (both studies) and 15 weeks (cow-driven study only). By default, observations occurred between 00:00 and 23:59 h; during three observation periods, adjustments to the start time were made to avoid periods with missing video data or major disturbances in the pen. Blinding the observers for study (cow-driven, calf-driven) or cow-calf relationship (dam vs. alien cow) was not possible as a result of the measures collected and methods used (i.e., video observations, where the entire pen was visible).

Continuous recording using behavior sampling (23) was used to record suckling bouts and close-to-udder events. The definitions for both behaviors were developed by the first and second authors following Fröberg and Lidfors (14) and tested using a 2-h subset of video data (hereafter referred to as the “training dataset”). The final definitions used for all data collection are as follows: a suckling bout was defined as the calf being near (<10 cm) or touching the udder with its mouth for ≥ 1 min and visibly, rhythmically suckling throughout. Contact between the mouth and udder could be broken for periods of <1 min, and suckling bouts that occurred within 10 min on the same cow were considered part of the same event (24, 25). Meanwhile, a close-to-udder event was defined as the calf being near (<10 cm) or touching the udder with its mouth, but with <1 min or no visible suckling activity. Close contacts that occurred <1 min apart and on the same cow were considered a single close-to-udder event.

The cow and calf ID were recorded for all behavioral events. If the event occurring was not between a dam-calf pair, it was additionally recorded if the focal calf's dam was present (i.e., in a barn area accessible to the calf) upon initiation of the event. For both behaviors, event duration was calculated as the total time between first and last contact with the udder, including interruptions as permitted in the definitions.

For suckling bouts, the primary body position of the calf relative to the cow was recorded as being inverse parallel (IP), from the side (S), or from behind (B) (Figure 2). As calf body angle relative to the cow was the only scoring factor, it was possible, for example, for a calf to suckle from between the hind legs but be scored ‘S’ for body position. Additionally, one-zero sampling was used to record allogrooming during, or within 1 min before or after, a suckling bout. Allogrooming was defined as licking between a focal cow and calf, and could be directed to any part of the recipient's body. The individual(s) performing the licking (cow, calf or both) was not recorded.

The reason for termination of a suckling bout or close-to-udder event was additionally recorded as one of the following: (1) the focal calf walks or moves away, (2) the focal cow walks or moves away, (3) the focal cow kicks out or otherwise disrupts the bout (e.g., by butting or lunging at the calf, lying down or defecating), and (4) other. Reasons under ‘other’ included disruptions by non-focal animals, personnel or barn equipment (e.g., barn scrapers). Finally, it was binomially recorded (1 = yes, 0 = no) if at least one other calf was already engaged in suckling the focal cow when a suckling bout or



close-to-udder event began. The conditions for scoring a ‘1’ included that a non-focal calf had to have a confirmed suckling bout of their own, and physically be in contact with the udder at the start time of the focal behavioral event.

2.2.1 Inter-observer reliability

Following an initial training session, where a third observer was trained by the first and second authors (also observers) using the training dataset, all three observers performed independent behavioral recordings on video data from three separate days, covering a total 140 behavioral events. Each event was then scored binomially in terms of whether or not each observer recorded it, and the duration of each event (in seconds) was averaged across all observers. Initial visual analyses indicated that there was poor agreement between observers for very short events. This was confirmed when we performed initial statistical testing using the irr package (26) and calculated a Light's kappa of 0.126. Using an iterative process, we determined that an appropriate cut-off for behavioral event duration was 16 s, as removing observations shorter than this resulted in the highest kappa coefficient ($\kappa = 0.210$) while eliminating as few “true” events as possible. While the kappa statistic itself indicates poor agreement, it is well known that a large difference in relative probability of an event occurring or not (indicated by a high prevalence index) results in paradoxically low kappa values (27). For the 74 events remaining after removing events shorter than 16 s, we obtained an overall agreement of 85% between raters (i.e., all three observers agreed on these events). The Prevalence Index (possible values –1 to 1; 0 indicates no difference in relative probability) and Bias Index (possible

values -1 to 1 ; 0 indicates no bias between observers) were calculated for each pair of observers, resulting in a Prevalence Index ranging from 0.85 to 0.88 and a Bias Index ranging from -0.03 to -0.01 . Combined, these metrics lead us to conclude sufficient inter-observer reliability for events 16 s or longer. To further reduce the risk of error in data recording, observers were instructed to flag uncertain events. These events were then reviewed with all observers present, and a consensus was reached.

2.3 Calf weight recordings

Calves in both studies were weighed at birth (mean (SD): cow-driven study = 38 (6.5) kg, calf-driven study = 40 (6.6) kg) and monthly thereafter throughout each study period. For calculations of average daily gain (ADG), we used birth body weight and the body weight collected in nearest proximity to the end of each study period. For the calf-driven study, this measure was collected 11 days before the end of the study period. Body weights used for the cow-driven study were, for practical reasons, collected on 2 separate days, corresponding to 1 and 4 days after the study period ended. ADG was calculated by subtracting birth weight from the body weight near the end of the study period and dividing by the difference in days between these two weighings.

2.4 Data handling and analysis

All data handling and statistical analyses were performed using R version $4.4.2$ (28) and the tidyverse package (29). Statistical significance was accepted at $p < 0.05$. For all linear mixed effects models, test statistics and p -values were obtained using the car package (30) and following Al-Sarraj and Forkman's (31) recommendations for analyzing unbalanced datasets. Results from linear mixed effects models were extracted using the emmeans package (32) and estimated responses are reported as LSMeans $\pm$ SEM. Raw data is presented as mean (SD) if normally distributed, while skewed data is reported as median and interquartile range (IQR). The individual calf was treated as the experimental unit in all analyses.

There were a total of 980 and 964 behavioral events recorded for the cow- and calf-driven studies, respectively; of these, 7 and 9 events (cow-, calf-driven study) were removed due to poor camera angles interfering with observer ability to determine start or end times, or to confirm suckling. Following the removal of events <16 s in length (see 2.2.1 for explanation; events removed in cow-driven, calf-driven study: 356 , 264), events occurring within 1 min between the same cow-calf pair – but that were previously separated by a short (i.e., <16 s) event on a different cow – were aggregated (cow-driven: 9 events; calf-driven: 12 events). This ensured that behavioral events followed the definitions as written in section 2.2, rather than being analyzed as separate events despite occurring on the same cow. One dam-calf pair was missing in the calf-driven study on the earliest observation period (i.e., age 3 weeks) due to treatment of the dam for mastitis in a sick pen.

2.4.1 Suckling and allosuckling behavior

The 380 (cow-driven) and 419 (calf-driven) suckling bouts remaining after the initial data cleaning were further binomially classified as “suckling on dam” (0) or “allosuckling” (1) events. Prior

to statistical analysis, the number of suckling bouts and total suckling time, regardless of whether performed on the dam or other cows, were summed per calf and day (defined here as a full, continuous 24 -h period). Linear mixed effects models were then run, separately per study, using the lme4 package (33) with the following suckling behaviors as outcomes: daily suckling bouts (no. bouts/d), suckling bout duration (s/bout) and total suckling time (min/d). Fixed effects included in the models were average calf age (weeks; numeric) and bout type (0 = suckling on dam, 1 = allosuckling; suckling bout duration models only), while calf ID (cow-driven: $n = 19$; calf-driven: $n = 24$) was specified as a random intercept. Additionally, for models pertaining to the cow-driven study, calf sex was included as a fixed effect (no male calves in calf-driven study). All possible two-way interaction effects were tested but ultimately not included in the final models due to non-significance ($p \geq 0.05$). Residuals were visually inspected to assess heteroscedasticity and normality for all models.

To explore possible factors related to allosuckling, we additionally used a generalized linear mixed model with a logit link function and binomial distribution [lme4 package (33)] for each respective study. In this case, the response variable was allosuckling ($1/0$). Model predictors included average calf age (weeks; numeric), calf sex (cow-driven study only), birth weight (kg) and presence of other suckling calves on the focal cow at the start of the bout ($1/0$), while calf ID (cow-driven: $n = 19$; calf-driven: $n = 24$) was included as a random intercept. Additionally, we wanted to explore factors associated with allosuckling when the dam was present in the cow-driven study, as dams could spend time in areas not accessible by calves. Therefore, the cow-driven dataset was first filtered to include only events where the dam was marked as present ($n = 284$ events). Then, a second generalized linear mixed model with logit link was run testing the same predictors ($n = 19$ calves), with allosuckling once again as the response, i.e., modeling the probability of allosuckling conditional on the dam being present. Log-odds estimates for all logistic regression models were transformed and reported as odds ratios.

Our literature review when planning the studies provided little evidence of breed influencing suckling behaviors in dairy calves, and as such breed was not included in our *a priori* hypotheses. However, since both our studies included two different breeds, additional exploratory *post hoc* analyses were performed including breed as a predictor. Results from these models are presented in Supplementary Tables 1, 2. The inclusion of breed resulted in only minor numerical changes in the estimates for the other predictors, with no effects on our main results.

Finally, we wanted to explore the relationship between the relative frequency of allosuckling per calf (% of all suckling bouts that were allosuckling) and ADG during the study period, as previous work on beef calves has suggested a slightly negative relationship between the two variables (34). Spearman's rank correlation coefficients were calculated per study using correlation tests and are reported alongside p -values and correlation plots. Interpretation of correlation coefficients followed guidelines by Schober et al. (35).

2.4.2 Suckling bout attributes

For each study, calf body position during suckling bouts, bout termination reason, and the occurrence of allogrooming were all descriptively reported separately for suckling bouts occurring on the dam and bouts of allosuckling. Data pertaining to allogrooming was not available for four of the recorded suckling bouts due to poor visibility of cow and/or calf head.

2.4.3 Close-to-udder events

Following the initial data cleaning, the time (in min) from each close-to-udder event to the next suckling bout (for the same calf, on that same day) was calculated; this was not possible for all events (cow-driven: 31, calf-driven: 38) due to no more suckling bouts occurring during the observed time. The resulting data for the difference in time had a strong right skew; consequently, the median difference in time was calculated, and this value was used to categorize close-to-udder events as occurring shortly before the next suckling bout or not (see [Supplementary Figures 1, 2](#)).

The strong right skew of time to next suckling bout suggests that during many close-to-udder events, calves may have been actively seeking opportunities to suckle. To further explore this notion, we additionally evaluated if the frequency of close-to-udder events occurring close in time before the next suckling event was correlated with the frequencies of allosuckling bouts and suckling bouts on the dam. Correlation tests were performed to test all four possible associations and used to calculate Spearman's rank correlation coefficients and corresponding *p*-values. Close-to-udder events were defined as occurring close in time if within the median time between close-to-udder events and subsequent suckling bouts.

3 Results

3.1 Suckling behavior

3.1.1 Cow-driven study

Calves performed an average (SD) of 4 (1.5) suckling bouts per day, with no significant differences between sexes or as calves increased in age ([Table 1](#)). Similarly, the suckling bout duration did

not change with calf age, but bouts of allosuckling were significantly shorter than suckling bouts between dam-calf pairs (LSMean ± SEM: 8 ± 0.6 vs. 12 ± 0.5 min/bout). Suckling bout duration and frequency did not differ significantly between male and female calves, but female calves tended to engage in more daily suckling than male calves (46 ± 2.9 vs. 36 ± 3.8 min/d). No effect of calf age was found for total daily suckling time, with calves spending an average of 42 (17.0) min/d engaged in suckling across the study period. Weekly average values for all suckling behaviors based on raw data can be viewed in [Supplementary Table 3](#).

3.1.2 Calf-driven study

As calves aged, they changed their behavior to perform fewer suckling bouts per day (3 weeks: 5 ± 0.3 bouts/d, 12 weeks: 4 ± 0.3 bouts/d; [Table 1](#)). The duration of individual suckling bouts increased during this time, with bouts occurring on the dam being significantly longer than bouts of allosuckling at all ages (11 ± 0.5 vs. 8 ± 0.8 min/bout). Suckling bouts between dam-calf pairs increased in duration from 9 ± 0.6 min/bout at 3 weeks to 13 ± 0.6 min/bout at 12 weeks of age. There was a tendency for calves to spend more time suckling per day as they aged (3 weeks: 42 ± 2.0 min/d, 12 weeks: 47 ± 2.0 min/d), although this finding was not significant. For all suckling behaviors, weekly average values based on raw data can be viewed in [Supplementary Table 3](#).

