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## **Ontogeny of suckling behaviour in cattle - a model for several mammalian species?**

### **Abstract**

Suckling behaviour of nine beef cow-calf-pairs (Hereford and Charolais) and five dairy cow-calf-pair's (Polish Holstein-Friesian) was video-recorded from day one *pp* to day 70 (beef) or 82 (dairy) *post partum* (*pp*) regularly. Cows were only suckled during that time and milk yield could not be recorded. Bout was defined as all activities of the calf from the first contact between the mouth of the calf at a specific teat and the last contact at this teat, i.e., as a small sub-unit of a meal. Number of suckled teats, uniformity of relative shares of suckled teats, number of bouts, average bout and relative number of bout-teat-repetitions described the course of ontogeny of suckling behaviour. The first model included the effects breed, cow (breed), and day *pp* as regression. The analysis revealed the following: (i) number of teats, uniformity of relative shares between suckled teats, and number of bouts increased with increasing day *pp*. (ii) Average bout, relative number of bout-teat repetitions and meal-bout-relationship decreased with increasing day *pp*. (iii) The same developments could be observed in both breeds, however, significantly slower in the dairy breed. The second model included the effects breed, cow (breed) and average bout as regression, representing milk yield. Breed changed from a very powerful into an almost negligible effect in that second analysis. The implications of the results for a wider group of mammalian species are discussed.

**Key Words:** Suckling behaviour, ontogeny, day of life, milk yield, cattle

### **Zusammenfassung**

**Titel der Arbeit: Die Ontogenie des Saugverhaltens beim Rind - ein Modell für Säugetierspezies?**

Das Saugverhalten von neun Fleischrinder- (Hereford und Charolais) und fünf Milchrinder- (Polnische Holstein-Friesian) Mutter-Kalb-Paaren wurde mit einer Videokamera zwischen Tag eins und Tag 70 (Fleischrind) und 82 (Milchrind) *pp* regelmäßig registriert. Die Kühe wurden in dieser Zeit nur besaugt und die Milchleistung konnte nicht registriert werden. Bout wurde definiert als alle Aktivitäten zwischen dem ersten und dem letzten ununterbrochenen Kontakt zwischen dem Kälbermaul und einer bestimmten Zitze. Bout ist also eine kleine Untereinheit eines Säugmahls. Die Zahl der besaugten Zitzen, die Uniformität der relativen Säugezeiten per Zitze, die Anzahl der Bouts, die durchschnittliche Bout-Länge und die relative Anzahl der Bout-Zitzen-Wiederholungen per Mahl beschrieben die Ontogenie des Saugverhaltens. Das erste Modell enthielt die Varianzquellen Rasse, Mutter (Rasse) und Tage *pp* als Regression. Die Analyse ergab: (i) die Uniformität der relativen Säugezeiten per Zitze und die Anzahl der Bouts stiegen, (ii) die durchschnittliche Bout-Länge und die relative Anzahl der Bout-Zitzen-Wiederholungen fielen je älter das Kalb war. (iii) Der gleiche Verlauf konnte in beiden Rassen beobachtet werden, allerdings brauchten die Milchrinder signifikant länger. Das zweite Modell enthielt die Varianzquellen Rasse, Mutter (Rasse) und durchschnittliche Bout-Länge als Regression als ein Hilfsmerkmal für die Milchmenge. In der zweiten Analyse wurde Rasse zu einer nahezu vernachlässigbaren Varianzquelle. Die Bedeutung der Ergebnisse für eine Gruppe von Säugetierspezies wird diskutiert.

**Schlüsselwörter:** Saugverhalten, Ontogenie, Lebenstag, Milchmenge, Rind

### **Introduction**

Calf suckling behaviour was recorded within the framework of developing a physiological milk harvest process. Substantial differences were observed between suckling behaviour shortly after birth and a few weeks later. Therefore the ontogeny of

suckling behaviour was in the focus of the research reported here. In a pre-study MAYNTZ (1996) proposed the ontogeny of suckling behaviour of *Bos taurus* being completed when the behaviour did not change qualitatively any more. The sequence of events listed below was essential for the course of ontogeny in that proposal. Those events were: (i) a bout pattern reflecting the milk flow in the gland (MAYNTZ and COSTA, 1998) had developed (for details see MAYNTZ et al., 2006); (ii) regular and frequent teat changes occurred between the suckled teats, (iii) all teats were suckled during a suckling meal (referred to as "meal" in the following), and (iv) the teats were suckled equally.

