

Temporal distribution of sucking behaviour in dairy calves and influence of energy balance

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ABSTRACT

So far, most authors in the literature have suggested that cross-sucking in dairy calves is elicited by milk ingestion, as sucking motivation persists for an additional 12–15 min after milk intake. However, cross-sucking without temporal association to milk ingestion has also been noted in studies with longer observation times. Furthermore, it is known that energy deficits influence sucking behaviour. This study is based on the hypothesis that cross-sucking is not only elicited by milk ingestion; hunger can also reinforce sucking behaviour. Seventy-five dairy calves (in groups of 24–27 animals) were observed two times for 20 h each during the milk feeding period, 1 week after grouping and 1 week before weaning. We noted all events of cross-sucking and related them to the calves' temporally closest visits to the milk feeder, with or without milk ingestion. The daily energy balance (consumed energy minus energy demand for growth and maintenance) was determined for each animal, and the influence of energy balance on the occurrence of cross-sucking was calculated. Thereafter, a daily energy balance was assigned to each cross-sucking bout. Of 919 cross-sucking bouts, 28.4% occurred within the first 15 min after receiving milk, and 71.6% of the sucking bouts occurred independently of milk intake. Of that 71.6%, half (36.3%) took place either during the 15 min before a visit to the milk feeder (with or without milk ingestion) or during the 15 min after an unrewarded visit to the milk feeder. The rest of the sucking bouts (35.3%) occurred without close temporal association to a visit to the milk feeder. The probability of exhibiting cross-sucking behaviour decreased with an increased energy balance ($P = 0.002$). Furthermore, the association between daily energy balance and time to the nearest visit to the milk feeder differed depending on the timing of the sucking bout (before or after the visit to the milk feeder) and if the calf received milk or not during that visit to the milk feeder ($P < 0.001$). Energy balance influenced sucking behaviour, indicating that animals with positive energy balance were less likely to perform cross-sucking and that the temporal occurrence of sucking bouts depended on energy balance. These findings show that milk-elicited cross-sucking must be differentiated from sucking bouts triggered by other motivational mechanisms, one of them likely being hunger.

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1. Introduction

It has been suggested that cross-sucking is mainly elicited by milk ingestion since non-nutritive sucking (e.g., cross-sucking and sucking inanimate objects) is often observed for 12–15 min after milk ingestion (so-called

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milk-dependent cross-sucking, e.g., Lidfors, 1993; de Passillé and Rushen, 1997; Margerison et al., 2003). It is also known that the taste of milk elicits sucking behaviour (de Passillé et al., 1997), and thus, milk-dependent cross-sucking is strongly influenced by milk feeding management. This might include, for example, the frequency of milk meals, milk intake via an artificial teat versus bucket, or the design of the teat (e.g., Sambras, 1984; de Passillé, 2001; Jensen, 2003; Lidfors and Isberg, 2003). In most of these studies, however, observation times were very short and only covered up to 30 min after milk ingestion. These studies were, therefore, unable to detect any sucking behaviour that was largely unrelated to milk ingestion. However, cross-sucking without obvious association to the ingestion of milk has been found in studies with longer observation times. This behaviour has accounted for a considerable proportion of all observed cross-sucking events (e.g., Veissier et al., 1998; Keil and Langhans, 2001; Weber and Wechsler, 2001; Jensen, 2003).

Question arises why cross-sucking occurs not only after milk intake but also before milk intake or seemingly independently in time of milk intake. Hunger is known to increase sucking motivation in calves (de Passillé and Rushen, 1997). This may be especially important during the weaning process, when milk is reduced and the calf has to adapt to nutrition on solid food only. It is thus possible that the general nutritional state of a calf is related to sucking behaviour. Keil and Langhans (2001) described a high correlation between energy deficit (difference between the energy density of the ration offered and needed) and the number of sucking bouts calves performed directly after weaning. Furthermore, Roth et al. (2008) showed that a feeding schedule during the weaning period that adequately compensated for the energy demands of each individual calf reduced the number of animals that cross-sucked after weaning. These results indicate that sucking behaviour is influenced by solid food intake and not only elicited by milk ingestion.

