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Effects of marked chromosome sections on milk performance in cattle

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Summary. The investigations of paternal half sibs start with the assumption that the transfer of an allele from a father to an offspring also indicates the inheritance of a distinct section of two homologous chromosomes from the father concerned. With the help of 20 gene systems, the transfers of single chromosome sections were marked and tested with regard to influences on milk performance traits. 1,457 German Friesian cattle, registered as daughters of three sires, were used. Some of the chromosome sections showed significant effects on the traits considered. Since especially those chromosomes which bear genes for milk proteins were involved, it was assumed that groups of linked loci influence the genetic variance of milk production. Possibilities for applying the results to the practical breeding situation and their significance are discussed.

Key words: Marker genes – Cattle – Genetic polymorphisms – Milk performance

Introduction

Several studies during the last two decades have been reported on statistically significant correlations between genetic polymorphic criteria and milk production traits (reviews, see Mitscherlich 1965; Zwiauer 1980). However, contradictory results and difficulties in their interpretation have prevented a fruitful development of that field of research. Therefore, Geldermann (1975, 1976) recommended an evaluation within groups of paternal half sibs for studies in cattle. As illustrated in Fig. 1, alleles then mark corresponding regions of homologous chromosomes and are in this sense used as "marker" genes, because offspring receive in addition to a definite allele ("allele transfer") a distinct chromosome section out of the two possible homologous paternal partners. In the present investigation genetic polymorphisms (blood group factors, blood and milk proteins, blood enzymes) served as marker genes, which were registered within groups of daughters from three sires together with the values of milk performance. The goal of the study was to test whether the allele transfer from father to daughters, and by this, the transfer of a marked chromosome section was connected with effects on milk production.

Material and methods

The investigations included 1,457 German Friesian ("Deutsche Schwarzbunte") cows from F.R.G. (Lower Saxony). Each cow was registered as a daughter of one of three A.I. bulls. In addition, the mothers of 156 of the cows could be evaluated.

Milk and blood samples were collected in 1978 and 1979 from January to April. During these periods, each of the daughters used was at the beginning of her first lactation and was chosen according to the following criteria:

- first calving age between 22 and 29 months,
- calving season between October and December,
- herd with milk-performance controls, more than 10 complete lactations per year, and average milk yields between 5,000 and 6,000 kg per year.

Usually only one daughter was considered per farm and father (for 83.1% of the daughters), in the remaining cases, two daughters.

Data of milk performance during the first lactations were corrected for first calving age by the computer centre responsible for the evaluation of breeding values (Lederer and Buthmann 1982). Afterwards the data of milk yield, fat content and fat yield were corrected for average herd production. In one computation, only cows with complete 305-day-performances were considered; in a second computation data from cows with shorter lactation intervals were also gathered and projected to 305-day-intervals according to Pabst (1975). The

Table 1. Details of the investigated animals

Sire no.	1	2	3
Estimation of breeding values			
Conditions of estimation:			
No. of daughters	230	157	218
No. of farms	189	134	182
Breeding values:			
Milk yield (kg)	+714	+1210	+637
Milk fat content (%)	+ 0.04	+ 0.05	+ 0.44
Milk fat yield (kg)	+ 30	+ 50	+ 47
No. of marker gene tested daughters:			
Total	509	476	472
Not excluded after parentage control	434	424	419
With additionally available lactation data from the computing center[a]	387 (324)	377 (281)	378 (267)
Milk performance (of those daughters not being excluded after parentage control)[b]			
Milk yield (kg)	5542±876	5869±851	5562±899
Milk fat content (%)	4.10± 0.36	4.06± 0.32	4.29± 0.38
Milk fat yield (kg)	227± 38	238± 38	238± 41

[a] In brackets: no. of animals with complete 305-day-performance
[b] 305-days and projected performances of the first lactation

Table 2. Utilized marker genes

Genetic polymorphic criteria	Descriptions concerning the breed German Friesian
Blood group systems:	Tolle (1960)
A, B, C, F, J, L, M, S, Z, R′	Köster (1983)
Blood proteins and enzymes:	Geldermann (1970)
Transferrins (Tf)	Thinnes et al. (1976)
Postalbumins (Pa)	Gebicke-Härter and
Posttransferrins (Ptf)	Geldermann (1976)
Amylases (Am_1, Am_2)	
NAD^+-dependent Malat-Dehydrogenases (mMOR)	
Milk proteins:	Kammer (1973)
β-Lactoglobulins (β-Lg)	Roth (1982)
α_{s1}-Caseins (α_{s1}-Cn)	
β-Caseins (β-Cn)	
$\varkappa$-Caseins ($\varkappa$-Cn)	

results of the second evaluation are shown in Tables 6–8. Details of the fathers and the daughters are given in Table 1.

