

Frequency and Heritability of Supernumerary Teats in German Simmental and German Brown Swiss Cows

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ABSTRACT

The incidence of supernumerary teats has been recorded in 179,793 German Simmental and 37,460 German Brown Swiss cows. Data were collected from first-crop daughters of test bulls from 1987 to 1998. The number of sires was 4298 and 1039, respectively. The average frequency of affected animals was 44.3% in German Simmental and 31.2% in German Brown Swiss. A significant yet small effect was found for herd-book membership (yes/no) and, in the Simmental data only, for inspector. The impact of year of birth and year of inspection was also significant, and more important, reflected a decrease of the population averages with time. Surprisingly, the incidence of supernumerary teats increased significantly with the parity number of dams in both breeds. A Bayesian threshold animal model approach was used to estimate the heritability of the occurrence of supernumerary teats. The posterior mean for the heritability was $h^2 = 0.45$ in German Simmental and $h^2 = 0.43$ in Brown Swiss, with standard errors of 0.01 and 0.03, respectively. Ranks of sires obtained from threshold and linear models showed a rank correlation of roughly 0.8 in both breeds. For a sound identification of the worst sires, a threshold model is recommended.

(Key words: hyperthelia, polythelia, hypermastia, extra teats, *Bos taurus*)

Abbreviation key: SNT = supernumerary teats.

INTRODUCTION

Supernumerary teats (hyperthelia, SNT) are an undesired and heritable trait in dairy cattle, particularly if supernumerary mammary glands are also present (hypermastia). This is due to aesthetic reasons, possible disturbances of machine milking, and because supernumerary mammary glands may act as a reserve for bacteria threatening udder health (Steiger and Grünen-

felder, 1988; Frerking and Lotthammer, 1981; Boodstein, 1972; Dragan, 1971; Schönberg, 1966).

SNT have been observed in various mammalian species. In humans (Urbani and Betti, 1996), sheep (Vainikainen, 1945), guinea pigs (Goertzen and Ibsen, 1951), and mice (Howard and Gusterson, 2000), a simple dominant/recessive inheritance has been found. In these species, special families, pedigrees, or lines and their crosses have been investigated. In cattle, larger samples that are more likely to exhibit greater variability have been analyzed. Literature reports show a frequency range for SNT in cattle of 15 to 69% (Juler, 1927; Ivanova, 1928; Johansson, 1957; Sommer et al., 1961; Dragan, 1971; Stavikova et al., 1982; Sieber, 1986; Lode, 1990). Clear differences between breeds were observable. For example, a frequency of 15% was found in German Holstein (Brka et al., 2000a) and 69% in German Simmental (Sommer et al., 1961). These differences suggest that SNT is heritable. Several contradictory proposals have been made for the mode of inheritance in cattle (Johansson, 1957; Thierley, 1968). From a maximum-likelihood analysis of 27 half-sib families with known phenotype of the sire, simple recessive or dominant inheritance was excluded (Brka et al., 2000b). From the results of this study, it was concluded that the inheritance in cattle either involves a more complex penetrance pattern or is oligo- or polygenic. Published estimates for the heritability of SNT were between 0.09 and 0.63 (recently reviewed by Brka et al., 2000a). With the exception of Sieber (1986), who analyzed a dataset of 26,823 German Simmental cows, only comparatively small datasets (200 to 1500 animals) were available. Threshold models are most appropriate for the genetic analysis of binary traits (Gianola, 1982), but this method has been used only once in the analysis of a small SNT dataset of 818 Holstein animals (Brka et al., 2000a).

This paper reports analyses of large datasets from two breeds, German Simmental and German Brown Swiss. First, the impact of several environmental factors on the occurrence of supernumerary teats was investigated. Second, a Bayesian estimation of the threshold model heritability for supernumerary teats was performed. Third, these values were compared with their

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Table 1. Structure of supernumerary teat datasets used for genetic analysis.