Data were collected to describe the ontogeny of suckling behaviour in cattle. The variables evaluated here, and the description of ontogeny resulting from that, were the final steps of a long process. The length of that process resulted from the two following facts: Only marginal hints about the beginning but not the course of ontogeny could be taken from the literature (e.g. SELMAN et al., 1970; EDWARDS and BROOM, 1982; LANGHOLZ et al., 1987; VENTORP and MICHANEK, 1991; SCHÄFFER et al., 1999) and the research consumed an unforeseeable amount of time. The long period of investigation itself resulted from the methods chosen. A lot of time had to be spent to record 193 voluntary suckling meals or 70 hours videotape, to translate the videotapes into quantitative data-files and to test different graphical translation of the data-files into figures showing the main characteristics of a suckling meal at one glance. Understanding biological processes by viewing (LORENZ, 1959) is an accepted form of gaining knowledge; however, only if proper testing of hypotheses follows - as we would state.

In all preliminary evaluations, the beef and dairy breeds differed significantly only concerning quantitative aspects of ontogeny and the dairy breed animals consumed a much longer period of time to reach the end of ontogeny of suckling behaviour described above. Viewing of the meal-graphs gave the impression, that the ending period of the dairy meals resembled the starting period of beef meals. Milk yield was higher in the dairy breed and milk yield generally should be higher in the starting period because the big number of short bouts during the long after-stimulation belongs to the ending period of a meal (MAYNTZ and COSTA, 1998). Thus the idea arose that milk yield could be a "common currency" between the two breeds.

MAYNTZ and COSTA (1998) had defined a bout as the period of "... all activities of the calf from the first contact between the mouth of the calf at a specific teat and the last contact at this teat, if there is suckling between these two events" i.e., as a small sub-unit of a meal. They showed e.g., that a pharmacological blockage of ejection resulted in very small bouts throughout an entire meal or that a pharmacologically induced additional ejection of residual milk during the partially non-nutritive after-stimulation (LIDFORS et al., 1994) resulted in a consecutive short series of prolonged bouts. Thus, longer bouts indicate more milk in the corresponding cistern and *vice versa*. It had not been feasible to record milk yield when the data analysed here were collected, but average bout length could represent the individual differences in milk yield. Therefore the description of the course of ontogeny given here falls into two parts: The evaluation before and after the hypothesis that average bout length representing milk yield was the common independent variable determining the course of ontogeny across breeds and individuals.

Thus the objectives of this study have been: (i) To establish the differences between the two breeds, and consequently (ii) to describe the course of the ontogeny of suckling behaviour along with lifetime within each breed and (iii) finally to repeat that description along with average bout across the breeds.

## Material and methods

### Animals

Nine beef calf-dam-pairs (CDP), eight Hereford and one Charolais, were randomly selected from a herd at the Research Station of Ecological Agriculture and Breeding of Endangered Animals in Popielno, Poland. A recording period from March 28 to April 8 was agreed before the onset of recording. CDP, the calves of which were born during this period were selected. One additional Hereford calf was born March 27 and two further on March 26 (number 21-23 in Table 3) and were incorporated in the data set. The lactation number of the dams thereby selected varied between one and five.

Additional five CDP (Polish Holstein-Friesian) were selected from another herd at the same Research station in a corresponding manner two years later. One additional Holstein calf was born one day before the agreed observation period (number 31 in Table 3) and was incorporated in the data set. That dairy herd averaged about 5500 litres per year on a grass-dominated diet during the year before the observations. The lactation number of the dams thereby selected varied between three and four.

### Management

The calving stable of the beef breed was equipped with single cubicles (5.5 m<sup>2</sup>) with a 5 to 10 cm thick straw mattress. (For further details see MAYNTZ et al., 2006).

The selected CDP were kept together with further 54 Hereford-CDP on a remote, forest-enclosed pasture from 0800 to 1800 during the third observation period. Calves and dams were kept in adjacent corrals separated by bars because calves were offered shelter and concentrates in their corral during night. (For further details see MAYNTZ et al., 2006).

The dairy cows gave birth in a conventional tied-up stall. The selected CDP were taken to a separate nearby pasture immediately before or after (one CDP) calving. During the following recording period, the six CDP stayed together on pasture separated from the rest of the herd. The dairy cows were not milked during observation.

Thus breed was partially confounded with management. Therefore the special "breed-management-interaction" analysed here is meant in the following when speaking about the effect "breed".

### Recording

Meals of the 12 selected beef cow-calf-pairs were observed during three periods, which were separated by 19 and 20 days. Recording was carried out during days of life 1 to 13, 21 to 36 and 60 to 80. The calves and their mothers stayed in the stable during the first and second observation periods. The beef cows were marked with large numbers on their flanks and thus could be selected as focal animals during the third observation period.

A single observer worked during the three observation periods. During the first and second observation period, the observer slowly patrolled the aisles between 5.00 and

20.00. The camera was started and the observer quickly chose a position for it on the cow's side opposite to the calf and close to the floor when a meal seemed to be initiated. Recording was carried out continuously until a few minutes after the voluntary separation of cow and calf.