Blood samples were obtained from cows and bulls. In addition, milk samples were collected from all cows. The methods described by Kammer (1973) and Thinnes et al. (1976) were used for the fractionation of samples. Afterwards, the genetic polymorphic criteria, as summarized in Table 2, were tested and considered as systems. They are associated with single gene loci, whereby, however, the phenogroups of complex blood group systems are controlled by series of closely linked loci (Sellei and Rendel 1968; Bouw and Fiorentini 1970). In these cases, each of the phenogroups are products of distinct haplotypes, although they are referred to as alleles in this paper. With the help of these criteria, paternity controls were executed and daughters of exclusable parentage rejected from the material (Table 1).

An allele transfer could only be traced for a sire heterozygous for the gene locus concerned and – in cases where the mother could not be determined – for a daughter possessing a genotype different from her father. Table 3 gives the formulae to calculate the expected values of the traceable allele transfers, by taking into account an equally numerous inheritance of both alleles from a paternal gene locus. Using these formulae, the detectable allele transfers depend on the genotypes of the mothers. For mothers, who were not investigated, genotype frequencies regarding systems with codominant alleles were estimated from the genotype frequencies of daughters on the basis of a random transfer of alleles from the father.

Within each sire's progeny the milk performances of daughters, which had inherited a distinct allele and therefore also a distinct chromosome section from the father were compared with those of daughters which had received the other allele of the gene locus concerned (Fig. 1). The group of daughters with indeterminable allele transfers was considered only in cases in which the detection rate of transfers of one allele reached less than 10% of the detection rate of the other allele. This daughter group was then added to the group of daughters that only had few detectable transfers.

First, each gene locus was evaluated separately by comparing the two daughter groups having the detectable transfer of allele 1 and 2 (group 1 and 2, resp.) of the father. In addition, the allele transfers of the linked casein gene loci were considered collectively, so that group 1 (2) consisted of those animals with at least one detectable allele transfer of the father's homologous chromosome 1 (2).

Comparisons were executed by using the χ^2- or the t-test.

Table 3. Expected frequencies for the detection of allele transfers at a gene locus assuming genetic equilibrium in the mother population

No. of alleles	n
Allele frequencies within the mother population	$P_1, \ldots, p_n$
Genotype of the father	$A_i A_j \quad (i \neq j)$
Expected frequencies of detectable allele transfers of allele A_i	
Without considering the mothers	$\frac{1}{2} p_i^2 + \frac{1}{4} \sum_{l \neq i}^{n} 2 p_i p_l + \frac{1}{4} \sum_{k \neq i,j}^{n} \left(\sum_{l=1}^{n} 2 p_k p_l \right) = \frac{1}{2} p_i + \frac{1}{2} (1 - p_i - p_j) = \frac{1}{2} (1 - p_j)$
With known mother's genotypes	$\frac{1}{2} \sum_{k=1}^{n} p_k^2 + \frac{1}{2} \sum_{\substack{(k,l) \neq (i,j) \\ k \neq l}}^{n} (2 p_k p_l) + \frac{1}{2} p_i p_j = \frac{1}{2} (1 - p_i p_j)$

Table 4. Allele transfers in the daughter groups for systems with codominant inheritance

Sire no.	1				2				3			
No. of daughters	434 (39)[a]				424 (28)[a]				419 (19)[a]			
	Allele transfers				Allele transfers				Allele transfers			
System	Allele	Obtained	Expected	P	Allele	Obtained	Expected	P	Allele	Obtained	Expected	P
	F	184	184.0									
F	V	43	47.4									
	?	207	202.6									
	A	85	84.9									
Pa	B	141	142.7									
	?	208	206.4									
					D_1	112	110.4		D_1	120	126.2	
Tf					A	192	198.4		A	166	176.2	
					?	120	115.2		?	133	116.6	
					A	119	116.8		A	113	117.7	
Ptf					B	101	102.3		B	113	104.1	
					?	204	204.9		?	193	197.2	
	B	100	106.2		B	96	106.4					
Am_1	C	121	129.4		C	104	116.7					
	?	213	198.4		?	224	200.9					
	A	93	92.1		A	96	88.1					
β-Lg	B	133	135.1		B	118	131.2					
	?	208	206.8		?	210	204.7					
					B	234	205.4					
α_{s1}-Cn					C	20	19.8	< 0.05				
					?	170	198.9					
	A_1	163	154.5		A_1	155	149.9		A_1	141	150.2	
β-Cn	A_2	83	77.2		A_2	83	75.1		A_2	69	75.5	
	?	188	202.3		?	186	199.0		?	209	193.3	