	Simmental	Brown Swiss
No. of animals	179,793	37,460
No. of sires	4298	1039
Mean number of progeny per sire	41.8 (1 to 65)	36.2 (1 to 100)
No. of animals in pedigree	532,665	163,729
No. of inspectors	17	5
Mean number of animals per inspector	10,576	7496
Years of birth	1984 to 1996	1984 to 1998
Years of inspection	1987 to 1999	1987 to 1999
Parity of dam	1 to 7, ≥8	1 to 7, ≥8

linear model analogues. In addition, the differences in the ranking of sires using linear and threshold models were investigated.

MATERIALS AND METHODS

Data and Animals

Two datasets with observations regarding the occurrence of supernumerary teats in German (dual-purpose) Simmental and German Brown Swiss dairy cows were provided by the Bavarian State Institute for Animal Production and the Ministry of Agriculture of the State of Baden-Württemberg. Simmental cows were born between 1984 and 1996, and Brown Swiss cows were born between 1984 and 1998. Data were collected as part of the examination of first-crop daughters of test bulls for exterior traits. Only animals that had been judged by inspectors with a minimum of 500 observations were retained for analysis (17 inspectors in Simmental and five inspectors in Brown Swiss). The proportion of herdbook cows was 82% in Brown Swiss and 69% in Simmental. Parity of dam varied from 1 to 15, and for analysis, parities >8 were grouped together.

For the description of udder-clearness, grades from 1 to 9 were used. Grade 9 was given for a clear udder and grades 1 to 8 for different locations and types of SNT. However, SNT present at the rear udder (grades 7 and 8) was observed in >90% of all cases. A binary definition of the trait was used with a value of 1 for affected animals (grades 1 to 8) and a value of 0 for unaffected animals (grade 9). After editing, 179,793 Simmental daughters from 4298 sires (41.8 daughters/sire) and 37,460 Brown Swiss daughters from 1039 sires (36.2 daughters/sire) were available for analysis. The structure of both datasets is summarized in Table 1.

STATISTICAL ANALYSIS

The impact of five systematic environmental effects was investigated in a fixed-effects analysis, ignoring random genetic effects: year of inspection, year of birth, inspector, herdbook membership of the cow (yes/no),

and parity of the dam. This analysis was done with a generalized linear model with probit link-function using the GENMOD procedure of the SAS package (SAS, 1992) and likelihood-ratio tests. Statistical testing of each factor was done by removing a particular factor from the model and comparing the likelihood of the reduced model to the likelihood of the full model.

Variance components were estimated with an animal threshold model with two categories (Dempster and Lerner, 1950; Gianola, 1982). This model included all the fixed effects mentioned above plus a random genetic animal effect (breeding value):

$$\pi_{ijklmn} = \Phi (I_i + G_j + C_k + B_l + K_m + a_n), \quad [1]$$

where

π_{ijklmn} is the expected percentage of animals with SNT,

Φ is the cumulative probability function of the standard normal distribution,

I_i is the effect of the inspector i ,

G_j is the effect of the year of birth j ,

C_k is the effect of the year of inspection k ,

B_l is the effect of the herdbook membership (yes/no),

K_m is the effect of the parity of the dam ($m = 1$ to 8),

a_n is the breeding value of animal n .

The size of the pedigree file was 532,665 animals for Simmental and 163,729 animals for Brown Swiss.

A Bayesian approach was used with flat priors for fixed effects and variance components, and the multivariate normal prior distribution $N(0, A\sigma_a^2)$ for the breeding values. Posterior distributions of the additive genetic variance and the heritability for the liability for SNT were determined with the Gibbs sampling algorithm implemented in the LMMG_TH program, a threshold model derivative of LMMG (Reinsch, 1996). Mean values of the posterior distribution are reported as parameter estimates.

For each dataset, 120,000 cycles were generated, and the results from each cycle were retained. Convergence was determined by visual inspection. The results of the first 20,000 iterations were discarded (burn-in plus a safety margin), and the results of the remaining 100,000 rounds were used to calculate the estimates for heritability and additive genetic variance. The effective sample size of the estimates was determined by time-series methodology (Sørensen et al., 1995). For comparison, Bayesian estimates from the equivalent linear models were also calculated using LMMG software (Reinsch, 1996). The number of iterations and post-Gibbs analyses were identical to the threshold model analyses.