3.1.3 Allosuckling behavior

Out of a total 380 (cow-driven study) and 419 (calf-driven study) suckling bouts recorded, 36% and 14% were bouts of allosuckling in each study, respectively (see [Figure 3](#) for a weekly breakdown). There were a number of calves that suckled exclusively on their own dams during the observation days in both studies, although this behavior was descriptively more prevalent in the calf-driven study (cow-driven:

TABLE 1 Fixed-effect estimates (est.) and SE for all linear mixed effects models of suckling behavior in either a cow-driven (*n* = 19 dam-calf pairs) or calf-driven (*n* = 23 dams, *n* = 24 calves) CCC system.

Behavior	Cow-driven					Calf-driven				
	Est.	SE	<i>F</i> -value	df1, df2	<i>p</i> -value	Est.	SE	<i>F</i> -value	df1, df2	<i>p</i> -value
Total suckling bouts (bouts/d)										
Calf age	0.04	0.029	1.75	1, 75	0.19	−0.10	0.033	9.30	1, 70	0.003
Calf sex ¹	0.68	0.462	2.16	1, 17	0.16	–	–	–	–	–
ICC ²	0.31					0.45				
Suckling bout duration (s/bout)										
Calf age	5.24	3.348	2.45	1, 362	0.12	24.53	3.541	47.92	1, 397	<0.001
Bout type ³	−192.71	31.676	36.65	1, 376	<0.001	−177.59	41.121	18.44	1, 415	<0.001
Calf sex ¹	69.28	54.891	1.59	1, 18	0.22	–	–	–	–	–
ICC ²	0.12					0.25				
Total suckling time (min/d)										
Calf age	0.38	0.357	1.11	1, 75	0.30	0.54	0.275	3.78	1, 70	0.06
Calf sex ¹	9.63	4.766	4.09	1, 17	0.06	–	–	–	–	–
ICC ²	0.21					0.31				

Calf age (cow-driven study: 3–15 weeks, calf-driven study: 3–12 weeks) was included as a numeric variable, and bout type referred to suckling on dam vs. allosuckling. *p*-values are shown for main effects, and *F*-statistics and degrees of freedom were estimated using the Kenward-Roger method.
¹Male calves were considered as the baseline; no male calves included in the calf-driven study.
²Intra-class correlation coefficient.
³Suckling bouts on dam were considered as the baseline.

2 calves, calf-driven: 12 calves). For the remaining calves (i.e., those that allosuckled at least once), the proportion of all suckling bouts that were performed on alien cows ranged from 8–61% (median: 40%) for the cow-driven study, and 4–61% (median: 15%) for the calf-driven study.

The odds of allosuckling increased significantly with calf age in both the cow-driven and calf-driven studies (Table 2). In the cow-driven study, the odds of allosuckling increased by 4.4 from 3 to 15 weeks of age. The odds of allosuckling at 12 weeks in the calf-driven study were 7.3 times greater than the odds at 3 weeks of age. There was also a strong influence of other calves already suckling the focal cow on the odds of allosuckling, with 170 (cow-driven study) and 141 (calf-driven study) times higher odds of a calf successfully suckling on an alien cow if other calves were already suckling the same cow, compared to cases where that calf was the first to suckle. In 86% (cow-driven study) and 89% (calf-driven study) of occasions where a calf joined an alien cow already nursing at least one other calf, the cow's own calf was among them. In general, allosuckling was more commonly observed as a group as opposed to solitary behavior, with calves suckling on an alien cow containing other suckling calves in 81% (cow-driven study) and 62% (calf-driven study) of all suckling events. Additionally, when the data set for the cow-driven study was filtered for suckling events occurring when the dam was present in the contact area, the odds of allosuckling increased as the calves grew older (Figure 4).

There was a tendency for a weak positive correlation between ADG throughout the study period and the relative frequency of allosuckling (% of all bouts that were allosuckling) for calves in the calf-driven study (Figure 5A). In the cow-driven study, no such correlation was found (Figure 5B).

3.2 Suckling bout attributes

When suckling on the dam, calves were primarily in an IP position (see Table 3). In contrast, allosuckling rarely occurred in this position,

with calves instead positioning themselves perpendicular to or behind alien cows when suckling. Allogrooming occurred in 40% of bouts between dam-calf pairs in the cow-driven study, while it was observed only in 1% of allosuckling events. Similarly, in the calf-driven study allogrooming was observed in 49% of suckling bouts occurring on the dam, and during none of the allosuckling bouts.

Suckling bouts between a dam and her calf were most often terminated by the calf (Figure 6). Conversely, approximately half of all allosuckling bouts (cow-driven study: 49%, calf-driven study: 53%) came to an end due to actions on part of the focal cow. The average duration of allosuckling bouts in the calf-driven study that were cow-terminated was numerically shorter than those terminated by calves, a pattern that was less pronounced in the cow-driven study (Table 4). Bouts ending due to kicking or other disruption (i.e., lunging, lying down or defecating) by the focal cow were, proportionally, quite similar between dam-calf pairs (8%) and unrelated cow-calf pairs (13%) in the cow-driven study. Meanwhile, in the calf-driven study, suckling bouts ending for this reason occurred more often in cases of allosuckling than for suckling on dam (12% vs. 4%).

3.3 Close-to-udder events

A total of 233 (cow-driven study) and 265 (calf-driven study) close-to-udder events were recorded across the different calf ages. This behavior occurred between calves and their dams in 35% and 64% of events for the cow-driven and calf-driven study, respectively. The duration of close-to-udder events was most commonly very short (median [IQR]; cow-driven study: 48 [27–85] s; calf-driven study: 55 [26–101] s).

Of the close-to-udder events in the cow-driven study, half occurred within 16 min of the next suckling bout (Supplementary Figure 1); these close-to-udder events were mainly terminated by cows (40%) or calves (56%), with a low number of events ending due to miscellaneous reasons. The number of

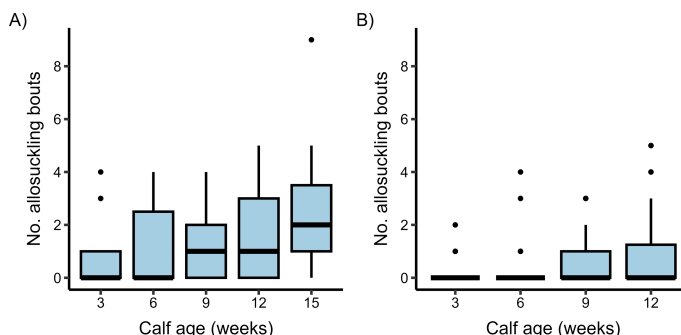


FIGURE 3
Boxplots presenting the number of allosuckling bouts per calf and observation day in a cow-driven (A) and calf-driven (B) CCC system across different ages. In the cow-driven study, dam-calf pairs ($n = 19$) could have full contact in a designated contact area within the pen, which cows could choose to leave at any time. For the calf-driven study, full contact between dams ($n = 23$) and calves ($n = 24$) was possible in all parts of the freestall pen. Box boundaries show interquartile range (IQR), whiskers represent 1.5 times the IQR, and the midline indicates the median value per calf age. Dots show values for all individual calves outside the whisker boundaries.

TABLE 2 Fixed-effect estimates, SE and *p*-values for all logistic mixed regression models of allosuckling behavior in either a cow-driven (*n* = 19 dam-calf pairs) or calf-driven (*n* = 23 dams, *n* = 24 calves) CCC system.

Behavior	Cow-driven			Calf-driven		
	Estimate	SE	<i>p</i> -value	Estimate	SE	<i>p</i> -value
Allosuckling (1/0)						
Calf age	0.12	0.046	0.01	0.22	0.074	0.003
Other calves	5.14	0.514	<0.001	4.95	0.795	<0.001
Calf birth weight	−0.04	0.039	0.27	0.03	0.065	0.68
Calf sex ¹	0.42	0.467	0.36	–	–	–
ICC ²	0.01			0.40		
Allosuckling with dam present (1/0)						
Calf age	0.25	0.082	0.003	–	–	–
Other calves	5.59	0.950	<0.001	–	–	–
Calf birth weight	−0.12	0.077	0.13	–	–	–
Calf sex ¹	−0.27	0.908	0.77	–	–	–
ICC ²	0.24			–		

Calf age (cow-driven study: 3–15 weeks, calf-driven study: 3–12 weeks) and birth weight were included as numeric predictors. Other calves refers to whether or not any non-focal calves were suckling the focal cow at the start of the focal suckling event and was scored binomially (1/0). Separate models were run for allosuckling in general and allosuckling only when the dam was present (i.e., physically available to the calf), which was not possible in the calf-driven study as the dam was always present.
¹Male calves were considered as the baseline; no male calves included in the calf-driven study.
²Intra-class correlation coefficient.

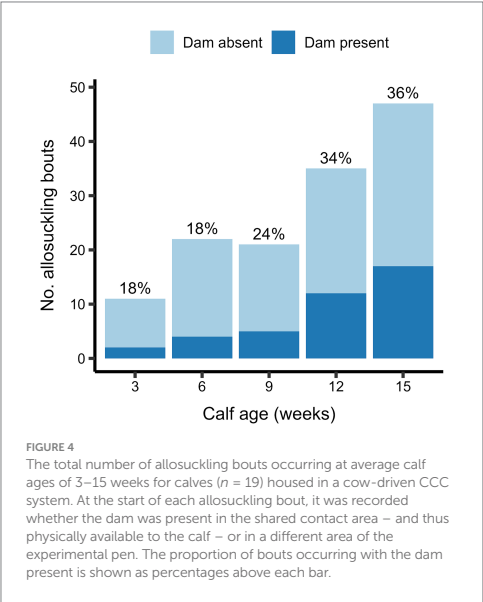


FIGURE 4 The total number of allosuckling bouts occurring at average calf ages of 3–15 weeks for calves (*n* = 19) housed in a cow-driven CCC system. At the start of each allosuckling bout, it was recorded whether the dam was present in the shared contact area – and thus physically available to the calf – or in a different area of the experimental pen. The proportion of bouts occurring with the dam present is shown as percentages above each bar.

close-to-udder events per calf occurring within 16 min of the next suckling bout was positively correlated with the number of allosuckling bouts performed by the calf during the study period (Figure 7A). Conversely, no correlation was evident between the frequency of close-to-udder events and suckling bouts performed on the dam (Figure 7B). As calves aged, close-to-udder events involving the dam decreased (59% at 3 weeks vs. 21% at 15 weeks), with calves instead directing this behavior toward alien cows to a higher degree.

The median time between close-to-udder events and subsequent suckling bouts in the calf-driven study was 71 min (Supplementary Figure 2). Of the events occurring within 71 min of suckling, the majority were terminated by calves (66%) as opposed to cows (30%). There was a moderate positive correlation between the number of allosuckling bouts per calf and number of close-to-udder events within 71 min of the next suckling bout, but it was less common for calves in the calf-driven study to allosuckle more than once (Figure 7C). In the calf-driven study, no correlation was found between the number of close-to-udder events and the frequency of suckling bouts involving dams (Figure 7D). Overall, close-to-udder events were primarily directed toward the dam in the calf-driven study, although the proportion decreased with increasing calf age (3 weeks: 84%, 12 weeks: 55%).

4 Discussion

In brief, calves in the cow-driven study allosuckled more frequently as they aged, but no other changes in suckling behavior were found. Calves in the calf-driven study performed fewer but longer suckling bouts as they aged, and allosuckling increased with age. While suckling behavior has previously been described for dairy calves housed together with their high-yielding dams indoors, we believe we are the first to do so beyond an average calf age of 9 weeks.