[a] In brackets: no. of marker gene tested mothers taken into account to calculate the expected values

?: Groups with not detectable allele transfers

Table 5. Allele transfers in the daughter groups for open and complex blood group systems

Sire no.		1		2		3	
No. of daughters		434		424		419	
		Allele transfers		Allele transfers		Allele transfers	
System	Allele no.	Allele	Obtained	Allele	Obtained	Allele	Obtained
	1	A_1D	13	A_1D	15	A_1DH	15
A	2	D	186	–	206	D	173
	?		235		203		231
	1	BO_1Y_2I''	208	BI''	223		
B	2	P_2I''	219	$O_1Y_2E_3'G'G''I''$	152		
	?		7		49		
	1	X_2	11	C_1ER_2	211	E	187
C	2	–	1	X_2L'	198	X_1	133
	?		422		15		99
	1	J	10	J	3		
J	2	–	143	–	159		
	?		281		262		
	1					L	16
L	2					–	181
	?						222
	1					M	23
M	2					–	185
	?						211
	1	H'	2	H'	208	H'	4
S	2	–	75	H'UH''	10	–	81
	?		357		206		334
	1	Z	6				
Z	2	–	142				
	?		286				

?: Groups with not detectable allele transfers

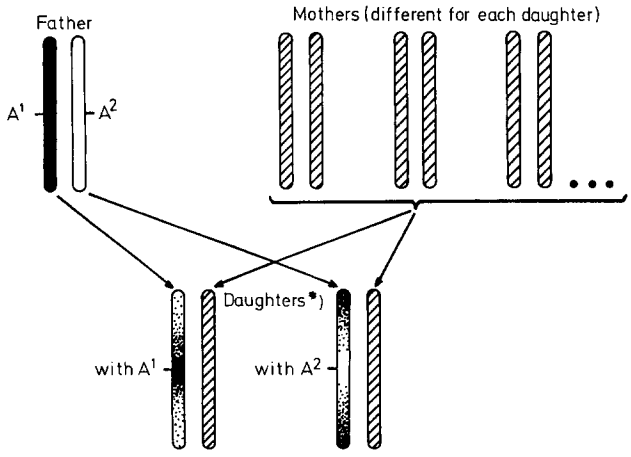

Fig. 1. Principle of the investigations illustrated on a chromosome with alleles 1 and 2 at a marker gene A. * Arrangement of genetic material in the investigated chromosome averaged over many individuals

Results

Numbers of detectable allele transfers are given in Tables 4 and 5. For heterozygous sires and gene loci with codominant inheritance, the expected detections of allele transfers were determined by assuming an equal probability for the transfer of the two different alleles. By comparing the expected with the obtained values, a significant difference arose for daughters of sire no. 2 regarding the α_{s1}-caseins for which more transfers of the allele B occurred than expected.

Regarding the inheritance of alleles of two gene loci simultaneously, the linkage between the loci of α_{s1}- and β-caseins could be verified by the offspring of sire no. 2. The map units amounted to 10 Morgan; the alleles α_{s1}-Cn^B and β-Cn^A1 were situated on one chromosome, and the alleles α_{s1}-Cn^C and β-Cn^A2 on the other. In the case of an equal number of transfers of both homolo-

gous chromosomes, transfers of chromosomes with alleles α_{s1}-Cn^B and β-Cn^A1 occurred more frequently than expected.

Tables 6–8 show the relationship between allele transfers and milk performance within daughter groups of each sire.

In the daughter group of sire no. 1, transfers of postalbumin alleles affected milk yield. Allele transfers on the Am_1 locus which were differentiable for daughters of the sires no. 1 and no. 2 caused effects on the milk fat content (significant only for daughters of sire no. 1).