During the pasture period the observer followed the herd to the pasture. He focused one CDP per day and recorded a voluntary meal between 12.00 and 18.00. Rules for start and end of recording were equivalent to those in the stable periods.

Only one of two observers was available at a time for recording the dairy cows. One meal was recorded for each single CDP every day during the first week of life. Thereafter, one meal per week was recorded at the end of each week. These later recordings were made during a three-day window at the end of a week. Recording continued roughly 11 weeks *pp*.

### **Data handling**

A time code was copied on the videotapes, showing hours, minutes, seconds and frames (25 frames / second) thus allowing different activities to be separated with an accuracy of 0.04 seconds.

The tapes were read meal-by-meal concerning activities and places of the calf's mouth. The end of one activity coincided with the start of a new one. The activities are listed below.

(i) Suckling, i.e., teat stretched in the mouth and sucking movements of the lower jaw, (ii) stimulate, i.e., lick, bite, massage, very slight push, take teat in mouth, (iii) transport of mouth, (iv) push, i.e., retraction of the head from the teat base and a consecutive strong push towards the teats base. The initial retraction of the head is missing in the "very slight push" mentioned above. (v) Strip, i.e. lengthening the teat considerably and stripping it from base to tip between the upper jaw and the front teats without sucking movements, (vi) calf not at udder, (vii) cow moves and (viii) cow kicks.

The activities "push" and "stimulate" appeared in two versions each, with or without the teat in the mouth. All activities could be combined, except with "calf not at udder". The following places of the calf's head were noted together with the activities: at (i) a specific teat, e.g., front right; (ii) between two specific teats, e.g., between front right and hind right; (iii) udder, i.e., at almost equal distance from all teats; and (iv) cow's body.

Duration of every activity was calculated and a time scale created by cumulative addition of all activities. Later the bout durations at every teat were transferred to a column for each corresponding teat at its starting point on the time scale.

The standard area-graph of the Excel program was chosen to visualise time scale and bouts of each teat. The main weakness of that graphical routine is that it does not allow free scaling of x- and y-axis, and thus is not fit for easy graphical comparisons. Its main advantage is that a graph can be produced very fast.

### **Dependent variables**

During data handling, the questions listed below arose. An example of such a question can be seen in Fig. 1. At first that meal was a two-teat-meal (hind right and front right) with complete meal structure. Apparently the amount of milk suckled from these two quarters did not satisfy the calf. Thus it addressed a third teat (hind left) close to the end of after-stimulation of the first two quarters. The cistern of that late addressed

quarter was full because stimulation had elicited an ejection also there (ZAKS, 1962). Consequently the first bouts at that third quarter were very long. From that graph the idea for the question arose when the suckled teats were addressed for the first time during a meal (see (ii) below).

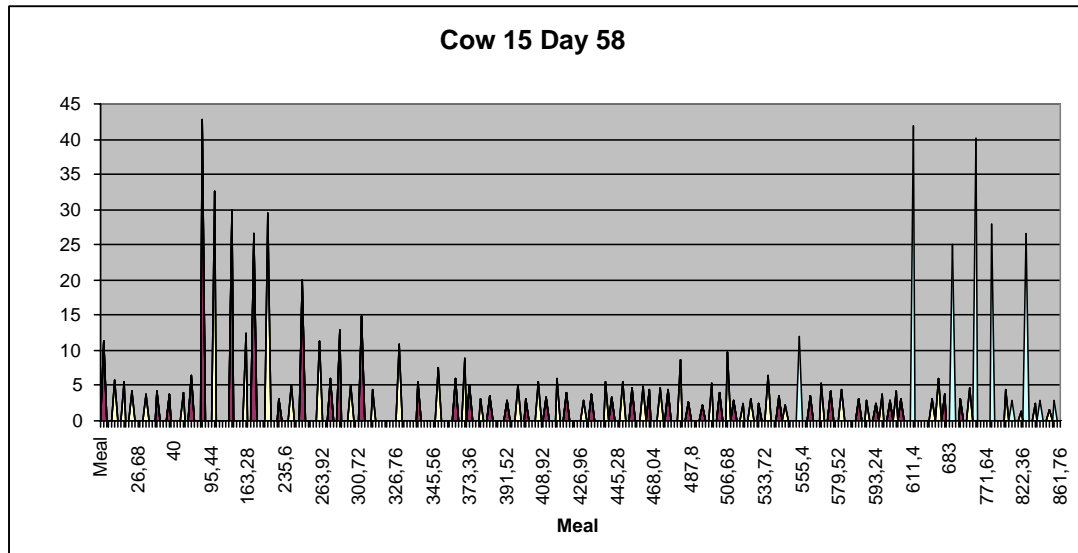


Fig.1: Graph of meal of dairy calf no. 15 at day 58 *pp* (Graphik der Mahlzeit des Kalbes Nr. 15. am 58. Tag *pp*)