4.1 Suckling behavior of calves

Calves in the calf-driven study followed a pattern of behavioral change (i.e., fewer but longer suckling bouts) that aligns with expectations based on research of pastured beef (3, 6) and free-ranging Maremma (7) cattle. Similar age-related changes have been observed for dairy calves in various dam-rearing systems with whole-day contact. Calves housed with their dams in an indoor deep-bedded

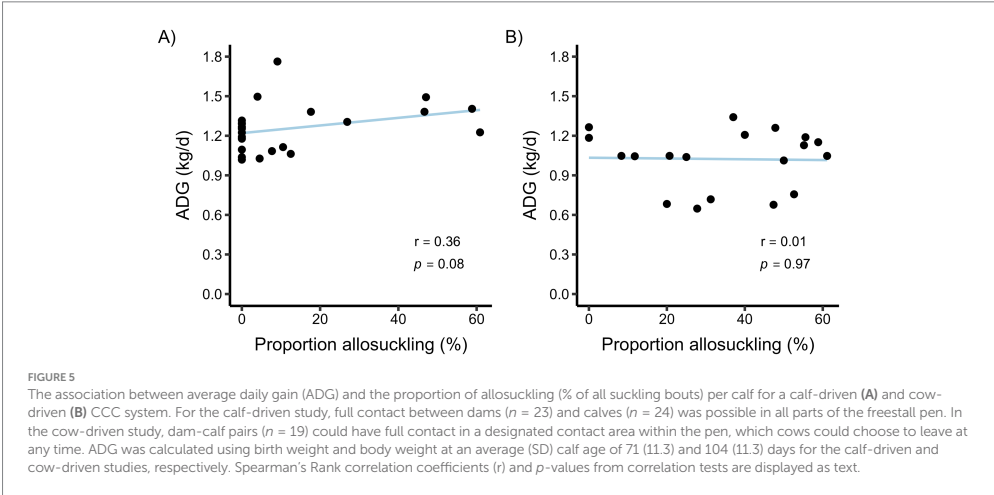


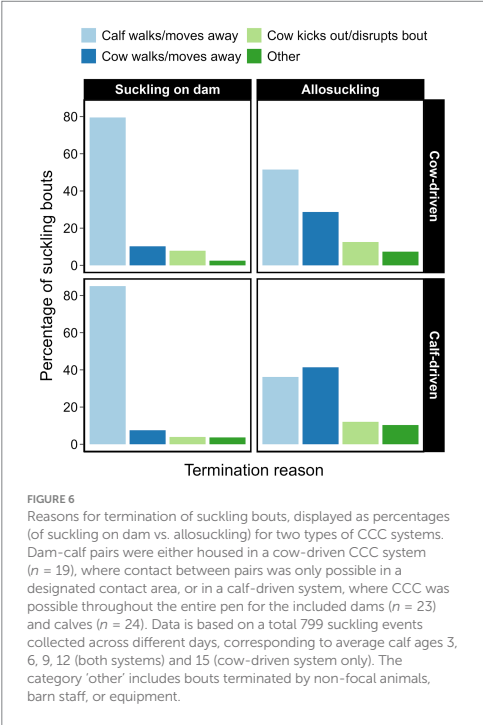
TABLE 3 Percentage of suckling bouts performed in inverse parallel (IP), or from the side (S) or back (B) of the focal cow.

Study	Bout type	Total events	Calf body position (% of total events)		
			IP	S	B
Cow-driven	Suckling on dam	243	70	24	6
	Allosuckling	136	11	61	28
Calf-driven	Suckling on dam	361	86	9	5
	Allosuckling	58	15	47	38

Dam-calf pairs were freestall-housed with either cow-driven ($n = 19$ pairs) or calf-driven CCC ($n = 23$ dams, 24 calves) and observed for suckling behavior at average calf ages of 3, 6, 9, 12 (both studies) and 15 (cow-driven study only) weeks.

pack [calf ages: 2 & 4 weeks; (17)] or on pasture [ages: 3 & 6 weeks; (36)] suckled for longer durations as they grew older. Decreases in suckling bout frequency have also been reported from 3–8 weeks of age for calves in indoor CCC systems (14, 16). These changes in the frequency and duration of milk meals observed in other studies and our own may be, in part, due to the increasing stomach capacity of the calf as it ages. However, one question remains: Why were the same behavioral patterns not evident in the cow-driven study?

In the cow-driven study, neither the duration nor the frequency of suckling bouts was significantly influenced by calf age, although bout duration increased numerically between 3 and 12 weeks of age. One explanation is that perhaps the available time for contact – and thus, suckling – was more limited than in the calf-driven study. Johansson et al. (37) evaluated the time budgets of the dams in our cow-driven study, and reported that they spent on average at least 32% of their daily time budget outside the contact area (based on time spent on activities that could not have been performed in this area, e.g., milking and consuming forage in the feed alley). This would suggest that in terms of hours of dam-calf contact per day, the cow-driven study may have been closer to a half-day CCC system (i.e., 12 h/d), at least for some calves. Similar to our findings, Bertelsen and Jensen (16) reported that dairy calves reared with half-day CCC had



no difference in the number of daily suckling bouts at 3 and 7 weeks of age, citing the restriction in contact time as the probable cause. The lack of changes in suckling behavior in our cow-driven study could thus be a sign of substantial restrictions in suckling time, potentially as a result of our pen set-up.

TABLE 4 Mean (SD) duration of suckling bouts, per bout type (suckling on dam or allosuckling), as terminated by the cow, calf, or for another reason (e.g., bouts terminated by non-focal animals, barn staff or equipment).

Study	Behavior	Terminator of bout		
		Cow	Calf	Other
Cow-driven	Suckling bout on dam duration (min/bout)	12 (5.8)	11 (4.5)	12 (3.7)
	Allosuckling bout duration (min/bout)	9 (4.7)	10 (4.9)	7 (3.5)
Calf-driven	Suckling bout on dam duration (min/bout)	12 (6.0)	10 (4.4)	11 (5.1)
	Allosuckling bout duration (min/bout)	8 (4.0)	11 (5.6)	5 (2.8)

Dam-calf pairs were freestall-housed with either cow-driven ($n = 19$ pairs) or calf-driven CCC ($n = 23$ dams, 24 calves) and observed for suckling behavior at average calf ages of 3, 6, 9, 12 (both studies) and 15 (cow-driven study only) weeks. Mean values are based on raw values.

Alternatively, the lack of overall linear increase in suckling bout duration for this study may have been due to the numerically low value at 15 weeks of age. Since no obvious disruptions were noted in the barn during this observation period, it is unclear what may have caused suckling bouts on this day to be approximately 4 min shorter than at 12 weeks. One possibility is that the increase in this behavior for indoor-housed dairy calves is limited to the first 3 months of life, potentially due to increased suckling efficacy or greater solid feed intake beyond this point, but further investigation is needed to verify this notion.

In both the cow-driven and calf-driven study, allosuckling bouts were approximately 3–4 min shorter than suckling bouts performed on the dam. While comparisons of duration for bouts between calves and dams vs. alien cows have not been previously reported for dairy cattle, our findings are similar to that of beef calves kept on pasture (19) or indoors (38). Our results are logical if we consider that around half of all allosuckling bouts were terminated by the cow, and these bouts were often shorter than calf-terminated allosuckling bouts. As described further in section 4.3, allosuckling frequently occurred on cows that were already engaged in an ongoing nursing event, which in 86–89% of cases included the cow's own calf. While cows that are nursing their own calves may be more tolerant of alien calves (14, 19), this tolerance likely dissipates once their calf has left.

Calves in the calf-driven study tended to spend more time suckling per day as they aged, likely due to the increasing bout duration. Meanwhile, daily suckling time in the cow-driven study remained stable with age. Only two previous studies have examined 24-h suckling time across different ages, and both reported no age effect (3, 24). However, these studies involved very young dairy calves [3–11 days old; (24)] or pasture-kept beef calves (3), limiting comparability with our findings.

Although age did not influence daily suckling time in the cow-driven study, female calves tended to spend more time suckling per day compared to male calves. Comparatively, other work has found no effect of calf sex on suckling behavior (14, 18). Although neither suckling bout frequency nor bout duration was statistically affected by calf sex, female calves had numerically more frequent and longer suckling bouts; hence, the combination of these two behaviors may have resulted in the greater daily suckling time for female calves.

Across all ages, the calves in both our studies performed approximately 4–5 suckling bouts/d, for 9–13 min/bout, which is within range of that reported by other studies that consider suckling within a 10-min period to be the same suckling bout

(14, 24). Further direct comparisons of similarly-aged calves in literature are difficult due to differences both in study conditions and in suckling bout definitions; new bouts have been defined after pauses of anywhere between 3 s (15) and 2 min (19). Due to the definitions we used, it is likely that the bout durations and total suckling times reported in our own work are overestimated to an extent, as calves were occasionally noted to resume suckling bouts after relatively long pauses (i.e., nearly 10 min), and thus what we report as suckling bouts may closer represent suckling meals [see Špinka and Illmann (25)].

4.2 Allosuckling frequency in cow- and calf-driven CCC systems

As our two studies were performed in different pens, resulting in substantial differences in pen set-up and management, we were not able to statistically evaluate if allosuckling was affected by the type of CCC system. Descriptively, allosuckling was observed more frequently in the cow-driven study than in the calf-driven study (36 vs. 14% of all suckling bouts). In other recent work, calves in half-day CCC systems tended to be more likely to allosuckle compared to calves reared with whole-day CCC [ages: 3 & 7 weeks; (16)]. Johnsen et al. (15) similarly noted more frequent allosuckling when dams had restricted compared to free access to a contact area. If we continue the assumption that our cow-driven study more closely reflected half-day CCC, it is plausible that the calves in this study resorted to allosuckling if they were hungry when their dam was not present in the contact area.

Interestingly, Fröberg and Lidfors (14) reported a relative allosuckling frequency of only 16% for a cow-driven CCC system. This may be at least partially explained by less severe restrictions on contact time, as their contact area included all lying stalls within the experimental pen instead of only part of the lying area as in our cow-driven system. This highlights the importance of pen design for cow-driven CCC systems, as the direction of cow traffic and availability of shared resources (e.g., stalls) may influence the amount of time spent by cows in the contact area – and thus the amount of time available for calves to suckle and receive other maternal care.

In addition to its prevalence in other ungulate species [see review by Mota-Rojas et al. (39)], allosuckling has been reported for dairy calves across a variety of ages and systems (14–16, 18, 40, 41), as well as for indoor-housed beef calves (34, 38, 42), twin beef calves on pasture (19) and Zebu dairy calves with restricted suckling (10).

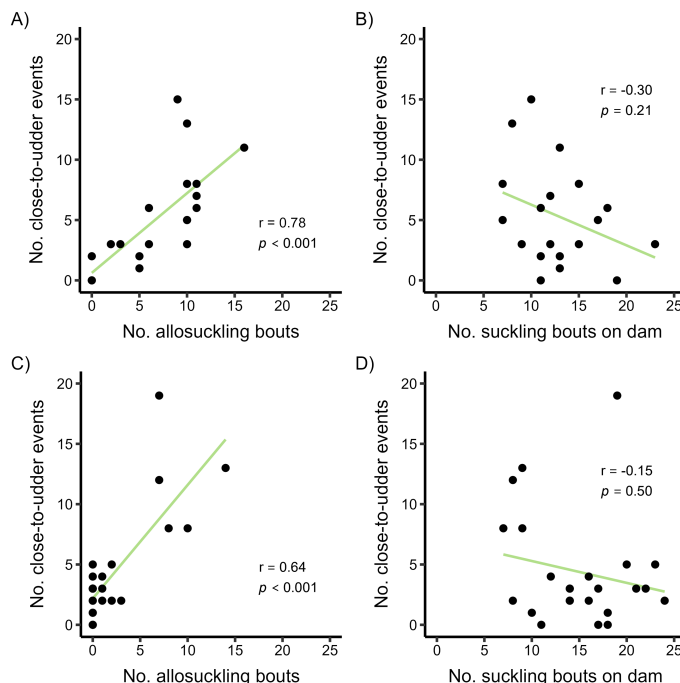


FIGURE 7

Correlation plots showing the frequency of close-to-udder events occurring shortly (defined as less than the median time difference) before the next suckling bout and the frequency of allosuckling bouts or alternatively number of suckling bouts on the dam per calf for a cow-driven (A,B) and calf-driven (C,D) CCC system. In the cow-driven study, dam-calf pairs ($n = 19$) could have full contact in a designated contact area within the pen, which cows could choose to leave at any time. For the calf-driven study, full contact between dams ($n = 23$) and calves ($n = 24$) was possible in all parts of the freestall pen. Spearman's Rank correlation coefficients (r) and p -values from correlation tests are displayed as text.

Under extensive conditions, allosuckling in beef and Zebu cattle has been reported as non-existent (43), with attempts by calves being thwarted by dams from an early age (6). In contrast, dairy calves may find more success in allosuckling due to a selection for docility during milking (41, 44); indeed, few allosuckling bouts in our own studies ended due to kicking or lunging by the cow. It is also possible that dairy cattle are generally more accepting of alien calves; Loberg and Lidfors (45) reported that nearly all of 46 foster dairy cows permitted suckling by groups of four alien calves only using minimal human interference (e.g., tying up the cows). Yet without a direct comparison of dairy and beef breeds under matching circumstances, it is unclear if differences in allosuckling frequency are the result of differences in genetics, housing, management, or a combination of all three, since dairy breeds have not been evaluated for allosuckling under similarly extensive conditions as beef cows are typically kept.