We assume that cross-sucking is triggered not only by the taste of milk but also by other motivational mechanisms, one of them likely being hunger. To verify our hypothesis, we estimated the daily energy balance (the difference between energy demand for growth and maintenance and energy consumption) for dairy calves fed by automatic milk and concentrate feeders. We examined the influence of energy balance on the probability to perform cross-sucking. Likewise, we noted the influence of energy balance on the temporal association of cross-sucking events with the nearest visit to the milk feeder. The aim of this study was to investigate the temporal relationships among cross-sucking bouts, rewarded and unrewarded visits to an automatic milk feeder, and the current energy balance of a calf.

2. Animals, material and methods

2.1. Animals and housing

The data presented in this paper originate from two experiments, in which the effects of two weaning methods on cross-sucking (see Roth et al., 2008) and rumen

development (see Roth et al., 2009) were analysed. The experiments were conducted from March to June 2004 and May to November 2005 at the Agroscope Reckenholz-Taenikon Research Station ART in Taenikon (Ettenhausen, Switzerland). The subjects included 75 dairy calves in total (47 Swiss Brown, 4 Swiss Brown \times Limousin, 16 Red Holstein, 1 Red Holstein \times Limousin and 7 Holstein Friesian). Calves of each experiment were kept together in the same pen with an area of 37.5 m² (27 calves, 1.4 m²/animal, first experiment) and 48 m² (24 calves in each of two batches, 2.0 m²/animal, second experiment), in deep litter without access to barnyard or pasture. Hay and water were available ad libitum in both experiments. All calves were fed by a milk feeder and a concentrate feeder (FA Foerster-Technik GmbH, Engen, Germany). Both feeders were computer controlled. All calves had free access all the time to both feeders. A chip in the neckband of each animal allowed the feeders to recognize individual calves and to feed each with an individually defined amount of milk and concentrate. Consumed milk and concentrate amounts as well as all visits to the milk and concentrate feeders (with and without consumption) were recorded automatically. The milk feeder was equipped with a self-enclosing mechanism (according to Weber and Wechsler, 2001), which ensured that calves could not be displaced by other calves and could thus perform non-nutritive sucking at the teat as long as they wanted, regardless of whether if they had received milk or not.

2.2. Recording of cross-sucking events and the relation to the temporally closest visit to the milk feeder

Each calf was observed directly for the occurrence of cross-sucking on two consecutive days for 10 h per day (06:00–11:00 and 16:00–21:00) at two points in time during the milk feeding period. The first data collection took place 1 week after the formation of the group at the age of 6 weeks (SEM \pm 1.1 day, range 4–10 weeks, milk allowance 6 l/day). The second data collection took place 1 week before weaning at the age of 11 weeks (SEM \pm 1 day, range 8–14 weeks, milk allowance 2.5–1 l/day). The differing milk amounts at the same age resulted from the concentrate-dependent weaning method that was applied to half of the animals (see Roth et al., 2008). All observed cross-sucking events were related to the visit to the milk feeder that was closest in time on the same day. The time difference of cross-sucking and visit to the milk feeder was calculated in relation to the time when a calf entered or left the stall for cross-sucking bouts before and after the visit to the milk feeder, respectively. The duration of time in which the calf was inside the stall was not further taken into account. Data on whether milk ingestion took place during this visit to the milk feeder or not were generated by the computer connected to the feeder. Therefore, each cross-sucking event was assigned to one of the following categories: “before calf entered the stall” or “after calf left the stall”; if the visit to the milk feeder was “with milk ingestion” or “without milk ingestion”. Due to technical problems on two observation days, seven of 926 cross-sucking bouts (of five animals) could not be related to a visit to the milk feeder on the same day and were therefore omitted from further analysis.

According to Roth et al. (2008), cross-sucking bouts were defined as milk-dependent and milk-independent. Milk-dependent cross-sucking was recorded if sucking bouts occurred within 15 min after a calf had left the stall with milk intake (Weber and Wechsler, 2001). All other cross-sucking was defined as milk-independent.