Considerable effects on milk production were measured in relation to allele transfers of the milk protein polymorphisms. Transfers of β-lactoglobulin alleles could be identified for the daughters of sires no. 1 and no. 2. In both daughter groups the effects on the milk production were similar and affected milk yield and milk fat content. Allele transfers of the α_{s1}-caseins could be examined only for the daughters of sire no. 2; they related to milk yield and milk fat yield.

Among the blood group systems, demonstrations of allele transfers in the C system were possible for daughters of sires no. 2 and 3. Corresponding effects were found for sire no. 2 on milk yield and milk fat yield. For presenting allele transfers the S system could be used in all three daughter groups. A relationship between those transfers and milk fat yield was recognized among daughters of sire No. 2. For daughters of sire no. 1 allele transfers have been demonstrated for the Z system with corresponding effects on milk fat content.

The closely linked loci of caseins allowed multiple marks of a chromosome section. Only for the daughters of the sire no. 2 could two of these gene loci – α_{s1}-Cn and β-Cn – been used simultaneously (Table 4). After defining the haplotype, the effects on milk performance were proven for the case that at least one of both alleles located on a distinct chromosome had been transferred. Thus, as shown in Table 7, effects were established on milk yield.

Discussion

If suitable test conditions are adhered to, chromosomes can be marked in breeding populations with the help of genetic polymorphisms identified by simple qualitative tests, e.g. blood grouping or electrophoresis. Many studies during the last two decades have been concerned with the demonstration of relationships between

Table 6. Milk performances in daughter groups with different allele transfers from sire no. 1

System	Allele	n	Milk yield (kg)		Milk fat content (%)		Milk fat yield (kg)	
			$\bar{x}\pm s$	P	$\bar{x}\pm s$	P	$\bar{x}\pm s$	P
F	F	166	5547±911		4.13±0.37		228±37	
	V	40	5577±710		4.12±0.34		220±30	
Pa	A	79	5477±812	<0.05	4.10±0.32		224±33	
	B	122	5696±698		4.05±0.31		230±28	
Am_1	B	92	5445±748		4.15±0.35	<0.05	225±32	
	C	107	5546±900		4.05±0.35		223±34	
β-Lg	A	81	5666±806	<0.01	4.06±0.33	<0.01	229±33	
	B	125	5356±706		4.19±0.38		224±29	
β-Cn	A_1	143	5596±711		4.11±0.36		229±30	
	A_2	75	5449±828		4.10±0.34		223±35	
A	1 or ?	222	5481±844		4.13±0.38		225±35	
	2	165	5624±751		4.08±0.31		229±31	
B	1	183	5485±813		4.11±0.34		224±33	
	2	198	5596±814		4.10±0.36		229±34	
J	1 or ?	263	5492±819		4.11±0.35		225±34	
	2	124	5647±790		4.10±0.34		231±33	
S	1 or ?	323	5538±813		4.12±0.34		227±33	
	2	64	5561±815		4.05±0.40		224±34	
Z	1 or ?	266	5538±825		4.14±0.36	<0.05	228±35	
	2	121	5551±786		4.05±0.32		224±29	

Table 7. Milk performances in daughter groups with different allele transfers from sire no. 2

System	Allele	*n*	Milk yield (kg)		Milk fat content (%)		Milk fat yield (kg)	
			$\bar{x}\pm s$	*P*	$\bar{x}\pm s$	*P*	$\bar{x}\pm s$	*P*
Tf	A	169	5818±743		4.05±0.28		235±31	
	D_1	98	5851±697		4.10±0.30		239±30	
Ptf	A	108	5844±763		4.07±0.29		238±33	
	B	88	5912±720		4.07±0.29		241±32	
Am_1	B	84	5900±718		4.03±0.29		237±28	
	C	93	5765±728		4.09±0.33		235±32	
β-Lg	A	81	5973±715	<0.01	3.99±0.34	<0.01	238±31	
	B	105	5709±665		4.15±0.30		237±30	
α_{s1}-Cn	B	204	5974±721	<0.01	4.05±0.30		241±31	<0.05
	C or ?	173	5745±755		4.08±0.27		234±32	
β-Cn	A_1	133	5929±681		4.04±0.29		239±30	
	A_2	75	5791±750		4.09±0.27		236±30	
A	1 or ?	199	5840±768		4.04±0.29		235±32	
	2	178	5902±718		4.09±0.27		241±31	
B	1	198	5825±764		4.05±0.27		235±32	
	2	136	5951±718		4.07±0.30		242±29	
C	1	191	5967±745	<0.01	4.06±0.28		242±32	<0.05
	2	171	5756±724		4.06±0.28		233±31	
J	1 or ?	238	5857±738		4.08±0.29		239±32	
	2	139	5890±758		4.03±0.28		237±31	
S	1	182	5808±755		4.05±0.31		235±31	<0.05
	2 or ?	195	5927±732		4.07±0.26		241±31	
α_{s1}- and β-Cn	B and/or A_1	202	5985±705	<0.05	4.04±0.29		241±31	
	C and/or A_2	77	5778±744		4.09±0.27		235±30	