Regardless, it is clear from both our own studies and those of others that allosuckling likely cannot be avoided in systems where dairy cows and calves are housed together. This raises the question: is allosuckling something we should strive to avoid? One potential concern with cows being suckled by multiple calves is that there is some evidence suggesting short-term damage to teats in dairy cows

that were suckled by 3–4 calves for 15 min twice daily without additional milking (46). Given the study design, this finding may primarily be due to low milk yield of the cows combined with a high competition for teats, although it is unclear from available information if the calves were additionally supplemented with milk. Furthermore, the notion that calves may act as vectors for pathogen transmission between cows – and thus negatively impact udder health – remains unsubstantiated (47). Suckling by one or more calves can instead be beneficial for the dams in reducing the risk of mastitis, especially in early lactation, likely largely due to more complete udder emptying [see review by Beaver et al. (48)]. Yet not all dams are equally accepting of nursing alien calves, which is reflected in our work by the numerically higher proportion of allosuckling bouts (compared to suckling bouts between dam-calf pairs) that were terminated by the dam. In cow-driven CCC systems, cows have the possibility to physically remove themselves from situations of unwanted allosuckling by leaving the contact area, which dams in our cow-driven study were anecdotally noted to do on several occasions. In contrast, reprieve from calves was not possible in our calf-driven study; thus, from the perspective of cow welfare, calf-driven CCC may negatively impact dam agency.

Looking instead from a calf perspective, allosuckling may serve as a strategy to obtain adequate milk to maintain high growth (39), particularly in situations when dam access is limited. In both our studies, calves that frequently allosuckled had similar or slightly higher ADGs compared to calves that suckled more from their dams. Although the number of allosuckling bouts was numerically higher in the cow-driven study, the total daily time spent suckling and the frequency of suckling bouts were similar in both studies. This finding suggests that the calves in the cow-driven study were able to compensate for any restrictions in dam-calf contact through allosuckling. Ultimately, the question of how to weigh the benefits of allosuckling for calves against potential welfare consequences for dams (e.g., reduced agency) is beyond the scope of our research, but must be addressed as attention toward CCC systems continues to grow.

4.3 Calf-level factors associated with allosuckling

As the calves in our studies aged, we found that the odds of suckling on alien cows increased significantly, albeit to a numerically greater extent in the cow-driven study. This contrasts with recent work by Bertelsen and Jensen (16), who found that dairy calves were more likely to allosuckle at 3 versus 7 weeks of age. In beef calves, allosuckling has been reported to increase [calf age 1–100 d, (38); 2–5 mo, (19)] or remain constant [1–203 d, (34)] as calves age. It is unclear what exactly is driving this increase in the behavior in some settings. In our cow-driven study, allosuckling likely initially manifested primarily out of hunger, based on the high proportion of allosuckling bouts at ages 3 and 6 weeks that occurred when the dam was absent from the contact area. At the same ages, only a few calves in the calf-driven study were observed to allosuckle at all. Our findings in the calf-driven study align with other work indicating that young dairy calves prefer to suckle their own dam [i.e., <1 week old (25)].

One possibility for increased allosuckling is that as the calves grew older, those that had previously learned to allosuckle (e.g., out of hunger or opportunity) continued to do so at increasing frequencies, with each successful attempt reinforcing the behavior. Recent work indicates that dam-calf pairs form strong bonds even when suckling is prohibited (49), suggesting that from the calf's perspective, a primary function of suckling is to provide it with nutrition, regardless of who acts as the provider (i.e., dam or alien cow). This might explain the increasing percentage of allosuckling observed in the cow-driven study even when the dam was present. While allogrooming may accompany suckling, this behavior was almost exclusively observed between dam-calf pairs in our studies, which aligns with the findings of others (7, 14) and suggests a separate motivation for this affiliative behavior than what motivates suckling.

Social factors may also to an extent explain the frequent observations of allosuckling. Increased intake of solid feeds has previously been attributed to social facilitation in group- (50) and pair-housed (51) calves, while pair-housed calves also demonstrate a higher frequency of milk-replacer meals than calves housed individually (52). In our studies, the odds of allosuckling were increased by over 140-fold when at least one other calf was already engaged in suckling. We deem it possible that the calves were socially influenced to start suckling when they saw and heard a

suckling calf nearby, and often simply joined at the source of the milk (i.e., the cow already being suckled).

In the current studies, birth weight was not associated with allosuckling. Birth weight has previously been negatively associated with allosuckling frequency in beef and cross-bred calves, although this variable was interactive with the frequency of maternal suckling; more specifically, calves that weighed less at birth and suckled their dam less frequently were more likely to allosuckle (34). It is possible that in their study, calves with a low birth weight also had lower-producing dams, and thus sought milk elsewhere, as other work has suggested a positive relationship between birth weight of beef calves and milk supply of the dam (53). Furthermore, in our cow-driven study, no influence of calf sex on allosuckling was evident, aligning with work by Das et al. (10) on Zebu dairy calves in restricted suckling systems. In contrast, Víchová and Bartoš (34) noted higher frequencies of allosuckling in female versus male calves, although the authors themselves could not explain this finding.

Finally, there are likely calf-level factors beyond those explored in these studies that explain the degree of allosuckling observed for individual calves, as there were still a number of calves in both studies that were never observed to allosuckle. Though beyond the objectives of our studies, which focused on calf factors, specific dam-calf dyad factors and cow-level factors (e.g., parity, previous CCC experience) may also have influenced our findings. For example, an investigation that observes calves from the same cow, over different lactations, for similarity in allosuckling patterns in the offspring might clarify the dam's contribution (if any) to this behavior.

4.4 Close-to-udder events

In the cow-driven study, close-to-udder events frequently involved alien cows and closely preceded suckling bouts; indeed, half of all close-to-udder events occurred within 16 min of an ensuing suckling bout, potentially representing feed-seeking in times of hunger. Considering that close-to-udder events in the calf-driven study often did not occur as close in time to the next suckling bout (median: 71 min), this lends support to our theory that calves in the cow-driven study at times were hungry when their dam was not available, and thus attempted to seek meals elsewhere. Moreover, the frequency of close-to-udder events occurring shortly (i.e., < 16 or 71 min) before the next suckling bout was found to be positively correlated with allosuckling frequency on calf-level in both studies, meaning that calves that frequently suckled on alien cows also often were scored as being very close to an udder without suckling shortly before their next successful suckling bout. Interestingly, only 30–40% of these close-to-udder events (i.e., occurring within 16 or 71 min of suckling) were recorded as terminated by cows. However, we urge caution in interpretation of the termination reasons, as they do not necessarily tell the whole story. For example, a cow may have kicked repeatedly at a calf suckling, but if the calf then made one last brief contact with the udder before walking away the event would be scored as calf-terminated.

Our intention with the recording of close-to-udder events was primarily to capture unsuccessful attempts at suckling, although the

difficulty of detailed observations via video recordings from top-mounted cameras resulted in quite a broad definition of the behavior. As such, the nearly 500 close-to-udder events in our studies may also have included instances of sniffing or licking an udder, without the calf taking a teat into their mouth. As comparison, Fröberg and Lidfors (14), during direct observation, reported only 32 unsuccessful suckling attempts for 16 calves over seven different 24-h observation periods, likely due to their definition of suckling attempt including a teat being in the calf's mouth. It would be interesting to see what fraction of our close-to-udder events – especially those close in time to suckling bouts – accurately represent attempts at suckling. For future studies, we would recommend using alternative observation methods (e.g., direct observations) that allow a refinement of our definition. Additionally, future research could consider combining observations of these two behaviors (i.e., close-to-udder events, suckling bouts) with data on other feeding behaviors; perhaps calves that learn to allosuckle (as an alternative food source to the dam) also begin to experiment with solid foods at an earlier age.

5 Conclusion

Dairy calves reared with cow-driven CCC did not alter their suckling patterns over time. Contrarily, calves with calf-driven CCC changed their behavior to perform fewer, but longer, suckling bouts as they aged. In both studies, the odds of allosuckling increased with calf age and were higher when performed in groups of at least two calves. However, allosuckling was more frequently observed among the calves with cow-driven CCC, even when their own dam was present. Our findings indicate that allosuckling can be expected in multiple types of dairy dam-rearing systems, although the extent to which it occurs may be related to calf-level factors and the duration of available daily contact time. This behavior may offer calves opportunities to satisfy their hunger when the dam is not available and thus maintain high growth during the contact period.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Zenodo data repository, doi: [10.5281/zenodo.14778954](https://doi.org/10.5281/zenodo.14778954).

Ethics statement

The animal study was approved by the regional Animal Ethics Committee (ID-No: 5.8.18–18,138/2019) in Uppsala, Sweden. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

CW: Formal analysis, Conceptualization, Data curation, Methodology, Writing – review & editing, Investigation,

Writing – original draft, Visualization. CC: Writing – review & editing, Methodology, Investigation. LR: Formal analysis, Writing – review & editing, Supervision. SA: Funding acquisition, Conceptualization, Supervision, Writing – review & editing. LL: Writing – review & editing, Methodology. HE: Writing – review & editing, Visualization, Formal analysis, Conceptualization, Methodology, Supervision.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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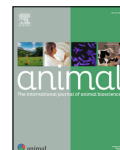
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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fvets.2025.1617158/full#supplementary-material>

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Behavioural responses of dairy cows and calves to fenceline weaning after 4 or 6 months of full cow-calf contact

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ABSTRACT

Cow-calf contact (CCC) systems, where cows and calves are housed together during all or part of the milk-feeding period, foster strong social bonds within dam-calf pairs. However, calves are still generally weaned and separated at younger ages than have been observed for semi-feral cattle. This study aimed to evaluate behavioural responses of dairy cows and calves to fenceline weaning after 4 or 6 months of full CCC. Additionally, the proportion of time spent by dam-calf pairs in close proximity (< 4 m indoors or < 8 m outdoors) prior to weaning was tested for its effect on behavioural responses. Dairy cows ($n = 25$) and their calves ($n = 26$) were housed in a freestall pen with free access to pasture for either 4 (4MO) or 6 months (6MO), after which calves were weaned outdoors via fenceline separation. Daily activity (lying time and step count) was recorded for all animals using accelerometers for 6 days before and for 11 days after weaning, while vocalisations and feed-seeking behaviour were collected for calves postweaning through direct observations. Scan sampling on 3 days during the end of the contact period was used to estimate proximity within each dam-calf pair, and calves were weighed regularly throughout the study. Calf feed-seeking behaviour and differences in lying time or step count (calculated as changes from a preweaning baseline value) for cows and calves were fitted with polynomial regression models. Directly after weaning, calves responded by decreasing their lying time, increasing their step count and vocalisations, and spending little time on feed-seeking; these responses were greater for 4MO calves. The calves, especially those weaned at 4 months, had reduced growth rates for several weeks postweaning, suggesting a lack of nutritional independence prior to weaning. Cow activity responses were similar but with no clear treatment differences in the first 3 days and with faster recovery times than for calves. Dam-calf proximity varied greatly between pairs but did not influence any of the modelled responses. Our results suggest that fenceline weaning causes behavioural responses indicative of distress in both calves and (to a lesser extent) cows, even when calves are weaned at a higher age.

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Implications

Cow-calf contact systems allow dairy calves to form strong bonds with their mothers, but this can lead to stress when they are inevitably separated and the calves weaned from milk. In this study, we aimed to evaluate behavioural responses to weaning calves via fenceline separation at 4 or 6 months of age. Weaning at either age caused similar behavioural response patterns for both calves and cows, although younger calves' responses were stronger in the first few days. Methods for gradual weaning are needed to

reduce weaning-related stress and encourage social and nutritional independence prior to weaning, especially in younger calves.

Introduction

Dairy production systems that allow some form of contact between cows and calves beyond the colostrum period – commonly known as cow-calf contact (CCC; Sirovnik et al., 2020) systems – are gaining recognition amongst consumers (Sirovica et al., 2022) and producers for being more natural and promoting good animal health and welfare (Eriksson et al., 2022; Neave et al., 2022). These systems provide cows and calves with increased opportunities to perform important behaviours (e.g., suckling) than if they are separated at calving, and facilitate the formation of

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social relationships, such as that between a dam and her calf. The dam-calf bond is a preferential mutual and emotional attachment, characterised by affiliative behaviours (e.g., allogrooming, maintaining proximity) and demonstrated in cattle to survive short periods of separation (Newberry and Swanson, 2008). This bond is established within the first few days after parturition through the dam's engagement in maternal behaviour (see review by von Keyserlingk and Weary, 2007), although quite quickly afterwards the dynamic begins to shift, to where the majority of interactions within the dam-calf pair are initiated by the calf (Jensen, 2011).