To compare the ranking of sires from linear and threshold models, breeding values with linear animal

models and the PEST program (Groeneveld, 1990) were first estimated. Second, for threshold models, posterior means for the breeding values of sires were obtained by Gibbs sampling with a fixed heritability. These posterior means were taken as breeding values from threshold models. In all cases, heritabilities were estimated as before.

RESULTS AND DISCUSSION

The frequency of SNT was 44.3% in German Simmental and 31.2% in German Brown Swiss. These frequencies are relatively high when compared to values found for other breeds such as Holsteins (15%, Brka et al., 2000a; 20%, Stojanovic, 1971). For Simmental, however, the literature reports even higher values (69%, Sommer et al., 1961; 61%, Thierley, 1968). The frequency was remarkably higher compared with the 29% proportion of affected animals in the study of Sieber (1986). The frequency in Brown Swiss was clearly lower by > 10%—a difference also found by Sommer et al. (1961). These authors obtained the value of 55.6% in the era before the reimportation of Brown Swiss genetics from the United States.

Likelihood-ratio test statistics and error probabilities for analyses of fixed effects are shown in Table 2. Almost all error probabilities had a magnitude of <0.001, except for the value of the inspector effect in the Brown Swiss dataset with an error probability of 16%. This effect was, however, retained in both models for heritability estimation because of the significance in the Simmental data.

Raw mean differences between inspectors ranged from 2.6 to 16% in Simmental, and may reflect differences

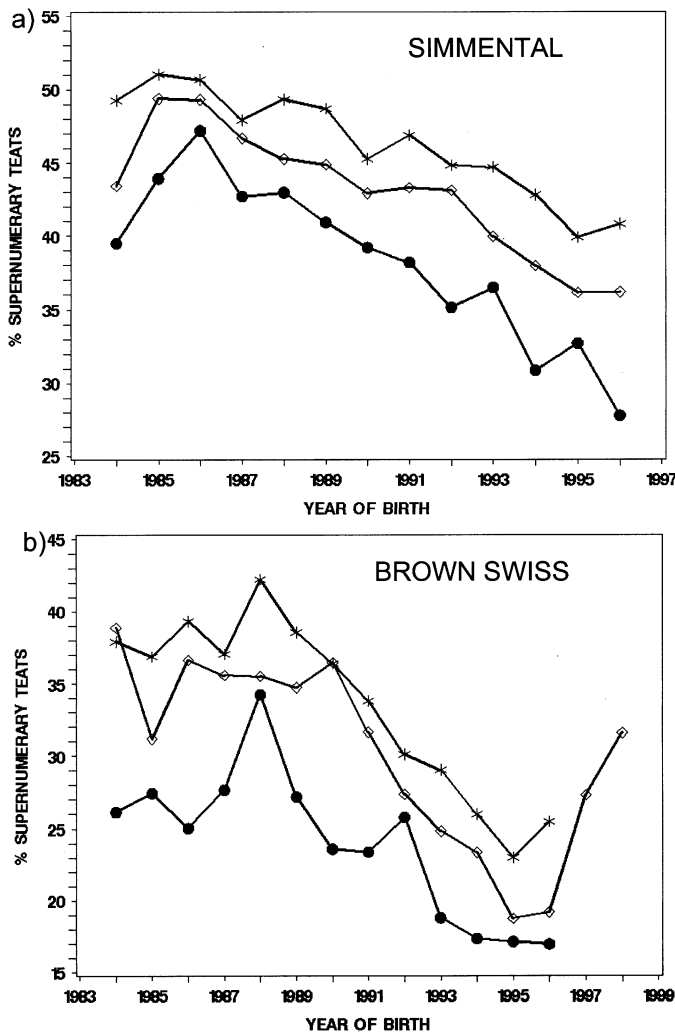


Figure 1. Incidence of supernumerary teats in German Simmental (a) and German Brown Swiss (b) against year of birth. Time trends are shown separately for cows from first (●), second (◇), and higher parities (*).