2.3. Recording of weight and estimation of energy balance

Animals used in the first experiment were weighed twice weekly; animals used in the second experiment once weekly. For each animal, the daily energy balance at each observation was calculated. To do so, we used estimated weight and weight gain at the observation days (based on a linear interpolation) to individually estimate the energy demand (MJ/day) necessary for growth and maintenance (after Kirchgessner, 2004, p. 386–387):

Energy demand for growth [in MJ/day] = $0.53 \times \text{weight}^{0.75}$ [in kg].

Energy demand for maintenance [in MJ/day] = $(7.08 \times \text{weight gain [in kg/day]} - 0.48)/0.4$.

The daily energy consumption (MJ/day) was known based on the quantity of consumed milk (crude protein: 200 g/kg; fat: 170 g/kg; energy: 19.2 MJ/kg) and concentrate (crude protein: 180 g/kg; fat: 80 g/kg; fibre: 40 g/kg; energy: 7 MJ/kg). Hay intake was not taken into account. The daily energy balance was then estimated for each calf by subtracting consumed energy on a given day from the energy demand on that day calculated:

Energy balance = energy consumption – (energy demand for growth and maintenance)

Example: a calf with a weight of 100 kg and a weight gain of 0.5 kg/day has an estimated energy demand of 24.4 MJ/day (16.75 MJ/day for maintenance and 7.65 MJ/day for growth).

2.4. Statistical analysis

To account for the hierarchical study design and for the repeated measures of the same animal, generalised linear mixed effects models were used to analyse the influence of energy balance on sucking behaviour (Pinheiro and Bates, 2000; Venables and Ripley, 2002). We evaluated two models, using two different response variables. The first variable that we analysed was whether an animal exhibited cross-sucking (model A). Likewise, we analysed the temporal occurrence of each cross-sucking bout in relation to the closest visit to the milk feeder (model B). For model A, cross-sucking was defined as a dichotomous response variable. For each observation day, calves were either classified as animals exhibiting or not exhibiting cross-sucking. The fixed continuous explanatory variable for model A was the energy balance per day (MJ/day). We thus tested how the energy balance influenced the probability (risk reflected by odds-ratios) of cross-sucking on that day. In model B, the response variable was the time

difference of each cross-sucking bout in relation to the temporally closest visit to the milk feeder (in minutes, logarithmically transformed). Daily energy balance (MJ/day), milk intake (yes/no), timing of the visit to the milk feeder (before/after visit to the milk feeder) and all their two-way plus the one three-way interactions were included as explanatory variables.

The random effects of the calf nested within the experiment (first experiment/first batch of second experiment/second batch of second experiment) were included in both models. The 5% significance level of the partial *F*-statistic was applied as a threshold for exclusion of explanatory variables from the model in a step-wise backward approach in which main effects and lower-level interactions were retained if they still occurred in higher-level interactions. We examined the assumptions of normally distributed errors and homoscedasticity graphically with the use of the normal plot (residual quantiles versus quantiles of a normal distribution), the Tukey–Anscombe plot (residuals versus estimates), and plots of the residuals versus variables. All calculations were done using lme (Pinheiro and Bates, 2000) and glmmPQL (Venables and Ripley, 2002) in R (version 2.6.1, R Development Core Team, 2007).