Spatial proximity (i.e., physical distance), a suggested measure of attachment between dam and calf (Claramunt et al., 2020), has been reported to be influenced by factors such as calf sex (Kour et al., 2021) or number of offspring (Price et al., 1985). To date, studies exploring spatial proximity in the context of dam-calf attachment have been largely limited to free-ranging beef cattle (Claramunt et al., 2020), Maremma cattle (Vitale et al., 1986) and the first 5 weeks postpartum in dairy cattle (Wenker et al., 2021). Time spent in close proximity provides opportunities for the calf to receive maternal care independent of suckling bouts (Johnsen et al., 2015; Kour et al., 2021). Thus, dam-calf pairs that spend more time at further distances may be said to exhibit a greater degree of social independence from one another. It could therefore be expected that pairs that spend more time in close proximity react more strongly to weaning.

Under extensive management conditions, weaning occurs gradually as calves gain nutritional and social independence, and may coincide with attempts by the dam to reject suckling by the calf (reviewed by Enríquez et al., 2011). Observations of semi-feral *Bos indicus* cattle have shown this process to occur between 7 and 14 months of age, with marked differences between calf sexes (Reinhardt and Reinhardt, 1981). Calves in CCC systems are instead often weaned by human intervention at 12–17 weeks (Eriksson et al., 2022), which is earlier than the weaning age observed in *Bos indicus* but later than the European average of 9 weeks for artificially-reared calves (Marcé et al., 2010). Near or concurrent to the time of weaning, calves in CCC systems are also separated from their dams, resulting in the cessation of both social contact and suckling, and therefore causing distress for the bonded individuals. Behavioural responses to early weaning and separation have been well-documented for cows and calves and often include increased vocalisations and locomotion for several days, paired with a temporary reduction in time spent lying and – for calves – feeding (see review by Lynch et al., 2019). Work on beef cattle suggests that weaning and separation at a higher calf age may reduce (but not eliminate) observed stress responses in calves (Lambertz et al., 2015b; de Souza Teixeira et al., 2021).

The question of when to wean and separate bonded dam-calf pairs in order to minimise the stress experienced by the animals still remains unanswered. To tackle this question, our study aimed to evaluate behavioural responses of dairy cows and calves to weaning via fenceline separation at two different calf ages (4 and 6 months), the older of which was chosen to be closer to the weaning ages observed for free-ranging *Bos indicus* cattle. The null hypotheses were that there would be no significant differences regarding time spent feed-seeking (calves), step count and lying time (cows and calves) after fenceline weaning at 4 or 6 months. Additionally, the study aimed to determine if dam-calf proximity prior to weaning influenced the responses postweaning, with the prediction that dam-calf pairs that were more spatially dependent (i.e., spent more time in close proximity) would show greater behavioural responses. To further understand the effects of fenceline weaning calves at these two ages, vocalisations and average daily gain in BW were explored descriptively.

Material and methods

Animals and treatments

This study enrolled 24 dam-calf pairs and one dam-calf triad with twin heifers and was conducted at the Swedish University of Agricultural Sciences' Swedish Livestock Research Centre in Uppsala, Sweden from 2 February 2022 to 3 March 2023. The study was an experimental trial with a parallel group design, with the total sample size selected based on the number of animals that could realistically be housed in the experimental pen. Cows were enrolled into a dam-calf contact system over a 6-week period and consisted of two breeds: Swedish Holstein (SH; primiparous: $n = 5$, multiparous: $n = 4$) and Swedish Red (SR; primiparous: $n = 6$, multiparous: $n = 10$). Enrolment was on the basis of birthing a heifer calf and containing no history of *S. aureus* mastitis prior to calving. Dam-calf pairs were kept for an average ($\pm$ SD) of 4 ± 1.0 days in individual calving pens before being moved to the experimental pen and introduced to the herd. One SR dam-calf pair (dam parity: > 1) was removed 37 days after the enrolment period had ended due to the cow contracting and succumbing to *E. coli* mastitis. Another SH dam-calf pair (dam parity: 1) was removed due to the treatment and eventual euthanasia of a calf (age: 87 days) with congenital impaired digestive functioning. Both pairs were removed before the onset of data collection for this study.

Dam-calf pairs were blocked by parity of the dam (primiparous or multiparous) and breed (resulting in four blocks in total) and randomly assigned to one of two treatments: weaning at 4 (4MO) or 6 (6MO) months of age. Randomisation was achieved by listing pairs within each block by calf birth date and switching every third and fourth pair, then using an online, randomised coin flipper to determine to which treatment group the first listed pair in each block should be assigned to. After this, every other pair within a block was assigned to that group, with the remaining animals assigned to the other treatment. An online coin flipper was further used to elect which treatment group would receive an additional pair of animals for blocks with uneven numbers. During treatment allocation, the dam-calf triad containing heifer twins was treated as a single unit. Following weaning through physical separation (hereafter referred to as fenceline weaning) at 123 ± 12.8 (4MO group) or 182 ± 9.6 (6MO group) days of age, calves remained on fenceline contact for 4 weeks. After this, they were moved to a separate area of the farm and therefore fully separated from any form of contact (auditory, visual or olfactory) with dams. One SR 6MO cow (parity: > 1) exited the trial on the day her calf was weaned due to a diagnosis of *S. aureus* mastitis in two quarters. The final number of animals available for statistical analysis was 11 4MO calves, 11 4MO cows, 12 6MO calves and 11 6MO cows (Fig. 1). After the final separation, the 4MO calves were kept as a group on a remote pasture for 37 days, where they were provided access to the same resources (i.e., feed, dry lying area) as the 6MO calves. The 4MO calves thereafter joined the general population of young stock, as did the 6MO calves immediately following their fenceline contact phase.

Housing and management

Indoor area

All animals were housed in an insulated barn with free cow traffic (VMS™, DeLaval International, Tumba, Sweden), freestalls and automatic milking. The experimental pen (Fig. 2) operated with full (i.e., whole-day, unrestricted contact; see Sirovnik et al., 2020 for definition) CCC and was calf-driven, so that calves had the primary initiative in choosing contact with cows. All resources – with the exception of a milking robot (DeLaval VMS™ V300, DeLaval AB

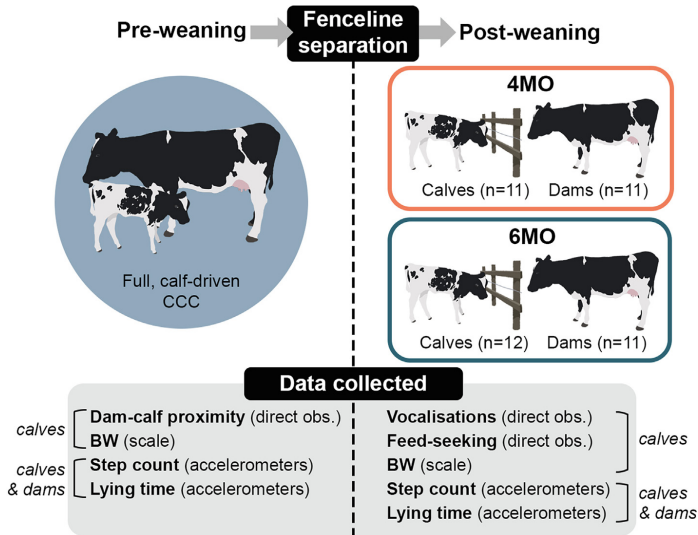


Fig. 1. Graphical summary of study design and data collection. Swedish Red and Swedish Holstein dams and calves were housed together, and calves were weaned via fenceline separation after either 4 (4MO) or 6 (6MO) months of cow-calf contact (CCC). Abbreviations: obs. = observations.

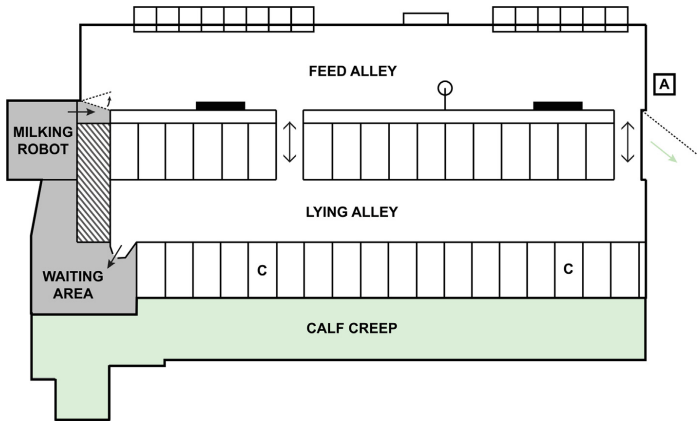


Fig. 2. Schematic illustration of the indoor areas available to dairy cows (n = 25) and calves (n = 26). Calves had access to these areas until weaning via fenceline separation at 4 (4MO) or 6 (6MO) months. All cows retained access until 4 weeks following weaning of the 6MO calves. Areas in grey are only accessible to cows, while the green area is exclusive to calves; all remaining areas are shared by both cows and calves. Arrows indicate the direction(s) of cow traffic. Observer location is depicted with an 'A' and a green arrow shows outdoor access from the pen (only available during summer). Cow concentrate feeding stations are indicated by a 'C', although they remained inactive for the duration of this study.

International, Tumba, Sweden), waiting area and calf creep – were shared between cows and calves. Access to the waiting area was restricted to only cows by use of a spring-loaded one-way gate (FeedSelect, GEA Farm Technologies GmbH, Bönen, Germany). A metal self-closing gate, modified with large plastic flaps, prevented calves from entering the robot in reverse.

The pen contained 33 freestalls bedded with rubber mattresses and a layer of sawdust, which was topped up two to four times per day using a rail-suspended bedding dispenser (JH miniStrø COW, MAFA i Ängelholm AB, Ängelholm, Sweden). Each stall was manu-

ally scraped several times per day to remove soiled bedding. There were also two concentrate feeding stations (DeLaval feed station FSC400, DeLaval International AB, Tumba, Sweden) located in the lying area, but these were turned off to encourage cow traffic through the milking robot; the robot was instead programmed to act doubly as a milking unit and concentrate feeding station.

In the feed alley, cows and calves had *ad libitum* access to one swinging brush (DeLaval SCB, DeLaval International AB, Tumba, Sweden), two self-filling water troughs (175 × 34.5 cm), salt blocks and feed. A grass-clover silage-based partial mixed ration (**PMR**)

(grass-clover silage with 2% straw inclusion and 5–7 kg concentrate) was available for the cows via 14 individual feed bins (CRFI, BioControl AS, Rakkestad, Norway) and a feeding table containing eight headlock spaces. A 1.9 m long portion of the feeding table was modified to allow access for calves; in this area, headlocks were removed and replaced with horizontal bars that prevented calves from escaping, and a trough was used to bring feed within reach for calves. PMR was delivered to all feeding areas 5 times per day via a rail-suspended distribution wagon (DeLaval FS1600, DeLaval International AB, Tumba, Sweden). Flooring through the lying area and feed alley was rubber, while the milking and waiting areas contained slatted rubber flooring. Initially, automatic scrapers were run manually in both alleys to prevent calf injury; once the calves were deemed old enough by barn staff, scrapers were set to run automatically once per hour.

The calf creep was an 80 m² area that ran adjacent to the lying area, spanning the length of the pen, and was accessible through the fronts of lying stalls. As such, the head and neck rails on two stalls were eventually adjusted to prevent the growing calves from developing skin lesions on their backs when moving between the creep and lying area. Within the creep, calves had free access to hay and water, as well as controlled access to two concentrate feeding stations (DeLaval concentrate station calves, DeLaval International AB, Tumba, Sweden). Bedding in the calf creep was deep-bedded wood shavings, which was topped up as needed to maintain a dry lying surface. Additional wooden boards were placed between the creep and waiting area for milking; this was done to discourage cows from seeking contact with calves in this area and potentially disrupting cow traffic through the robot.