The questions mentioned above were: (i) How many teats were suckled during a meal? (ii) When was a specific teat addressed for the first time during a meal? (iii) How uniformly were the teats suckled? (iv) How many bouts were counted? (v) How long was the average bout? (vi) How often was a bout followed immediately by another one at the same teat? (vii) How long was the meal? (viii) How much time was spent on suckling or on non-suckling activities? (ix) How long was the longest bout? (x) When was a complete meal structure, i.e., including at least pre-stimulation, ejection and after-stimulation recorded for the first time? The variables described below were developed to answer these questions.

*Variables describing the use of teats.* (i) Number of suckled teats, (ii) relative entrance of first, second, third and fourth suckled teat into the meal i.e., time until suckling at that specific teat started for the first time in % of meal, (iii) uniformity of relative shares of suckled teats. Uniformity was calculated in the following way: (a) the standard deviation between the relative shares (sum of bouts at a specific teat in % of all bouts) of all four teats, i.e., including the not-suckled ones was calculated. (Perfect uniformity, i.e., 25 % suckling at every teat: 25, 25, 25, 25%,  $s = 0$ . Totally missing uniformity, i.e., only suckling at one teat: 100, 0, 0, 0%,  $s = 50$ ). (b) The actual standard deviation was multiplied by 2 (Perfect uniformity:  $0 \times 2 = 0$ . Totally missing uniformity:  $50 \times 2 = 100$ ). Thus any distribution of relative suckling time between the four quarters was expressed on a gliding scale between 0 and 100. (c) The scale was turned by subtracting the actual figure from 100 (Perfect uniformity:  $100 - 0 = 100$ . Totally missing uniformity:  $100 - 100 = 0$ ). The third step was done exclusively to ease reading by linking perfect uniformity to 100 and totally missing uniformity to 0, (iv) number of bouts. (v) average bout, being sum of bouts divided by number of bouts and (vi) relative number of bout-teat-repetitions. The graphs mentioned above had revealed that mostly younger calves returned to the teat just suckled after a completed

bout, but that this behaviour disappeared gradually. Because the different meals included a wide variety of bouts, the number of bout-teat-repetitions had to be expressed in % of all bouts.

*Variables describing the meal as a whole.* (i) Meal length, (ii) meal-bout-relationship (= meal length / number of bouts) expressing how much time of a meal was spent mainly on suckling (small figures) or also on not-suckling activities (high figures) and (iii) longest bout.

*Qualitative variables indicating a complete meal structure.* (i) Day *pp*, at which the occurrence of a complete meal structure could be recorded for the first time and (ii) number of suckled teats during that meal.

### Models and levels of probability

The model for testing differences between breeds included the following effects: breed, cow (breed), and day *pp* as regression. The model using average bout instead of day *pp* included the following effects: breed, cow (breed), and average bout as regression. Data were analysed by GLM procedure of SAS (SAS/STAT, 1989).

Least square means were calculated for the variables significantly effected by the applied model. Contrasts between least square means were compared with Dunnett's t-test. Only contrasts between the fixed effect breed are shown.

The composition of the data set and the number of replications were not planned to falsify *a priori* established hypotheses. Therefore the actual probability levels are given, however, not those  $\geq 0.1$ .

## Results

Tables 1 summarises the results of analysis of variance including the effects breed, cow (breed), and day *pp* as regression. Table 2 gives the contrasts between the breeds. Table 3 gives the day *pp*, at which a complete structure of a meal could be recorded for the first time (on average day 4 *pp* for the beef and day 12.3 *pp* for the dairy breed) and the number of suckled teats at the corresponding meal (2.92 and 1.83 respectively).

Table 1

Results of analysis of variance for the model breed, cow (breed), and day *pp* as regression (Resultate der Varianzanalyse mit den Varianzquellen Rasse, Mutter (Rasse), und Tag *pp* als Regression)

Variable	Pr > F for model	R <sup>2</sup>	Pr > F for breed	Pr > F for
No. of suckled teats	< 0.0001	0.493	< 0.0001	0.0112
Relative entrance of the first suckled teat	0.0357	0.153	0.0117	n.s.
Relative entrance of the second suckled teat	< 0.0001	0.372	< 0.0001	n.s.
Relative entrance of the third suckled teat	< 0.0001	0.494	< 0.0001	n.s.
Relative entrance of the fourth suckled teat	< 0.0001	0.588	< 0.0001	0.0023
Uniformity	< 0.0001	0.657	< 0.0001	0.002
No. of bouts	< 0.0001	0.547	< 0.0001	0.0269
Average bout	< 0.0001	0.539	< 0.0001	0.0001
Relative no. of bout-teat-repetitions	< 0.0001	0.655	< 0.0001	0.0009
Meal length	< 0.0001	0.265	0.0026	n.s. (0.0785)
Meal-bout-relationship	< 0.0001	0.421	< 0.0001	0.0075
Longest bout	< 0.0001	0.433	< 0.0001	< 0.0001

Table 4 gives the regression equations for the beef and table 5 for the dairy breed with day *pp* as independent variable. Figure 2 demonstrates the relationship between the relative entrance of the different teats into a suckling meal and day *pp*.