3. Results

3.1. Frequency and temporal distribution of cross-sucking events

In total, 919 sucking bouts were observed. Of the 75 calves, 62 showed cross-sucking at least once (82.7% overall, 85.2 and 81.3% in the first and second experiments, respectively). Fifty-six of the 62 calves showed more than one sucking bout. Forty-four calves were observed cross-sucking on both data collections. Seven calves were observed cross-sucking only in the period 1 week after grouping, and 11 calves were observed cross-sucking only in the period 1 week before weaning. Inter-individual differences in the frequency of cross-sucking were large. The number of cross-sucking calves as well as the absolute number of cross-sucking bouts (in total and per calf) is shown in Table 1. Time to the nearest visit to the milk feeder ranged between 0.02 and 651.67 min (median before visit to the milk feeder with milk intake: 6.57 min; before visit to the milk feeder without milk intake: 23.05 min; after visit to the milk feeder with milk intake: 2.89 min; and after visit to the milk feeder without milk intake: 8.09 min). Of all observed cross-sucking bouts, 28.4% ($n = 261$) occurred during the first 15 min after the calf had left the stall with milk intake. These sucking bouts were classified as milk-dependent cross-sucking (Fig. 1). Within 15 min before a visit to the milk feeder (with or without milk intake), 21.1% ($n = 194$) of the sucking bouts were observed. Another 15.2% ($n = 140$) were observed during the first 15 min after the calf had left the stall without milk ingestion, and 35.3% ($n = 324$) occurred more than 15 min before or more than 15 min after a visit to the milk feeder (milk-independent cross-sucking, Fig. 1). Mean duration of stall visit with and without milk intake was 71.23 and 42.72 s, respectively.

Table 1

Number of cross-sucking bouts, cross-sucking calves, and range of cross-sucking bouts per calf per observation period.

Time of observation	Total number of cross-sucking bouts (observed in 20 h/individual)	Number of calves cross-sucking (total $n = 75$)	Range (and mean \pm SEM) of total number of cross-sucking bouts per calf
1 week after grouping	550	51	1–60 (10.80 \pm 1.85)
1 week before weaning	369	55	1–40 (6.69 \pm 0.90)

3.2. Energy balance and the occurrence of cross-sucking

Energy balance ranged from -47.99 to $+20.03$ MJ/day (median: -14.00 MJ/day, first quartile: -22.79 MJ/day, third quartile: -9.27 MJ/day). The probability of exhibiting cross-sucking decreased with higher values of the energy balance (OR = 0.69 per one unit MJ/day, $t_{240} = -3.15$, $P = 0.0018$, model A). This indicates that, with lower (more negative) energy on the observation day, the probability for the animals to perform cross-sucking was higher.

3.3. Energy balance and time difference between cross-sucking and the temporally closest visit to the milk feeder

In model B, the interaction between energy balance, milk intake (yes/no) and timing of visit to the milk feeder (before/after, model B) had a significant influence on time difference between sucking and the temporally closest visit to the milk feeder ($F_{1,850} = 13.36$, $p = 0.0003$, Fig. 2). For sucking bouts that occurred before a visit to the milk feeder with milk intake, relation to energy balance was positive (Fig. 2a). These results indicate that, with increasing energy balance, the time between a cross-sucking bout and the next visit to the milk feeder increased. For the other three combinations (after visit to the milk feeder with milk intake (b), and before (c) and after (d) visit to the milk feeder without milk intake), the relation between time to the nearest visit to the milk

feeder and energy balance was markedly weaker and slightly negative (Fig. 2). Slopes were found to be 0.05, -0.01 , -0.02 and -0.01 in Fig. 2(a)–(d), respectively.

4. Discussion

The results of the present study showed that more than two-thirds (71.6%) of all sucking bouts seem to occur independently of milk intake. Furthermore, energy balance influenced the occurrence and the temporal pattern of cross-sucking.

4.1. Temporal distribution of cross-sucking events

As described in other studies with similar observation times (Veissier et al., 1998; Keil and Langhans, 2001; Weber and Wechsler, 2001; Jensen, 2003), the calves showed cross-sucking outside a close temporal association to milk ingestion in our study. Only 28.4% of all sucking bouts in this study seemed to be elicited by milk, as they occurred within 15 min after the calf left the stall after it had received milk. Following the findings of previous studies (e.g., de Passillé and Rushen, 1997; Weber and Wechsler, 2001), we classified these sucking bouts as milk-dependent cross-sucking. However, 71.6% of the sucking bouts were not elicited by milk intake. This is a remarkable proportion and clearly emphasises the importance of long observation times of at least several hours. With respect to the total amount of cross-sucking and observation time, this proportion is very similar to Weber and Wechsler (2001). We classified these sucking bouts as milk-independent cross-sucking.