Outdoor areas

From 17 May onwards, cows and calves were granted free access to a shared outdoor pasture (2.4 ha), located 227 m from the barn and accessible via a walkway (Supplementary Fig. S1). Fencing surrounding the pasture and walkway was both wooden and electric, and water was available *ad libitum* via two water troughs. When each group of calves was weaned, they were moved to a separate calf pasture (1.1 ha), located between the shared pasture and the barn. The calf pasture contained one water trough and a shelter (48 m²; PLAYMEK mobilt vindskydd, PLAYMEK, Röke, Sweden) that encompassed a deep-bedded straw area. Fresh feed (identical to that available in the barn) and minerals were freely available via a separate roofed feed wagon. A 5.4 m long portion of fencing was modified to allow for limited CCC (Supplementary Fig. S2); at this area, cows and calves could physically touch one another through a 0.4 x 5.4 m opening. The bottom of the opening was located at a height of 0.9 m from the ground, and suckling was prevented via closely placed horizontal beams below.

Data collection

To facilitate the identification of individuals, all cows were marked with a unique symbol on their sides and back using an animal-safe marking spray (blue, white or yellow). Markings were refreshed 2–3 times per week throughout the preweaning and postweaning observation periods, and all calves were equipped with coloured collars to aid in differentiation. Binoculars were used to identify animals at greater distances. A visual overview of the data collected pre- and postweaning is presented in Fig. 1.

Preweaning

In the week prior to fenceline weaning for each respective group, direct observations were conducted on 3 consecutive days by two trained individuals per day to determine the spatial proximity within dam-calf pairs. One observer was positioned indoors, standing on a 1.7 m tall step ladder, while a second observer was

outdoors, sitting on a 3.3 m high hunting tower (Frisport AB, Malmö, Sweden) with a clear view of the pasture and walkway. There were a total of four 2-hour observation periods each day, spanning over an 11-hour period each day (0700–1800 h). Each observation period was preceded by an additional 10-min period, to allow both cows and calves to acclimate to the observer's presence. During each 2-hour observation period, scan sampling was conducted at 10-min intervals, where each dam-calf pair was scored based on whether or not they were in "close" proximity. Close proximity was defined as a dam and calf being within 4 or 8 m of one another in the indoor or outdoor areas, respectively. Instances where the dam was located within the milking robot or milking waiting area were automatically scored as not being in close proximity. If the distance between a pair could not be determined (e.g., dam or calf were out of sight), this was additionally noted. Finally, whether or not a calf was engaged in suckling a cow was recorded during each interval using one-zero sampling.

Postweaning

Direct observations were conducted on days 1, 2, 3, 5, 8 and 11 postweaning, with the day of fenceline weaning considered as day 0. Observations were carried out by one of three trained observers from a hunting tower with a view over all experimental pastures (Supplementary Fig. S1). Similar to the preweaning observations, there were four 2-h observation periods daily, each with a 10-min acclimation period prior and spanning over 11 h (0800–1900 h). During each observation period, calves were scanned at 10-min intervals and noted for a presence or absence of feed-seeking behaviours, as well as if they were out of sight. Feed-seeking was defined as "actively picking at or consuming grass, hay, silage or minerals"; the calf could be still or moving. Additionally, one-zero sampling in 5-min intervals was used to detect vocalisations on a per-calf basis. No distinction was made between types of vocalisations (i.e., high-pitched vs low-pitched), but a calf was only recorded as having vocalised if the observer witnessed that particular individual emit a noise. As such, recorded vocalisations were primarily open-mouthed.

Activity and calf BW

All cows and calves were equipped with leg-mounted tri-axial accelerometers (IceQube, IceRobotics, Edinburgh, UK) which were used to record the time spent lying and number of steps taken each day, as reported in 15-min time periods. IceQubes were attached to one of the hind legs and scanned once weekly using an IceReader device (IceRobotics, Edinburgh, UK) and computer containing the IceManager software (IceRobotics, Edinburgh, UK) to download the raw data. IceQubes have been previously validated for recording daily lying time in dairy cows (Borchers et al., 2016) and calves (Finney et al., 2018). Step count has been validated against video observations for IceTag (IceRobotics, Edinburgh, UK) devices (Nielsen et al., 2010), which are similar to IceQubes but sample at a rate of 16 (compared to 4) Hz. All calves were weighed at birth and thereafter on a monthly basis. Animal weights were always recorded on the first Thursday of each month, so calf age at the first monthly weighing could vary between a few days and almost a month. Additionally, calves were weighed weekly from the day of fenceline weaning to 3 weeks after, resulting in four consecutive weeks of weight records for each respective treatment group. Weight data included all recorded weights from the first monthly weighing after the enrolment period ended (calf age: 42 ± 11.4 days) to the first monthly weighing after the experimental period ended (calf age: 372 ± 11.4 days).

Statistical analysis

All data handling and statistical analysis procedures were conducted using R version 4.4.2 (tidyverse, Wickham et al., 2019; R

Core Team, 2024). Significant differences were accepted at $P < 0.05$. The experimental unit for all analyses was the individual cow or calf. For the triad, one twin was randomly selected using an online coin flipper, and her data were used for all analysed variables. Data pertaining to the second twin heifer were removed. All analyses pertaining to calves were run both with and without the single twin heifer, and as this did not substantially affect the results, it was ultimately decided to retain this individual in the final dataset.

Dam-calf proximity

Fifty-five of 3 456 observations were initially removed due to noted external disturbances during the 10-min scan periods. Additionally, all observed instances when either the cow or calf could not be seen were considered missing values and thus removed ($n = 99$). An additional 18 observations were missing due to observer errors. From the remaining 3 284 observations, the number of scans recorded in close proximity was first summed per calf-day, then averaged across the 3 days to create a single mean value for each dam-calf pair. This value thus represents the average daily number of observations recorded in close proximity, and was thereafter used to calculate the mean percentage of observed time that each dam-calf pair spent in close proximity.

Calf growth performance

Calf weight measurements were examined visually and two erroneous weight records were removed, as they were 100–200 kg higher than those recorded for the same individuals both 1 week prior and later. Average daily gain (ADG) was calculated for four separate periods: from birth to weaning, and weekly from weaning until 3 weeks postweaning. ADG was calculated by taking the difference in BW over the observed time period (e.g., weaning weight subtracted from the weight 1-week postweaning) and dividing by the number of days. Calf BWs and ADG are reported descriptively due to a lack of *a priori* predictions.

Activity data

Raw IceQube data were converted to.csv files using the IceManager software and thereafter imported into R, where step count and lying time were handled separately. To correct for invalid recordings of step count due to leg movement whilst lying, all 15-min periods where the recorded time spent standing was 0 min were removed. Step count and lying time were then summed per cow- or calf-day, and each daily summary was assigned a day number relative to the day of fenceline weaning (Day 0). Afterwards, the dataset was filtered to include only data from Day –6 to Day 11 per treatment group. Overall, of the 374 possible cow-days and 391 calf-days (not including Day 0), 62 cow- and 48 calf-days were removed (see [Supplementary Table S1](#) for details). Per day, at least 22 animals were available for analysis, with an average of 13.6 ± 0.80 and 15.5 ± 0.95 observation days for 4MO and 6MO animals, respectively. Data from Day 0 were not analysed due to data sampling of the animals on this day (e.g., calf weighing, accelerometer data download), which likely affected their behaviour. Finally, a preweaning baseline value was created per individual for both daily step count (steps/day) and daily lying time (min/day) by averaging the available data between Day –6 and Day –1. The two response variables used in the statistical analyses corresponded to the difference in steps or lying time for each day postweaning compared to the baseline value for either activity.

The effect of day after weaning was fitted as a polynomial function for both lying time and step count in linear mixed models. The mixed-effects polynomial regression analyses were performed using the lme function from the nlme package (Pinheiro et al., 2023). Fixed effects included treatment (4MO or 6MO), time (Day 1–11 as a numeric time-series), treatment $\times$ time, dam-calf proximity (percentage of observed time spent “close”) and parity (primiparous or mul-

tiparous; in cow models only), while cow or calf ID was specified as a random intercept. A first-order autoregressive correlation structure was specified to account for temporal autocorrelations between days. The difference in step count for cows and calves was transformed to fulfil the assumption of normal distribution of residuals. Second-order polynomial models were used for the fourth-root-transformed difference in step count, as well as the untransformed difference in lying time for both cows and calves. Likelihood ratio tests were performed to check model fit using the lrtest function in the lmerTest package (Zeileis and Hothorn, 2002), wherein each final model was tested against a lower-order polynomial model. Likelihood ratio tests were also used to determine whether or not the treatment $\times$ time interaction had a significant effect on the response variables. Only interaction effects with $P < 0.05$ were included in the final models; as such, treatment $\times$ time interactions were removed from the cow model for differences in step count ($P = 0.590$). Results are reported as back-transformed values.

Vocalisations and feed-seeking behaviour

Data from two 10-min observation periods were removed due to cows blocking the observer's view of the calf area, making it impossible to identify which calves were vocalising and if they were feed-seeking. Additionally, due to visual observations of oestrus behaviour in some calves, three calf-day observations were excluded from further analyses of feeding behaviour and vocalisations. Individual observations were further removed or missing due to external disturbances, such as barn staff entering the calf enclosure ($n = 22$), the calf being out of sight ($n = 19$), the observer not being in place ($n = 13$) or calves having escaped the enclosure ($n = 26$). At most, four of a total possible 48 daily observation periods were excluded from a single day; eight of the 12 postweaning observation days had no missing observation periods. Observations of vocalisation occurrence and feed-seeking behaviour were summed per hour and day to create an hourly average per calf per day. Due to a lack of independence between calves (vocalisations generally occurred clustered), vocalisations are reported descriptively as mean and SD per treatment group and observation day. A second-order polynomial model was used to analyse the time spent feed-seeking (min/h) after weaning, with treatment, time, treatment $\times$ time and dam-calf proximity included as fixed effects. Calf ID was included as a random intercept, and the covariance structure was specified as first-order autoregressive. Likelihood ratio tests were performed to test both model fit and the significance of interaction terms; treatment $\times$ time was ultimately removed from the final model ($P = 0.207$).

Results

Dam-calf proximity

When allowed full, free access to one another, 4MO dam-calf pairs spent an average 34% (range: 20–65%) of observed time within 4 and 8 m from one another in the inside and outdoor area, respectively. Descriptively, this was similar to 6MO pairs, who spent approximately 41% (range: 30–59%) of their time in close proximity to one another. Average dam-calf proximity did not have a significant effect on any of the changes in daily step count or lying time observed for dams and calves following fenceline weaning, nor on the feed-seeking behaviour of calves ([Table 1](#)).

Calves

Growth performance and vocalisations

Average calf BWs from the age of 6–53 weeks are displayed in [Fig. 3](#). From birth to weaning, ADG appeared similar between treat-

Table 1
Regression estimates and SE for the daily difference in step count and lying time of dairy cows and their calves in the 11 days after weaning, measured as the difference from a baseline value (mean daily value in the 6 days prior to weaning) for either behaviour. Model estimates and SE for feed-seeking behaviour of calves on Days 1, 2, 3, 5, 8 and 11 are also reported. Dam-calf pairs were housed together with full cow-calf contact for 4 (4MO; n = 11) or 6 (6MO; calves, n = 12; cows, n = 11) months, after which the calves were weaned via fenceline separation. P-values are based on ANOVA output of main effects unless noted otherwise.