Table 8. Milk performances in daughter groups with different allele transfers from sire no. 3

System	Allele	*n*	Milk yield (kg)		Milk fat content (%)		Milk fat yield (kg)	
			$\bar{x}\pm s$	*P*	$\bar{x}\pm s$	*P*	$\bar{x}\pm s$	*P*
Tf	A	153	5514±786		4.28±0.34		235±33	
	D_1	103	5631±889		4.28±0.34		241±39	
Ptf	A	104	5656±804		4.27±0.35		241±36	
	B	103	5450±793		4.34±0.34		236±36	
β-Cn	A_1	126	5482±759		4.33±0.37		236±33	
	A_2	61	5655±762		4.29±0.29		242±35	
Å	1 or ?	219	5515±807		4.32±0.35		238±35	
	2	159	5628±801		4.25±0.32		239±35	
C	1	156	5599±833		4.29±0.36		239±35	
	2	125	5512±801		4.30±0.31		237±37	
L	1 or ?	214	5579±862		4.29±0.33		238±35	
	2	164	5541±727		4.30±0.35		238±35	
M	1 or ?	211	5500±781		4.31±0.36		236±37	
	2	167	5640±831		4.28±0.31		240±32	
S	1 or ?	309	5554±828		4.28±0.34		237±36	
	2	69	5600±699		4.36±0.33		243±30	

genetic polymorphic criteria and the inheritance of performance traits (e.g. Mitscherlich et al. 1959; Neimann-Sørensen and Robertson 1961; Brum et al. 1968; Arave et al. 1971; Zwiauer 1980). However, these studies led to contradictory results as some researchers have reported a high correlation between a particular allele or genotype and the multifactorial performance trait in question while others have found little or no degree of correlation at all. Statistical methods employed may account for this. On the one hand, significant differences may have been observed accidentally and, on the other hand, some relations may not become obvious because of the small number of animals used. Above all, it is likely that the effects of marker alleles or genotypes on the control of the observed quantitative feature are only small in relation to other, yet undefined gene loci.

The effects of unknown genes, which influence a quantitative trait, can be neutralized if animals of several families are included in an evaluation. Such genes can lie in the same chromosome section as a marker gene. Certainly then, for animals of a population, different alleles can be linked. Thus, in the case of genetic equilibrium, the effects on the quantitative trait, measured with each marker allele, cancel each other out. In a given population however, distinct haplotypes can occur more frequently than expected accidentally (Merlin and Di Stasio 1982). Even alleles of unlinked loci can appear more or less frequently than would be expected in the case of genetic equilibrium, if, for example, the allele complexes of a well established sire become widespread and those of an other sire are eliminated by withdrawing him and his offspring from the breeding stock (Lherminier 1968). Consequently, relationships between monogenic and multifactorial determined traits in populations reflect not only effects of the monogenic character itself, but also, and, perhaps more importantly, the influence of allelic disequilibria which can vary according to population as well as breeding generation.

For that reason, in the analyses presented here, the connections between monogenic and multifactorial traits were for the first time examined within daughter groups of individual sires. Considering allele transfers within each daughter group, the effects on milk production caused by alleles of the marker genes used along with the alleles in the corresponding chromosome sections were traced. This evaluation is not influenced by allele disequilibria in the population, but the measured effects of allele transfers on quantitative traits arise from substitution effects of paternal homologous chromosomes (Geldermann 1975). Besides, there can also be dominant-recessive effects which depend on the frequencies of different chromosome types in the mothers.

Gaining as few environmental influences as possible only daughters of distinct first calving age and season were used which had been located in different herds of a homogeneous breeding region. In addition, the animals were included during the onset of their first lactation to avoid a selectional loss. The congruence between observed and expected frequencies of allele transfers indicated an appropriate choice of animals (Table 4).