Table 2

Contrasts between least square means (LSM) of beef and dairy breed for variables significantly influenced by breed in the model breed, cow (breed), and day *pp* as regression (Kontraste zwischen least square means (LSM) von Fleisch- und Milchrindern für die Variablen, die im Modell Rasse, Mutter (Rasse), und Tag *pp* als Regression signifikant beeinflusst wurden)

Variable	LSM <sub>beef</sub>	LSM <sub>dairy</sub>	H <sub>0</sub> : LSM <sub>beef</sub> = LSM <sub>dairy</sub> Pr >  t
No. of suckled teats	3.43	2.61	<0.0001
Rel. entrance of the first suckled teat	0.43	1.23	0.0117
Rel. entrance of the second suckled teat	5.60	22.84	<0.0001
Rel. entrance of the third suckled teat	11.03	36.33	<0.0001
Rel. entrance of the fourth suckled teat	17.74	44.28	<0.0001
Uniformity	70.04	38.25	<0.0001
No. of bouts	69.98	22.41	<0.0001
Average bout	8.12	15.95	<0.0001
Rel. no. of bout-teat-repetitions	19.74	51.55	<0.0001
Meal length	526.26	432.13	0.0026
Meal-bout-relationship	12.97	20.39	<0.0001
Longest bout	28.69	58.18	<0.0001

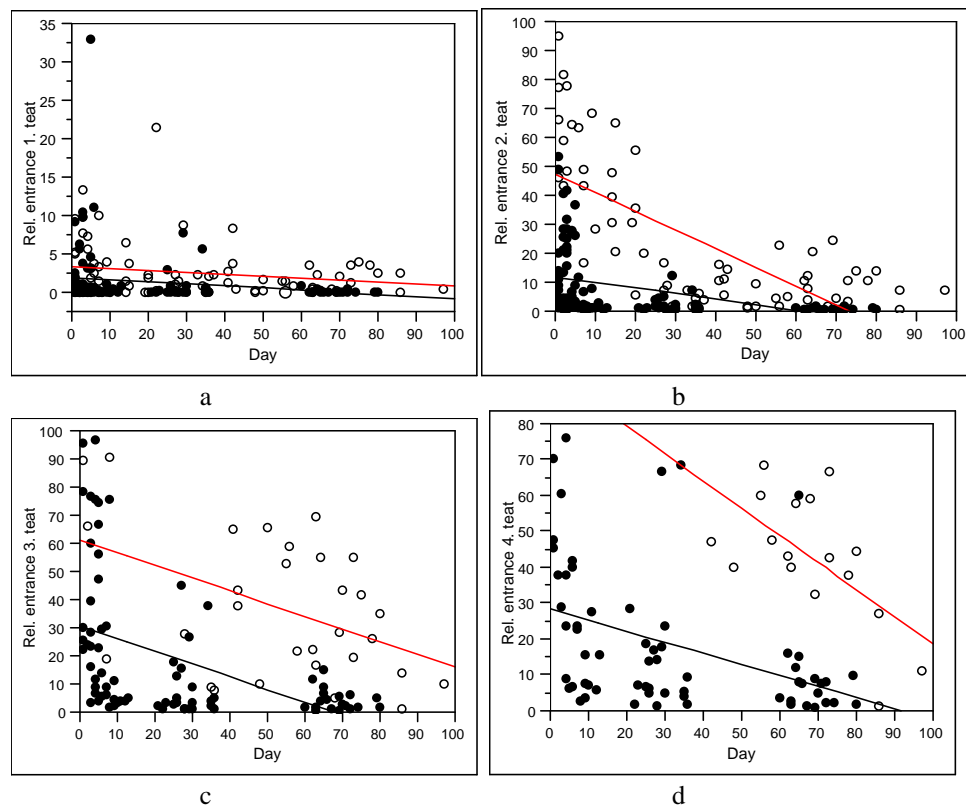


Fig. 2: Relative entrance of first (a), second (b), third (c) and fourth (c) suckled teat into the meal by day *pp*. X-axle: day *pp*, y-axle per cent of mealttime passed when the corresponding teat was suckled for the first time. Linear regressions for beef (lower line, filled circles) and dairy breed (higher line, empty circles). (Relativer Beginn des Saugens an der ersten (a), der zweiten (b), der dritten (c) und der vierten (d) Zitze. X-Achse: Tag *pp*., Y-Achse: Relative verfllossene Mahllänge bevor die entsprechende Zitze das erste mal besaugt wurde. Die linearen Regressionen für Fleischrinder (niedrigere Linie, ausgefüllte Kreise) und Milchrinder (höhere Linie, leere Kreise)