Model	Cows			Calves		
	Estimate	SE	P-value	Estimate	SE	P-value
Difference in steps (steps/day) ¹						
Treatment _(6MO)	−0.21	0.235	0.342	−0.77	0.514	0.482
Time	−0.77	0.102	<0.001	−1.16	0.128	<0.001
Time ²	0.05	0.008	<0.001	0.07	0.011	<0.001
Treatment × time	–	–	–	0.09	0.185	0.048 ³
Treatment × time ²	–	–	–	0.001	0.015	0.048 ³
Proximity	−0.003	0.010	0.777	0.01	0.010	0.374
Parity _(primiparous)	−0.08	0.222	0.732	–	–	–
ICC ⁴	0.10			0.16		
Difference in lying time (min/day)						
Treatment _(6MO)	6.21	48.290	0.537	183.64	57.790	0.334
Time	46.74	13.285	<0.001	105.09	14.887	<0.001
Time ²	−2.75	1.141	<0.001	−7.52	1.258	<0.001
Treatment × time	−3.31	18.768	0.015 ³	−71.06	21.054	<0.001 ³
Treatment × time ²	−0.08	1.566	0.015 ³	5.98	1.734	<0.001 ³
Proximity	0.84	0.748	0.181	−0.95	1.061	0.372
Parity _(primiparous)	−36.92	17.109	0.046	–	–	–
ICC ⁴	0.05			0.12		
Feed-seeking (min/h)						
Treatment _(6MO)	–	–	–	1.23	0.936	0.242
Time	–	–	–	4.32	0.450	<0.001
Time ²	–	–	–	−0.24	0.037	<0.001
Proximity	–	–	–	−0.06	0.039	0.117
ICC ⁴	–	–	–	0.10		

Abbreviations: ICC = Intra-class correlation coefficient.
¹ Variable was square-root-transformed in order to maintain normal distribution of model residuals.
² Referring to the numeric variable time raised to the power of two.
³ Likelihood ratio test comparing models both with and without the interaction term was used to determine P-values.
⁴ ICC was calculated using the formula $\sigma^2_{\tau} / (\sigma^2_{\tau} + \sigma^2_{\epsilon})$, where σ^2_{τ} is the variance of random effects and σ^2_{ϵ} is the residual variance.

ments at (mean ± SD) 1.3 ± 0.14 kg/day for 4MO calves and 1.4 ± 0.13 kg/day for 6MO calves. ADG in the first week postweaning was on average negative for both groups (4MO: −0.4 ± 0.50 kg/day; 6MO: −0.4 ± 0.43 kg/day) but by the second week, the calves were again on average gaining weight (4MO: 0.2 ± 0.35 kg/day; 6MO: 1.1 ± 0.76 kg/day). In the third week following weaning, 4MO calves increased their ADG to preweaning rates of 1.4 ± 0.29 kg/day while

calves weaned at 6 months once again reduced their ADG on average to 0.04 ± 0.68 kg/day. At the end of the study, when calves were around 12 months (372 ± 11.4 days) old, the 4MO and 6MO groups weighed 422 ± 24.4 kg and 451 ± 37.6 kg, respectively. Vocalisations across the 11 days immediately after fenceline weaning decreased numerically for both treatment groups, although 4MO calves were observed to vocalise in a higher proportion of sampling intervals than 6MO calves on Day 2 (Table 2).

Changes in activity and feed-seeking behaviour

Prior to weaning, 4MO and 6MO calves spent 15.6 ± 0.79 and 14.6 ± 0.94 h/day lying down, respectively. There was a significant effect of treatment × time for the difference in lying time ($\chi^2_2 = 19.34$, $P < 0.001$; Fig. 4A) after fenceline weaning, with 4MO calves showing stronger behavioural responses in the first few days.

Table 2
Average percentage (mean ± SD) of 5-min sampling intervals per hour during which dairy calves of two treatments – weaning via fenceline separation at 4 (4MO) or 6 (6MO) months – vocalised at least once. Sampling was performed 1, 2, 3, 5, 8 and 11 days after weaning of each treatment group, with a total of 96 sampling periods per day.

Day	Treatment	
	4MO (n = 11)	6MO (n = 12)
1	40.2 ± 10.26	43.0 ± 11.16
2	30.2 ± 13.04	12.2 ± 5.89
3	15.5 ± 5.83	12.9 ± 12.75
5	4.3 ± 2.49	1.4 ± 1.68
8	4.3 ± 3.48	0.9 ± 1.24
11	3.3 ± 3.62	1.1 ± 1.29

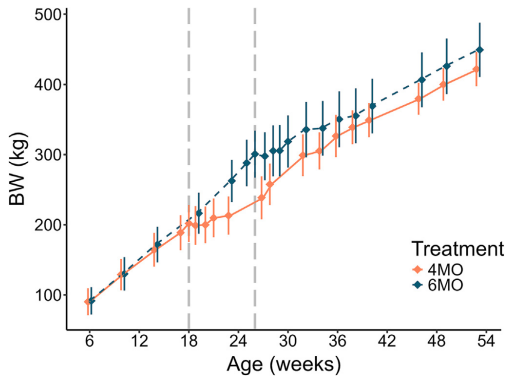


Fig. 3. Average BW (kg) for dairy calves of two treatment groups – weaning via fenceline separation after either 4 (4MO; n = 11) or 6 months (6MO; n = 12) of full contact with their dams. Vertical dashed lines represent weaning events. Error bars represent SD, while weeks refer to the average calf age.

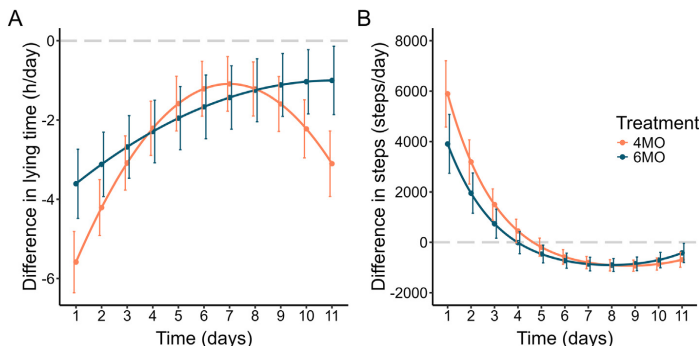


Fig. 4. Estimated quadratic regression lines for differences in lying time (h/day; A) and step count (steps/day; B) of dairy calves in the 11 days after weaning via fenceline separation at 4 (4MO; $n = 11$) or 6 months (6MO; calves, $n = 12$). Behaviours are displayed as the difference from baseline (indicated by the grey dotted line), which was calculated as the mean daily lying time or step count in the 6 days prior to weaning. Error bars show the estimated SE. Estimates for step count are back-transformed.

Across all calves, average daily step count increased from $2\,451 \pm 519.9$ steps/day before weaning to $10\,898 \pm 3\,298.5$ steps/day on Day 1. The difference in step count differed between treatments depending on the day ($\chi^2_2 = 6.08$, $P = 0.048$; Fig. 4B); 4MO calves had a higher step count on Day 1 and 2 postweaning.

While preweaning feed-seeking behaviour was not recorded, all calves were noted to engage in suckling on at least one occasion during the 3 preweaning observation days (median: 6, range: 1–12). From Day 1 after weaning, instances of feed-seeking behaviour increased in a quadratic manner but with no differences between 4MO and 6MO calves (Table 1). Across the days, calves increased their hourly time spent feed-seeking from 8.6 ± 3.32 min/h on Day 1 to a peak average of 24.8 ± 3.67 min/h on Day 8, after which there was a slight decrease to 21.7 ± 4.73 min/h on Day 11.

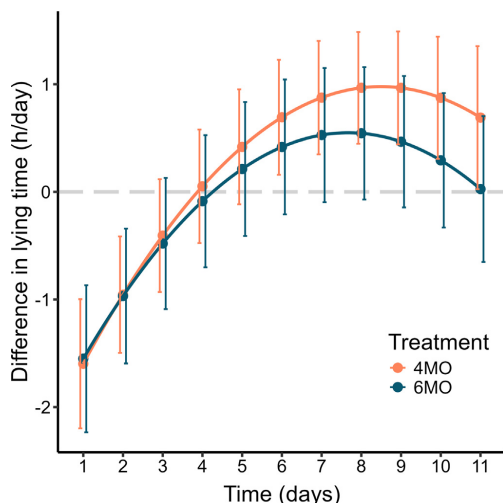


Fig. 5. Estimated quadratic regression lines for differences in lying time (h/day) of dairy cows in the 11 days after weaning of their calves via fenceline separation at 4 (4MO; $n = 11$) or 6 months (6MO; $n = 11$). Behaviours are displayed as the difference from baseline (indicated by the grey dotted line), which was calculated as the mean daily lying time in the 6 days prior to weaning. Error bars show the estimated SE.

Cows

Across both treatments, cows spent an average of 11.4 ± 1.16 h/day lying down and performed approximately $2\,397 \pm 753.8$ steps/day in the week prior to fenceline weaning. Following the weaning of calves, there was a significant treatment $\times$ time interaction effect on the response in cows' lying time ($\chi^2_2 = 8.46$, $P = 0.015$; Fig. 5), with both treatments initially reducing lying time to a similar degree but cows in the 4MO group increasing their lying time more than 6MO cows over the following days. However, this significant interaction was likely the result of a low number of 6MO individuals having extremely low values on Days 4 and 11 only (see Supplementary Fig. S3). Cows also responded to the weaning by increasing their step count but returned to preweaning levels by Day 2 and Day 3 for 4MO and 6MO cows, respectively, with no significant interaction between treatment and time (Fig. 6). Parity did not influence postweaning step count, but primiparous cows reduced their lying time to a greater extent than multiparous cows ($F_{1,18} = 4.62$, $P = 0.046$; Table 1).

Discussion

This is the first study to compare the effects of fenceline weaning in dairy cows and heifer calves after 4 or 6 months of full CCC. We expected that delaying weaning until the calves had gained a higher status of social and nutritional independence as an effect of being older would reduce behavioural indications of weaning distress. However, both groups of calves initially responded to fenceline weaning by spending less time lying down, increasing their step count and vocalisations, and spending very little time engaging in feed-seeking behaviour relative to 1 week later. As is in line with previous work in dairy (Fröberg et al., 2011; Wenker et al., 2022; Bertelsen and Jensen, 2023) and beef (Price et al., 2003; Lambertz et al., 2015a) calves, these behavioural responses were strongest the first days of fenceline. The responses were evident regardless of the age at which calves were weaned, although the 4MO calves' responses were slightly stronger. While this difference in initial response is potentially, in part, due to the difference in calf age upon weaning, only a handful of studies have explored age-related differences in weaning response and with mixed findings. Lambertz et al. (2015b) found response patterns similar to our own for beef calves abruptly weaned at 6 and 8 months, with the younger calves having spent more time walking and less time lying down on the second day after weaning compared to calves weaned at an older age. Another study observed that beef calves weaned at

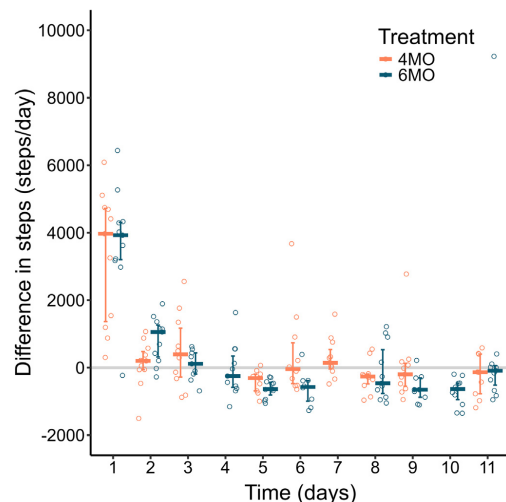


Fig. 6. Median values for differences in step count (steps/day) of dairy cows after weaning of calves via fenceline separation at 4 (4MO; $n = 11$) or 6 months (6MO; $n = 11$). Step count is displayed as the difference from baseline (indicated by the grey solid line), which was calculated as the mean daily step count in the 6 days prior to weaning. Presented data are raw, untransformed values. Error bars represent interquartile range, and daily individual cow observations are plotted as individual points.

30 or 75 days of age spent more time walking on the day of weaning than calves weaned at 6 months (de Souza Teixeira et al., 2021). Contrary to these findings, other work has reported a tendency for locomotor activity in beef calves to increase with weaning age (range: 5–8 months), although these results were based on only 6 h of postweaning observations (Stěhulová et al., 2017). Additionally, two of these studies reported the youngest calves to perform more frequent vocalisations than those weaned at later ages (Lambertz et al., 2015b; de Souza Teixeira et al., 2021), while Stěhulová et al. (2017) found no effect of weaning age on vocalisation frequency. In our study, vocalisations were measured with one-zero sampling, preventing us from evaluating the frequency of vocalisation. Nonetheless, on Day 2, younger calves were observed to vocalise in a visually greater proportion of sampling intervals than older calves.

Similar to calves, cows responded to the fenceline weaning by decreasing their lying time and increasing their locomotor activity. In the days immediately after weaning, the behavioural responses of cows did not differ between treatment groups. Contrary to our findings, other work on beef cattle has reported a potential effect of calf age, with dams of younger calves spending more time moving and vocalising in response to weaning (calf age range: 5–8 months; Stěhulová et al., 2017). Nevertheless, short-term behavioural changes are regularly observed for cows, irrespective of whether their calves are weaned at 8–10 weeks (Veissier et al., 2013; Ungerfeld et al., 2016; Neave et al., 2024) or 7 months (Lambertz et al., 2015a). Additionally, primiparous cows reduced their lying time to a greater degree in response to weaning compared to older cows. While previous work has generally reported dam age not to influence behavioural responses to weaning (Flower and Weary, 2001; Neave et al., 2024), it should be noted that some of the cows in our study had reared calves in a previous lactation. Meanwhile, the experience of being separated from a bonded calf was new for all of the primiparous cows. While our data did not allow us to investigate the potential carry-over effects

of dam-rearing on cow responses – either across lactations or due to being reared with dam contact – this remains an important area for future research.