In the investigation, daughters of three sires were included, each of which showed highly positive breeding values of milk performance. This selection was essential because only for qualified breeding sires a sufficient number of daughters was available during a limited period. Even for two of those sires, differences regarding the effects of homologous chromosome sections on milk production could be demonstrated. Hence, it follows that a heterogeneity of genetic material exists in the cattle population.

Stronger effects have to do with chromosome sections marked with polymorphic milk proteins. In connection with allele transfers of β-lactoglobulins, similar effects appeared for milk production in both daughter groups testable. Moreover, the β-*Lg*-locus is linked with the sex independent J-systems (Hines et al. 1968) so that through a twofold marking the transfer of certain chromosome material is judicable. This was shown by the results whilst similar effects on the milk production traits were obtained by marking with the J-system as well as with the β-*Lg*-locus, but the relations turned out significant only with the β-*Lg*-locus. A combined evaluation was omitted because of the small number of identified transfers of the allele *J* in the J-system (Table 5). However, for the daughters of sire no. 2, the casein loci allowed a double marking of one chromosome section (with α_{s1}-*Cn* as well as with β-*Cn*) so that the number of marked transfers could be enlarged. Separate consideration of transfers of alleles from both gene loci showed the expected similar effects of alleles located at a distinct homologous chromosome on the values of milk performance. It has to be mentioned that the haplotype α_{s1}-Cn^B/β-Cn^A1 connected with the higher milk production had been observed in the daughters more frequently than expected randomly.

For the systems Am_1 and C it could have shown that effects on quantitative traits measurable with the help of a marker gene can differ depending on the progeny. This has to be expected, if, depending on the sire, various alleles are combined within the marked chromosome section. Concerning the three closely linked casein loci that could have proved for the sires used.

The results give the impression that a considerable portion of the genetic variance for milk production are caused by genes within a few chromosome sections.

These findings correspond to data of an analysis executed simultaneously in mice (Kluge and Geldermann 1982). Perhaps clusters of genes for a special quantitative trait lie in some distinct chromosomes and react to selection as "super genes" as suggested by Lewontin (1973). A linkage of quasi selectively neutral and different superior alleles within a chromosome results in a stability for the frequency of the chromosome types against selection. This is valid also for the frequencies of alleles located there independent of their own selective significance. Moreover, in the case of dominant-recessive gene actions, heterosis is produced at the level of chromosomes. This leads to an accumulation of few and distinct allelic linkage types, which establish stronger units if epistatic effects between the alleles increase and recombination rates decrease. Thus, groups of linked gene loci (gene cluster, gene families, polygenes) were extensively investigated for genes of the immune response and histocompatibility (review, see Schreffer and David 1975). As shown for inheritance of blood groups (Bouw and Fiorentini 1970) and of caseins (Hines et al. 1968), gene clusters seem to be of importance also for phenotypes in cattle.

The main limitation of trying to measure the effects of single chromosome sections lies in the fact that a parent can only be examined with regard to its heterozygous genotypes. Besides, effects of homologous chromosome sections can vary between individuals and ought to be calculated for each testing animal by means of a large offspring number. The required number depends on the degree of effects from single chromosome sections so that only the more important chromosomes are judicable with a reasonable effort. The conditions are more convenient, however,

- if performances are controlled by gene clusters within few chromosome regions,
- if for this chromosome region several marker genes and/or multiple alleles per marker locus can be identified,
- if suitable statistical analyses are used, and
- if previous knowledge about the ancestors exists.

The effects found here on the traits of milk performance are interesting for the practical breeder. As relations appear within paternal halfsibs, several daughters should be included per sire for testing the effects of the marked chromosome sections on performance values. Subsequently, further offspring of the same sire can be estimated on the basis of marker genes with regards to their breeding values. As some of these tests can also be carried out in calves a prediction about the genetic controlled capacity of the development of an individual can be made. Male calves can also be tested in order to determine which ones should be selected for subsequent progeny test. But then for sex-limited milk proteins, an additional marking of the concerned chromosome sections with non sex-limited marker genes is of importance. Above all, the investigations can support decisions on the mating of parents, in order to get offspring which will have productive chromosome sections in an advantageous combination. Apart from the direct application of marker genes in cattle breeding, this kind of analyses can give a greater insight into the inheritance of milk performance.

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