The analysis with day *pp* as main effect (Tables 1 and 2) or independent variable (Tables 4 and 5) revealed the following: (i) Number of teats, uniformity of relative shares between suckled teats, and number of bouts increased with increasing day *pp*. (ii) Average bout, relative number of bout-teat repetitions and meal-bout-relationship decreased with increasing day *pp*. (iii) An additionally suckled teat was not suckled

Table 3

First occurrence of a complete meal structure and number of suckled teats during the corresponding meal (Erstes Erscheinen einer kompletten Mahlstruktur und die Zahl der besaugten Zitzen während dieses Mahls)

Breed	Cow no.	First day <i>pp</i> with a complete meal structure	No. of suckled teats at that meal
Beef	1	4	2
	2	9	3
	4	4	3
	5	2	2
	6	2	4
	7	5	2
	8	2	2
	9	4	2
	10	1	2
	21	4	4
	22	6	3
	23	5	3
	Dairy	11	14
13		13	1
14		14	1
15		13	2
16		7	3
31		13	2

Table 4

Linear regressions with day *pp* as independent variable (x) for beef breed (Lineare Regressionen mit Tag *pp* als unabhängige Variable bei Fleischrindern)

Variable (y)	Linear regression	R <sup>2</sup>
No. of suckled teats	$y = 2.95 + 0.02 x$	0.23
Rel. entrance of the first suckled teat	$y = 0.72 - 0.01 x$	0.02
Rel. entrance of the second suckled teat	$y = 11.66 - 0.18 x$	0.15
Rel. entrance of the third suckled teat	$y = 22.64 - 0.33 x$	0.27
Rel. entrance of the fourth suckled teat	$y = 31.17 - 0.38 x$	0.25
Uniformity	$y = 53.55 + 0.63 x$	0.40
No. of bouts	$y = 25.52 + 1.96 x$	0.55
Average bout	$y = 10.61 - 0.10 x$	0.24
Rel. no. of bout-teat-repetitions	$y = 35.86 - 0.56 x$	0.30
Meal length	$y = 421.95 + 4.27 x$	0.15
Meal-bout-relationship	$y = 18.63 - 0.22 x$	0.21
Longest bout	$y = 30.67 - 0.11 x$	0.02

Table 5

Linear regression with day *pp* as independent variable (x) for dairy breed (Lineare Regressionen mit Tag *pp* als unabhängige Variable bei Milchrindern)

Variable (y)	Linear regression	R <sup>2</sup>
No. of suckled teats	$y = 1.87 + 0.03 x$	0.48
Rel. entrance of the first suckled teat	$y = 2.06 - 0.03 x$	0.09
Rel. entrance of the second suckled teat	$y = 37.76 - 0.48 x$	0.32
Rel. entrance of the third suckled teat	$y = 59.68 - 0.63 x$	0.43
Rel. entrance of the fourth suckled teat	$y = 66.66 - 0.56 x$	0.35
Uniformity	$y = 16.98 + 0.81 x$	0.61
No. of bouts	$y = 13.26 + 0.55 x$	0.56
Average bout	$y = 19.54 - 0.15 x$	0.29
Rel. no. of bout-teat-repetitions	$y = 79.19 - 1.01 x$	0.73
Meal length	$y = 372.66 + 2.53 x$	0.17
Meal-bout-relationship	$y = 25.00 - 0.22 x$	0.41
Longest bout	$y = 58.74 - 0.07 x$	0.003

from the beginning of the meal at the first time. With increasing day *pp* suckling at such an additional teat started earlier in a meal. (iv) The same developments could be observed in both breeds, however, later in the dairy breed. The differences between



breeds concerning average bout indicate a close correlation between average bout and milk yield. Table 6 gives the results of analysis of variance of the complete meal data including the effects breed, cow (breed), and average bout as regression.

Table 7 gives the regression equations across the breeds with average bout as independent variable.

## Discussion

### Day *pp* as main effect and differences between breeds

The differences between breeds can be quantified with the help of the regression equations in Tables 4 and 5: All four teats would be suckled from day 52 in the beef and from day 71 *pp* onwards in the dairy breed and a very high uniformity (about 90) of suckling activities between the teats would be reached at about day 58 and 90 *pp* respectively.