Calves of both treatment groups experienced clear depressions in ADG upon cessation of suckling, likely indicating a lack of nutritional independence prior to weaning. Comparatively, beef calves that were fenceline-weaned at 7 months maintained similar ADGs in the 2 weeks postweaning compared to non-weaned controls (Price et al., 2003). Even at 6 months of age, our dairy calves likely had nearly unlimited access to whole milk, while similarly-aged beef calves may be forced to start experimenting with solid feeds due to the more limited milk supply of their dams (3 kg/day at 6 months lactation; Rodrigues et al., 2014). The effect of dam milk yield on nutritional independence in calves is additionally reinforced by findings from Ungerfeld et al. (2009), who reported that beef calves reared by cows with low milk yields spent more time grazing and returned to baseline activity levels faster after weaning at 6 months than those reared by high-yielding beef cattle. Although we do not have detailed data on the feeding behaviour of our calves prior to weaning, all calves were confirmed to still engage in suckling bouts, regardless of weaning age. Moreover, previous research has reported that dairy calves with unrestricted access to CCC consume very little solid feed during suckling periods of 2–3 months (Roth et al., 2009; Fröberg et al., 2011).

In our study, the growth check after weaning (i.e., number of weeks before the slope in Fig. 3 stabilises) was longer in duration for 4MO than that of 6MO calves, suggesting that they may have been more nutritionally dependent on their dams upon weaning. Nutritional independence plays a large role in how calves respond to weaning, as demonstrated by Johnsen et al. (2018) in a study where calves were granted half-day access to their dams – either with or without the opportunity to suckle. Calves with dam access but prevented from suckling instead obtained milk from an automatic feeder; they were thus considered to be nutritionally independent and produced significantly fewer vocalisations upon fenceline weaning at 6 weeks. Other work has attributed vocalisations at weaning to gut fill; abruptly-weaned calves vocalised more compared to calves with continued access to a milk feeder with warm water substituted for milk (Budzynska and Weary, 2008). Considering the descriptively higher proportion of vocalisations for 4MO calves on Day 2, it is plausible that the younger calves were simply hungrier after weaning due to a lack of nutritional independence. Furthermore, the differences in growth check severity were still visible at 1 year of age, with 4MO calves weighing approximately 50 kg less than 6MO calves. However, it should be noted that calves of both treatments were, at 12 months of age, still considerably larger (4MO: 422 ± 24.4 kg; 6MO: 451 ± 37.6 kg) than the recommended minimum BW for 15-month-old Swedish Holstein and Swedish Red heifers, which is 380 kg and 350 kg, respectively (Greppa Näringen, n.d.).

The behavioural responses and growth checks observed in response to weaning in our study suggest that producers should avoid ending suckling abruptly, especially for younger calves. Fenceline weaning – while preferable to other two-stage methods such as the use of nose-flaps, which have been reported to cause nasal abrasions (Lambertz et al., 2015a; Valente et al., 2022; Wenker et al., 2022) – still involves an abrupt cessation of milk. Instead, we encourage future research to focus on developing and evaluating weaning methods that implement a gradual decrease in milk allowance, thereby fostering nutritional independence in calves prior to weaning.

While we did not differentiate between low-pitched (close-mouthed) and high-pitched (open-mouthed) vocalisations (Johnsen et al., 2015) during behavioural observations, our recorded observations included primarily the latter due to the rel-

ative ease with which open-mouthed vocalisations can be associated to a specific individual. Vocalisations – particularly those that are high-pitched – are thought to be a behavioural mechanism intended to locate and, when paired with locomotion, eventually reunite bonded pairs (Watts, 2000; Newberry and Swanson, 2001; Johnsen et al., 2015). The vocalisations observed in our calves immediately postweaning were paired with a simultaneous increase in locomotor activity, and from our own anecdotal evidence were generally noted to cease upon the reunion of dam-calf pairs across the fence. These behaviours were thus, at least in part, serving in an effort to join calves with their respective dams, regardless of their ability to suckle afterwards. This theory is further supported by work on free-ranging beef (Price et al., 1985; Padilla de la Torre et al., 2015) and non-suckling dairy (Johnsen et al., 2018) cattle, where vocalisations have been noted to occur during reunions of dam-calf pairs following short bouts of separation. Vocalisations in our study appeared in the highest proportion of sampling intervals on Day 1 for both groups. On Day 2, 4MO calves vocalised more than 6MO calves, while the values were similar for both groups for the remaining study period. From Day 5 postweaning and onwards, vocalisation occurrence was minimal, with the observers noting that many vocalisations could be attributed to events likely not related to weaning distress (e.g., feed delivery).

Changes in locomotor activity and movement have been greatly detailed as a weaning response for both dam-reared dairy (range of weaning age: 1 day to 9 weeks; Stěhulová et al., 2008; Frøberg et al., 2011; Bertelsen and Jensen, 2023) and beef (range of weaning age: 6–7.5 months; Price et al., 2003; Haley et al., 2005; Lambertz et al., 2015a) calves, with a return to preweaning levels usually reported by 5 days after weaning. In our study, all calves increased their step count considerably the day after fence-line separation but returned to baseline levels around Day 4, aligning with the findings of others. In contrast, the substantial decrease in daily lying time compared to baseline, observed on the first day of fence-line, had still not normalised on the last day of the observation period (Day 11). It is difficult to compare the relative extent to which lying behaviour changed between studies due to differences in behavioural recording protocols. Nevertheless, in contrast to our own findings, other studies report a stabilisation of lying time by 2–3 days after weaning, regardless of weaning strategy (Enriquez et al., 2010; Lambertz et al., 2015b). Part of the initial decrease in lying time we observed may be linked to the high levels of locomotion performed by the calves, as they may have exchanged some lying time for time spent standing and walking. However, even as vocalisations lessened and step count returned to baseline levels, daily lying time remained lower, implying that factors other than weaning distress were at play. Adult cows housed on pasture are known to have lower lying times compared to those in freestall systems (see review by Tucker et al., 2021). One explanation provided is that on pasture, cows need to spend more time consuming feed (i.e., grazing) than indoor-housed cows. After weaning, our calves increased their time spent on feed-seeking activities to a peak average of 25 min/h on Day 8, so it is possible that calves exchanged some lying time during this period for time spent seeking food.

While we are unable to evaluate changes in feed-seeking behaviour due to our lack of preweaning observations, the postweaning responses of our calves follow a similar increasing pattern as is reported for 6-month-old beef calves (Hötzel et al., 2010; de Souza Teixeira et al., 2021). As a result of our study design, we cannot determine if calves initially decreased their feeding-related activities as a stress response to weaning, or instead were simply seeking out very little solid feed to begin with and increased this following the cessation of milk.

Cows also responded to weaning events by decreasing their daily lying time, although this behaviour was affected to a lesser extent than for calves. Compared to preweaning lying times of 11 h/day, cows only reduced their lying by an estimated 2 h immediately after weaning. Moreover, cows returned to baseline levels by Day 5 (4MO) and 6 (6MO) after weaning, whereas calves failed to recover their lying time within the observation period. This is a slightly longer recovery period than the 2 days reported for dairy cows whose calves were weaned – either abruptly or gradually through a reduction in contact time – after 10 weeks of whole-day CCC (Neave et al., 2024). Our own findings therefore do not indicate that weaning at a higher calf age reduces stress responses in dairy cows, at least in terms of changes in lying time. In further contrast, findings from beef cattle suggest even shorter-lived reductions in lying time (weaning age: 2 months; Ungerfeld et al., 2016) or no changes whatsoever (weaning age: 7 months; Boland et al., 2008) for dams following weaning. The reductions in lying time seen in our cows, at least on Day 1, are likely due to the simultaneous increase in locomotor activity.

In terms of locomotor activity, the changes seen on Day 1 were nearly identical between treatments, with cows increasing their activity by median values of nearly 4 000 steps/day. By Day 2 and 3, 4MO and 6MO cows had returned to preweaning activity levels and remained near or slightly below baseline for the remainder of the observation period. Postweaning changes in movement have previously only been reported for individually-housed dairy cattle after short periods (i.e., up to 14 days) of CCC (Flower and Weary, 2001; Stěhulová et al., 2008). Nonetheless, the results of these studies mirror our findings, with increases in general cow movement reported for the first day following separation only. Limited findings are also available for beef cows; Ungerfeld et al. (2016) saw an increase in the percentage of observed time spent on locomotor activity following the abrupt weaning and separation of their 7-month-old beef calves, with a return to preweaning levels within 5 days.

To our knowledge, dam-calf proximity has not previously been explored as a predictor when modelling behavioural responses to weaning. We initially hypothesised that dam-calf pairs that were more spatially dependent would demonstrate stronger responses to fence-line weaning. In general, there was a large inter-pair variation in terms of time spent in close proximity, with some pairs spending up to 65% of their daily observed time near one another while others spent as little as 20%. Wenker et al. (2021) made a similar reflection regarding individual variation when recording how much time free-stalled-housed dairy cows spent standing within 2 m of their calves. Yet, contrary to our hypothesis, we ultimately found no effect of dam-calf proximity prior to weaning on any of the postweaning behaviours analysed. It is possible that for some individuals, spatial proximity alone is simply not a good measure of dam-calf attachment. Personality assessments of growing heifers have demonstrated clear differences between individuals (e.g., sociable vs pessimistic; Lecorps et al., 2019), making it plausible that calves may perceive spatial proximity in different ways. For example, some calves may feel socially “secure” at farther dam-calf distances, while others require a close physical proximity to meet the same social needs. In this way, two calves with similar levels of dam dependence may differ in how much time they spend within a close distance. Furthermore, as it is impossible to separate the calf’s drive to maintain proximity from that of the dam in a free-ranging system, it is possible that socially and/or nutritionally independent calves were recorded as being in close proximity due to strong maternal behaviour on part of the cow – or vice versa. However, with so little existing work exploring spatial proximity in the context of dairy dam-calf attachment, it is

difficult to determine what factors ultimately influenced our measures of dam-calf spatial proximity.

Our findings suggest that fenceline weaning was stressful for dairy calves regardless of weaning age, as seen by the decreased growth rate, short-term changes in behavioural patterns and prevalence of vocalisations. It is possible that the greater changes seen in calves for both daily lying time and step count compared to cows were not solely the result of milk removal and partial restriction in dam contact, but also as a result of being introduced to a new environment. Based solely on the differences in initial postweaning stress responses and in BW at 1 year, the 6MO calves appear to have been slightly better equipped to handle the fenceline weaning. Nevertheless, we recommend a further exploration of gradual methods that encourage the development of social and nutritional independence in calves prior to weaning.

Conclusions

Overall, dairy calves demonstrated clear behavioural responses to fenceline weaning at both 4 and 6 months, as shown by increases in step count and vocalisations, decreases in lying time, and little time spent feed-seeking during the days immediately after weaning. The calves, particularly those weaned at 4 months, had a reduced growth rate for a number of weeks postweaning, suggesting that they were not nutritionally independent from the dams at weaning. Cows similarly increased their step count and reduced daily lying time in the first few days postweaning, but to a lesser extent than calves and with no clear differences between treatments. Furthermore, we did not find dam-calf proximity during the contact time to be a predictor of behavioural responses to fenceline weaning, but we encourage further exploration in this area and on dam-calf relationships as a whole.

Supplementary material

Supplementary Material for this article (<https://doi.org/10.1016/j.animal.2025.101525>) can be found at the foot of the online page, in the Appendix section.

Ethics approval

All animal handling was approved by the Animal Experiments Ethics Board in Uppsala, Sweden (ID-No: 5.8.18–18138/2019).

Data and model availability statement

The analysed dataset and final models were deposited in an official repository and are publicly available for download at <https://doi.org/10.5281/zenodo.11092911>. Information can be made available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

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Cow-calf contact systems facilitate contact between dairy cows and calves during the milk-feeding phase. This thesis assessed the behavioural development and productive performance of calves with 3–6 months of dam-calf contact. Dam-reared calves increased allosuckling behaviour with age, showed high preweaning growth, and responded strongly to fenceline weaning at both 4 and 6 months of age. As adults, they had a lower first-lactation milk yield compared to artificially-reared matched individuals, although differences in dam-calf management may influence this outcome.

Claire Wegner received her doctoral education at the Department of Applied Animal Science and Welfare at the Swedish University of Agricultural Sciences. She received her Bachelor of Science in Applied Animal Biology at the University of British Columbia.

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