To our knowledge, this is the first study that has analysed the temporal distribution of all sucking bouts in detail. For further studies, we recommend distinguishing between milk-dependent and milk-independent cross-sucking in order to detect different motivational mechanisms. Sucking bouts occurring 15–30 min after the calf had left the stall with milk intake could be omitted for a clear distinction between the two categories “milk-dependent” and “milk-independent” cross-sucking.

4.2. Energy balance and the occurrence of cross-sucking

To our knowledge, our findings are the first to demonstrate the connection between cross-sucking and energy balance. As we expected, the probability for a calf to cross-suck increased with decreasing energy balance. In other words, an inappropriate energy supply led to a higher risk of cross-sucking. Our findings are in line with the results of Keil and Langhans (2001), who found a high correlation between energy deficit (difference between

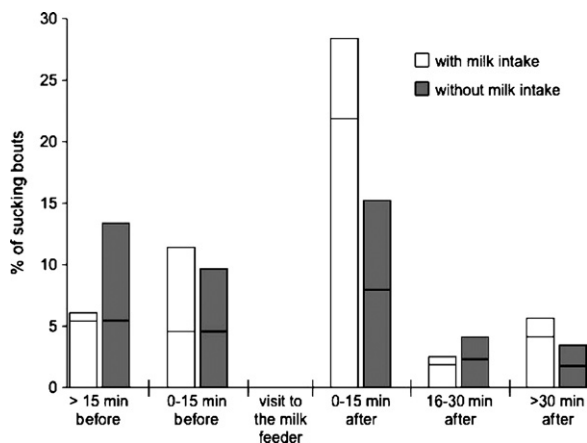


Fig. 1. Percentage of all observed cross-sucking bouts ($n = 62$ calves, 919 sucking bouts) in association to the temporally closest visit to the milk feeder on the same day. Cross-sucking bouts were classified as related to a visit to the milk feeder with milk intake (open bars) or without milk intake (grey bars). Bars are divided in first (6 weeks of age, lower part) and second observation (11 weeks of age, upper part).

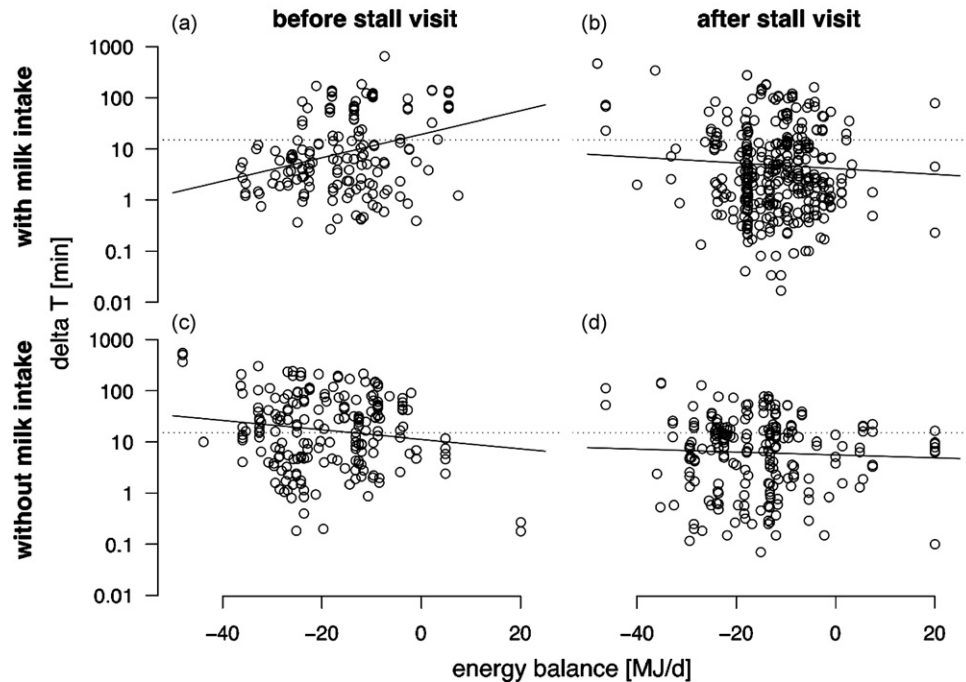


Fig. 2. Energy balance (MJ/day) of cross-sucking calves versus time to the temporally closest visit to the milk feeder (min): (a) before a visit to the milk feeder with milk intake, (b) after a visit to the milk feeder with milk intake, (c) before a visit to the milk feeder without milk intake and (d) after a visit to the milk feeder without milk intake. In order to identify cross-sucking bouts temporally close to the visit to the milk feeder more easily, the time span of 15 min before and after the visit to the milk feeder is indicated by dotted lines.