Table 6

Main results of analysis of variance for the model breed, cow (breed), and average bout as regression (Hauptresultate der Varianzanalyse mit den Varianzquellen Rasse, Mutter (Rasse) und durchschnittliche Bout-Länge als Regression)

Variable	Pr > F for model	R <sup>2</sup>	Pr > F for breed	Pr > F for cow (breed)	Pr > F for average bout
No. of suckled teats	<0.0001	0.450	n.s.	0.0003	<0.0001
Relative entrance of the first suckled teat	0.0292	0.157	n.s.	n.s.	0.0006
Relative entrance of the second suckled teat	<0.0001	0.307	n.s.(0.0889)	n.s.	<0.0001
Relative entrance of the third suckled teat	<0.0001	0.449	n.s.	n.s.	<0.0001
Relative entrance of the fourth suckled teat	<0.0001	0.488	n.s.	n.s.	<0.0001
Uniformity	<0.0001	0.554	n.s.	0.0390	<0.0001
No. of bouts	<0.0001	0.386	n.s.	0.0396	<0.0001
Relative no. of bout-teat-repetitions	<0.0001	0.490	n.s.	0.0019	<0.0001
Meal length	0.0268	0.159	n.s.	0.0496	0.0041
Meal-bout-relationship	<0.0001	0.686	0.0002	0.0047	<0.0001
Longest bout	<0.0001	0.553	<0.0001	0.0013	<0.0001

Table 7

Linear regression with average bout as independent variable (x) (Lineare Regressionen mit durchschnittlicher Bout-Länge als Unabhängige Variable (x))

Variable (y)	Linear regression	R <sup>2</sup>
No. of suckled teats	y = 3.96 - 0.08 x	0.30
Relative entrance of the first suckled teat	y = - 0.11 + 0.08 x	0.06
Relative entrance of the second suckled teat	y = - 1.54 + 1.38 x	0.21
Relative entrance of the third suckled teat	y = - 2.26 + 2.52 x	0.36
Relative entrance of the fourth suckled teat	y = 3.90 + 2.63 x	0.32
Uniformity	y = 87.46 - 2.8 x	0.47
No. of bouts	y = 92.60 - 3.88 x	0.28
Relative no. of bout-teat-repetitions	y = 4.98 + 2.62 x	0.36
Meal length	y = 536.68 - 4.89 x	0.02
Meal-bout-relationship	y = 2.24 + 1.23 x	0.60
Longest bout	y = 9.2 + 2.79 x	0.41

After day 52 or 90 *pp* mentioned above the description of an average meal would be: (i) The first and second teat in the dairy and the first three teats in the beef breed would be addressed as fast as possible at the beginning of a meal. Only for the fourth teat a small delay could be seen (about 9 % of meal in the beef, respectively 16 % in the dairy breed). (ii) A meal would include 139 (beef) and 63 bouts (dairy) with an average length of about 4.8 or 6 seconds respectively. (iii) No bout would be repeated

at the same teat immediately, likewise almost no none-suckling activities would be seen in either breed. (iv) A meal would last for about 11 (beef) and 10 (dairy) minutes, (v) but the longest bout would differ substantially with about 24 second in the beef and 52.5 seconds in the dairy breed.

An explanation for these differences between the breeds could be, that the initial over-secretion of the mother (MAYNTZ and SENDER, 2006) is bigger in the dairy breed and that therefore different periods of time were needed to level out secretion of the mother and need of the offspring.

That hypothesis demands that the mechanisms acting before levelling out were similar in both breeds. Assuming that this hypothesis cannot be falsified, we would see the same processes in e.g., wild species but during a much shorter period of time compared to the beef breed reported here.

### **A new approach: Average bout as main effect**

The hypothesis with different levels of initial over-secretion together with spontaneous impressions from the meal graphs led to the idea to replace day *pp* by milk yield as main effect. Average bout instead of milk yield had to be used because recording of milk yield had not been feasible. It was striking that the significance for the effect breed decreased, when average bout instead of day *pp* was used in an otherwise similar model (Table 6). Comparing Tables 1 and 6 shows that breed changed from a very powerful into an almost negligible effect in the second analysis.

Supposing that milk yield cannot be rejected in future tests as common factor between breeds, precise predictions are possible on the basis of that hypothesis. (i) All variables describing the end of ontogeny of suckling behaviour, especially the number of suckled teats, the uniformity of relative shares of suckled teats and the relative number of bout-teat-repetitions would reach the final stage earlier the lower the milk yield of the mother and *vice versa*. This alternative hypothesis is supported by the results of PASSILLÉ and RUSHEN (2006). (ii) Within that hypothesis it would not matter, why the milk yield of a specific mother is low or high: wild life or husbandry, first or later lactations (STEINHARDT and THIELSCHER, 2005), good or poor energy supply etc. All would influence the length and course of the ontogeny of suckling behaviour of the actual offspring via their effect on the actual milk yield of the mother. This hypothesis could contribute to further diminishing the black box between genetic potential, behaviour and phenotypic outcome of lactation (STEINHARDT and THIELSCHER, 2004; STEINHARDT and THIELSCHER, 2005). However, contributions of behaviour to different phenotypic outcome of lactation due to sex and/or birth weight of the calf could be explained by including the FIL-hypotheses (WILDE et al., 1988). (For further arguments see MAYNTZ and SENDER, 2006).