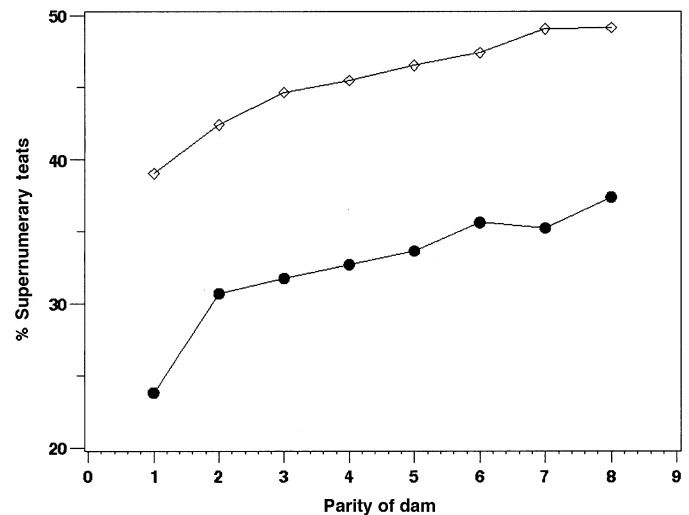


Figure 2. Incidence of supernumerary teats against parity of dam in Brown Swiss (●) and Simmental (◇) cows.

Table 2. Likelihood-ratio test statistic (χ^2) and error probabilities for analyses of fixed effects.

Fixed effects	Simmental			Brown Swiss		
	DF	Test statistic χ^2	Error probability	DF	Test statistic χ^2	Error probability
Inspector	16	583.7742	0.0001	4	6.5497	0.1617
Year of birth	12	52.1510	0.0001	14	39.6474	0.0003
Year of inspection	12	63.2336	0.0001	12	44.4354	0.0001
Herdbook membership	1	58.4658	0.0001	1	7.7826	0.0053
Parity of the dam	7	481.5357	0.0001	7	202.2575	0.0001

between regions rather than differences between inspectors, as each has a certain region as his own area of responsibility.

Herdbook membership was significant in both breeds. The differences between herdbook and nonherdbook cows were, however, small: 2.1% in Simmental (43.6% vs 45.7%) and 0.9% in Brown Swiss (31.0% vs 31.9%). The decrease of roughly 2% of the frequency of SNT in herdbook cows may be due to removal of SNT by surgery on some farms. In earlier years, this practice was uncommon for Simmental breeders, in contrast to many farms with German Holsteins (Thierley, 1968) but may today be practiced in some cases without recognition by inspectors.

A clear time trend was found in both breeds. This time trend is modeled by the effects of year of birth (Figure 1a and b) and year of inspection. The genetic component of this trend is accommodated by the breeding values in the animal model. Reasons for and size of the environmental aspect of this time trend are unclear and should be further investigated. Surprisingly, the parity number of the dams showed a clear impact on the frequency of SNT (Figure 2). An increase of SNT with parity was observed in both breeds. The magnitude of this increase is ~10% from parity 1 to 7, ≥ 8 , and is similar in Simmental and Brown Swiss (Figures 1a and b, and 2).

These differences between parities were constant over time (Figure 1), with more fluctuations in the Brown Swiss data because of smaller sample size.

Posterior means for the differences between parities from the Bayesian analyses, including genetic effects, are given in Table 3, together with standard errors and raw means of the frequency of SNT in different parities. Raw means and Bayesian estimates from both models show a trend of increasing frequency of SNT with parity number. The posterior means for the difference between first- and second-parity daughters was estimated as 5% in the linear model analyses in both Simmental and Brown Swiss, with further increases of only 1 to 2% per calving. The increase from first to second parity is perhaps less surprising, because first-parity cows are immature, and the weight of first-parity calves is known to be lower than the weight of calves from higher parities. This raises the question of whether phenotypic selection in dairy herds partially contributes to the fact that older animals have progeny with more SNT than younger animals. Cows with the worst milk production are culled in each lactation and replaced by young heifers. The proportion of culled animals is roughly 30% in each lactation. Higher parity cows are, thus, more intensively selected due to their own milk performance. Provided that milk production is phenotypically correlated with the incidence of supernumerary teats (high performing cows having a higher incidence), one would not expect an impact of such a selection on the frequency of supernumerary teats in the progeny of the selected dams, because this requires the correlation to be genetic. Genetic differences between dams are, however, accounted for

Table 3. Raw means for the occurrence of supernumerary teats by parity and Bayesian estimates of the effects of parity (posterior means) from linear and threshold models, together with their standard errors (SE).