energy density of the ration offered and needed) and the number of observed sucking bouts directly after weaning. Furthermore, the results supports our former findings (Roth et al., 2008) that a feeding schedule during the weaning period that accounts for the individual energy demand reduced the number of cross-sucking animals after weaning. We assume that energy balance could explain this reduction in number of cross-sucking animals very well.

4.3. Energy balance and time difference between cross-sucking and the temporally closest visit to the milk feeder

As mentioned above, less than one-third of all cross-sucking bouts could be classified as directly milk elicited. For these cross-sucking bouts, we did not expect the energy balance to be relevant. Milk-dependent cross-sucking can plausibly be explained by factors connected to milk intake (e.g., taste of milk; de Passillé et al., 1997). Our results revealed that energy balance did not influence the temporal pattern of cross-sucking after a visit to the milk feeder with milk intake.

Milk-independent cross-sucking, however, accounted for a remarkable proportion of all sucking bouts. Here, we assumed that this cross-sucking could be triggered by hunger, as hunger is known to enhance the sucking motivation (de Passillé and Rushen, 1997). One plausible motivation for a visit to the milk feeder is hunger (e.g., De Paula Vieira et al., 2008). Therefore, we expected to find a relationship between energy balance and time to

the nearest visit to the milk feeder with better (more positive) energy balance. A sufficient energy intake would lead to a larger time span between cross-sucking and the next visit to the milk feeder. A relationship showing this pattern was only found for cross-sucking bouts before a visit to the milk feeder with milk intake but not for cross-sucking bouts before and after a visit to the milk feeder without milk intake. This pattern supports the assumption that hunger could elicit cross-sucking before milk intake.

Additionally, hunger may not be influenced by milk intake only. Solid food intake increases with age as rumen development increases. As concentrate intake regulates hunger too, we therefore assume that concentrate intake could have an effect on sucking motivation. To our knowledge, the physiological regulations of food intake, “abomasal hunger” (satisfied by milk) and “ruminal hunger” (satisfied by solid food) are unknown.

In addition to hunger, further aspects should be taken into account to explain sucking motivation in our view. In particular, one must consider sucking bouts that occurred before and after a visit to the milk feeder without milk intake. Due to the similarity to a cow’s udder (a dark inguinal region characterised by softness, warmth and formability), the udder or scrotal region of another calf could be preferred to the rubber teat that does not provide these qualities, especially if the teat does not supply milk. Therefore, cross-sucking bouts after or before a visit to the milk feeder without milk intake could not only be triggered by hunger but also may be influenced by frustration when

a calf could neither obtain milk nor satisfaction by sucking the rubber teat during the visit to the milk feeder.

An additional motivational mechanism for sucking behaviour might be boredom, as Keil et al. (2002) showed that a stimulating environment was able to reduce cross-sucking in dairy calves. Furthermore, we believe that being sucked by another calf could initiate a sucking bout as we repeatedly observed two calves sucking on each other at the same time.

These results demonstrate that cross-sucking is influenced by more than milk ingestion. In further studies, we suggest analysing the physiological (e.g., hormonal state) and behavioural (e.g., if the cross-sucking calf is being sucked by another calf) situation of calves individually for each sucking bout in order to assign the motivational mechanisms initiating that sucking bout. All in all, this emphasises the need for further investigations into sucking behaviour and especially into nutritional aspects of rearing calves for the prevention of cross-sucking.