With the help of the regressions in table 7 we could describe the quantitative course of ontogeny of suckling behaviour in cattle across the breeds and individuals in the following way: The shorter the average bout, (i) the higher the number of suckled teat; however, 4 teats would hardly be suckled, instead the maximum would be about 3.95; (ii) the higher the uniformity of suckling activities between the teats; however, it would reach only a maximum of 87; (iii) the higher the number of bouts; however, almost never higher than 90; (iv) the lower the relative number of bout repetitions, however, immediate bout repetition at the same teat would not disappear completely; (v) the longer the meal; however, not longer than about nine minutes; (vi) the less not-

suckling activities and (vii) the shorter the longest bout; however, not longer than about 12 seconds.

Most of the quantifications above agreed well with the data analysed here, the third and the fifth, however, less. Probably these discrepancies resulted from: (i) the size of the data set analysed here might have been too small to fit second degree regressions; (ii) average bout is only an indirect measure for milk yield; (iii) an offspring might need a minimum number of sucking movements to realise that the corresponding cistern is empty, resulting in that a bout cannot fall below a lower threshold; (iv) the impression of the degree of filling of a cistern might also be subjected to experience and memory and therefore might not be based on the actual status of the cistern exclusively and (v) a minor part of variance might be effected by day *pp*.

### General aspects

The study presented here allows to hypothesise that species, which share the anatomical and endocrinological characteristics listed below, show the same principal course of ontogeny of suckling behaviour as *Bos taurus* because they all have to reduce the initial over-secretion of the mother (MAYNTZ and SENNER, 2006) without drying of single mammary glands. The characteristics mentioned above are: (i) the need of a pre-stimulation (ZAKS, 1962) before ejection of milk, (ii) a relative middle size milk duct area (CROSS, 1977), where the milk is not under capillarity (referred to as "cistern" in the following), the volume of which is 20 to 40 % of the total milk duct volume (BRUCKMAIER et al., 1994; DEWHURST and KNIGHT, 1994), (iii) the cistern being more of cavern type (WIRZ, 1913), (iv) a relationship between number of offspring and lactating mammary glands greater than one and (v) the number of active glands being constant within and between lactations even if the number of nursed offspring varies. Keeping several glands lactating demands that offspring suckle from several glands regularly. The cavern-like cistern weakens the relation between the inflow into that cistern and the flow from the alveoli and in all those small ducts, where the milk is under capillarity resulting from squeezing (true alveoli alone) respectively relaxing (small ducts, BRUCKMAIER, 2005). Only milk in the cistern is available for harvest. An outflow from the cistern larger than the inflow into it makes waiting for refilling of a cistern profitable for offspring (MAYNTZ and COSTA, 1998). Waiting for refilling a single cistern is optimised when several cisterns are emptied in a sequence. Several mammalian taxa share these characteristics.

Recording average bouts could be feasible in husbandry and in zoos. In zoos it would be much more worthwhile than the conventionally recorded "lock on-" (e.g., TAVOLGA and ESSAPIAN, 1957; MCBRIDE and KRITZLER, 1951) or "nipple-attachment-time" (e.g., MENDEL and PAUL, 1989), because its close correlation to individual milk yield. Average bout would also help to differ better between nutritive and non-nutritive phases in a meal (e.g., WOLFF, 1968; LIDFORS et al., 1994; TANAKA, 1997) and thus to estimate milk supply of mammalian offspring in human care better. It remains a challenge to define "milk yield" in relation to "need" to make full use of that approach.

Analysing the ontogeny of suckling behaviour under the aspect of milk yield revealed another aspect. Cattle offspring were apparently born with a very simple rule: "look for milk, where you found it last". The development of every variable describing the use of teats did not reject that hypothesis. A calf started to address other teats not

before the amount of milk harvested from the first addressed ones fell undoubtedly short. The strength of that rule can be judged from regression equations for relative number of bout-teat-repetitions in tables 4, 5 and 7. Starting from frequent repetitions, it takes a considerable number of days *pp* (64 in the beef and 78 in the milk breed) to get almost rid of these often vain attempts to get milk from "where you found it last". The big teacher in nature, i.e., shortage of resources, made a complicated behavioural pattern eventually emerge from a simple behavioural rule.

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