Parity of the dam	Simmental					Brown Swiss				
	Raw means (%)	Linear model estimates (%)		Threshold model estimates		Raw means (%)	Linear model estimates (%)		Threshold model estimates	
		$\bar{\chi}$	SE	$\bar{\chi}$	SE		$\bar{\chi}$	SE	$\bar{\chi}$	SE
1	39.1	0.0	0.0	0.0	0.0	23.8	0.0	0.0	0.0	0.0
2	42.4	4.9	0.4	17.0	1.6	30.7	4.6	0.7	18.8	2.9
3	44.7	6.8	0.5	23.8	1.7	31.8	6.3	0.8	25.5	3.3
4	45.5	7.5	0.5	26.1	1.8	32.7	6.8	0.9	27.1	3.6
5	46.5	8.3	0.5	28.9	1.9	33.7	7.9	1.0	31.0	4.0
6	47.4	9.1	0.6	31.4	2.2	35.7	9.7	1.1	37.8	4.5
7	49.1	10.5	0.7	35.9	2.5	35.3	8.7	1.4	33.9	5.3
≥ 8	49.2	10.7	0.7	36.9	2.5	37.4	10.5	1.2	40.1	4.7

Table 4. Estimates of additive genetic variance and heritability from threshold models for supernumerary teats with standard errors and effective sample sizes.

Breed		Estimate	Standard error	Effective sample size
Simmental	h^2	0.45	0.012	58.5
	σ^2_{animal}	0.831	0.041	58.4
Brown Swiss	h^2	0.43	0.026	82.6
	σ^2_{animal}	0.759	0.082	84.1

in the animal model. It is assumed that size and maturity of the mother changes the conditions for prenatal growth so that the likelihood of the occurrence of supernumerary teats increases with the age of the dam. It should be noted that in the data used for this investigation, almost no dams with more than one offspring with a phenotypic record were present. It is, however, not possible to rule out an existing bias of the estimated parity effects due to culling on a correlated trait such as milk production, because this would require a bivariate analysis including that correlated trait.

Heritabilities of 45% in Simmental (S.E. = 1.2%) and 43% in Brown Swiss (S.E. = 2.6%) were estimated. Posterior means for the additive genetic variance were 0.831 in Simmental (S.E. = 0.04), and 0.759 (S.E. = 0.08) in Brown Swiss. Monte-Carlo errors can be obtained from S.E. and effective sample sizes (Table 4).

As expected, the heritability estimates from linear models were considerably lower. The values were 28% for Simmental (S.E. = 0.008) and 25% for Brown Swiss (S.E. = 0.014). Most heritability estimates for Simmental in the literature are higher than the threshold model estimates reported here; for example, the linear model analysis of Sieber (1986), who found a value of 0.51 for German Simmental. The heritabilities for linear model estimates in the present study are at the lower range of literature values for SNT based on linear models estimates.

Heritability estimates on the (0.1) scale were similar for both breeds even though heritability estimates are known to be frequency-dependent when applying linear models to categorical data (Gianola, 1982). This similarity can, however, be explained by the intermediate level of both average population frequencies. Transforming the linear model heritabilities to the liability scale (Dempster and Lerner, 1950) results in values similar to the reported threshold model estimates.

As mentioned in the introduction, a simple dominant-recessive inheritance has been found in other species, but could not be confirmed in a maximum-likelihood analysis of Simmental half-sib data (Brka et al., 2000b). Assuming single gene inheritance, it was found that the

Table 5. Breeding value ranks for 10 worst sires (worst sire, rank = 1).