5. Conclusion

Because over two-thirds of the sucking bouts occurred independent from milk ingestion, we conclude that observation times longer than 30 min after milk intake are necessary to make a profound statement about the causation of sucking behaviour in calves. A differentiation between milk-dependent and milk-independent sucking bouts seems to be reasonable. The hypothesis that cross-sucking is motivated by the taste of milk and can be influenced by milk feeding management is plausible but takes into account only a small proportion of sucking events. Animals with appropriate energy supply were less likely to perform cross-sucking. Likewise, the temporal occurrence of sucking bouts depended on energy balance. Cross-sucking seems to be influenced by various motivational mechanisms, one of them likely being hunger. To substantially prevent cross-sucking in calves the feeding plan (milk and solid food rations) should be of relevance.

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References

- De Paula Vieira, A., Guesdon, V., de Passillé, A.M., von Keyserlingk, M.A.G., Weary, D.M., 2008. Behavioural indicators of hunger in dairy calves. *Appl. Anim. Behav. Sci.* 109, 180–189.
- de Passillé, A.M., Rushen, J., 1997. Motivational and physiological analysis of the causes and consequences of non-nutritive sucking by calves. *Appl. Anim. Behav. Sci.* 53, 15–31.
- de Passillé, A.M., Rushen, J., Janzen, M., 1997. Some aspects of milk that elicit non-nutritive sucking in the calf. *Appl. Anim. Behav. Sci.* 53, 167–173.
- de Passillé, A.M., 2001. Sucking motivation and related problems in calves. *Appl. Anim. Behav. Sci.* 72, 175–187.
- Jensen, M.B., 2003. The effects of feeding method, milk allowance and social factors on milk feeding behaviour and cross-sucking in group housed dairy calves. *Appl. Anim. Behav. Sci.* 80, 191–206.
- Keil, N.M., Langhans, W., 2001. The development of intersucking in dairy calves around weaning. *Appl. Anim. Behav. Sci.* 72, 295–308.
- Keil, N.M., Zwicky, U., Schrader L., 2002. Einfluss der Umweltkomplexität auf Verhalten und gegenseitiges Besaugen von Aufzuchtälbern in Gruppenhaltung. Aktuelle Arbeiten zur artgemässen Tierhaltung 2001-KTBL-Schrift 407, KTBL, Darmstadt, Germany, pp. 76–83.
- Kirchgessner, M., 2004. Tierernährung: Leitfaden für Studium Beratung und Praxis, 11th edition. DLG-Verlag, Frankfurt am Main.
- Lidfors, L., 1993. Cross-sucking in group-housed dairy calves before and after weaning off milk. *Appl. Anim. Behav. Sci.* 38, 15–24.
- Lidfors, L., Isberg, L., 2003. Intersucking in dairy cattle—review and questionnaire. *Appl. Anim. Behav. Sci.* 80, 207–231.
- Margerison, J.K., Preston, T.R., Berry, N., Phillips, C.J.C., 2003. Cross-sucking and other oral behaviours in calves, and their relation to cow suckling and food provision. *Appl. Anim. Behav. Sci.* 80, 277–286.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-Effects Models in S and S-PLUS*. Springer, New York.
- R Development Core Team, 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.r-project.org/>.
- Roth, B.A., Hillmann, E., Stauffacher, M., Keil, N.M., 2008. Improved weaning reduces cross-sucking and may improve weight gain in dairy calves. *Appl. Anim. Behav. Sci.* 111, 251–261.
- Roth, B.A., Keil, N.M., Gygas, L., Hillmann, E., 2009. Influence of weaning method on health status and rumen development in dairy calves. *J. Dairy Sci.* 92, 645–656.
- Sambras, H.H., 1984. Gegenseitiges Besaugen von Kälbern bei künstlicher Aufzucht. *Berliner Münchner Tierärztliche Wochenschrift* 97, 119–123.
- Veissier, I., Ramirez de la Fe, A.R., Pradel, P., 1998. Nonnutritive oral activities and stress responses of veal calves in relation to feeding and housing conditions. *Appl. Anim. Behav. Sci.* 57, 35–49.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, 4th edition. Springer, New York.
- Weber, R., Wechsler, B., 2001. Reduction in cross-sucking in calves by the use of a modified automatic teat feeder. *Appl. Anim. Behav. Sci.* 72, 215–223.