Threshold model	Simmental linear model	Brown Swiss linear model
1	1	50
2	31	16
3	3	9
4	333	12
5	257	18
6	304	83
7	62	14
8	21	557
9	492	41
10	30	13

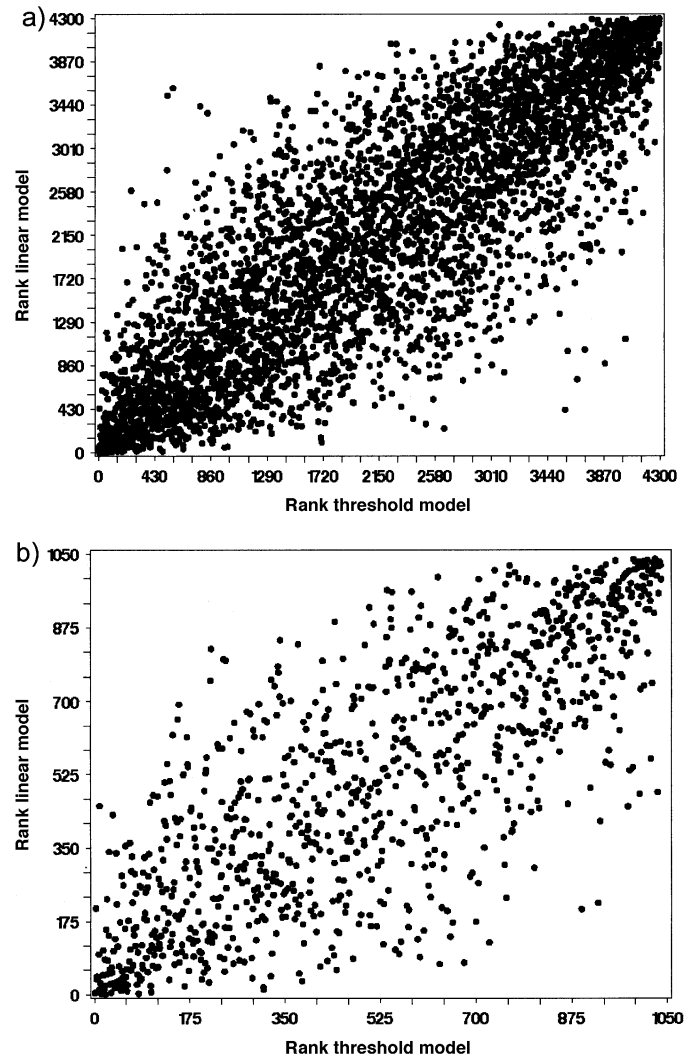


Figure 3. Bivariate plots of sire rankings from threshold and linear models from Simmental (a) and Brown Swiss (b).

penetrance pattern must be more complex. The increase of the incidence of SNT with parity number of the dam increases the need to reexamine the question of the existence of a major gene for SNT in cattle by using models allowing for an age-of-dam effect on the penetrances of one or several genotypes. An ideal dataset would comprise phenotypes of both parents and their progeny. Alternatively, such major genes could be identified in a linkage study.

Rank correlations between breeding values from linear models and threshold models were 0.85 in Simmental and 0.79 in Brown Swiss. Bivariate plots of sire rankings are shown in Figure 3.

The ranking of the 10 worst sires in both breeds shows that these values are not acceptable (Table 5): Both in Simmental and Brown Swiss, the largest rank difference between the linear model and the threshold model is roughly 500 among the 10 worst sires. As only limited selection pressure can be placed on SNT because of the economic importance of other traits, it is most important to identify the worst sires accurately. Since linear models can only be viewed as approximations in comparison to threshold models for binary data (Gianola, 1982), we recommend the use of a threshold model for sire evaluation. The role of the occurrence of SNT and supernumerary mammary glands as a component of udder health and udder conformation should be further investigated, as well as its importance relative to other traits, especially in breeds with a high frequency.

CONCLUSIONS

The frequency of supernumerary teats showed a clear decreasing time-trend (year of birth, year of inspection) both in German Simmental and German Brown Swiss. The incidence increased in offspring of higher parity dams. The threshold model heritability was 0.45 in Simmental and 0.43 in Brown Swiss. For the sound identification of the worst sires, a threshold model is recommended.

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