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On the Mode of Inheritance of Double-muscled Conformation in Bovines

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For this report, analysis of the results of an experiment conducted at the University of California at Davis and a critical review of the literature did not lead to rejection of the autosomal monohybrid model as an adequate explanation of the genetic transmission of the conformation associated with bovine muscular hypertrophy, commonly known as double-muscling. Conformational criteria for classifying a calf as double-muscled neonatally were developed and discussed herein, and a hypothesis is presented for prenatal selection against homozygous mutant embryos.

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On the Mode of Inheritance of Double-muscled Conformation in Bovines¹

INTRODUCTION

DOUBLE-MUSCLED CONFORMATION in bovines is characterized by the extraordinarily bulging muscles of the shoulder and thigh, a very rounded rear end (when viewed from the side), and a wide but shallow body throughout. The enlarged muscles and reduced subcutaneous fat brings into relief the intermuscular grooves. These characteristics, along with the animal's fine-boned skeleton, give it a sculptured appearance (fig. 1).

Extensive reviews of the literature on double-muscling have been made by Lauvergne, Vissac, and Perramon (1963) and Oliver and Cartwright (1968), and an annotated bibliography was published by Lauvergne, Boyazoglu, and Hubert (1968).

This paper reports a test of the hypothesis:

The body shape (conformation) associated with bovine muscular hypertrophy, commonly known as double-muscling, is a phenotypic expression of the homozygous mutant genotype (mm) resulting from a monohybrid autosomal mode of inheritance.

Variation in degree of dominance due to differences in breed, sex, and feeding regimes is under continuing study by the authors.

MATERIALS AND METHODS

Foundation and replacement females from our previous crossbreeding experiment with the Angus, Hereford and Shorthorn breeds (Rollins *et al.*, 1969 and 1970) were used as ++ (homozygous normal) cows in matings with mm, m+and ++ bulls. The foundation females (99 at the start of the crossbreeding experiment) were selected at weaning from various herds of the Angus, Hereford, and Shorthorn breeds as representative samples of the breeds. Since the *m* gene is segregating at a low frequency in all breeds, we cannot categorically say that these animals were all of ++ genotype. However, it can be said with assurance that none were of doublemuscled conformation or closely resembled it. During the crossbreeding experiment and the double-muscle ex-

TABLE 1

DISTRIBUTION BY GENOTYPE OF SIRE OF TERM CALVES PRODUCED BY COWS OBTAINED FROM A PREVIOUS U.C. CROSSBREEDING EXPERIMENT

Genotype of sire	Number of sires	Number of term calves
++	10	307
m+	4	86
mm	2	46
	Total	439

¹Submitted for publication January 21, 1972.



Fig. 1. Double-muscling conformation: (top) a six-year-old Piedmont bull; (bottom) a one-year-old Red Angus bull.



		Sires used				Br	eeding females			Resu	ltant calf crop
ear	Herd number	Genotype	Breed*		Source	e,† genotypic f	requency, and	breed*		Үеаг	Genotypic frequency
966	65 64	+ + ¤ ¤	A RA					I ++ - 65 H,A,S,HA,			
967	65 64 644	+ + # # # #	A RA RA			II m+ or ++ - 10 A		HS,AH,AS		1968	mm - 6 m+ or ++ - 3 m+ - 9
968	65 K401 644 718 250	+ + u u + u u u +	A A D SS RA A	·	$ \begin{array}{c} \text{III} \\ \text{m} + -2 \\ \text{m} + \text{or} + + \\ -8 \\ \text{A} \end{array} $		A, H, S, C, Hol, SH, SA, AH		VI m+ or ++ - 12 A.A.H.RAH, RAA,RA×AH	1969	mm - 7 m+ - 29 m+ or ++ - 1 ++ - 9
969	65 64 644 856 972 044	mm mm mm mm mm mm mm	A RA A A A A A	IV mm - 3 m+ - 10 m+ or ++ - 3 A						1970	mm - 18 mm or m + - 2 m + - 38 m + or + + - 15 + + - 15
$ \begin{array}{c} $	= Angus = Angus = Experi second acq ety of sou	s, H = Here where the sir imental cows juisition from irces. VI =	eford, S = eford, S = re is Angu from pre n the line Replacem	= Shorthorn, RA is and the dam is yyious crossbreedi in II. IV = Acc ient heifers bred	= Red Angus 5 Hereford. ing experiment juisitions from in the experim	s, C = Charols t (Rollins, et c 1 an Angus hei nental herd.	ais, Hol = Ho al. 1969 and 1 rd not closely	lstein. In the c 970). II $=$ A related to the l	ase of a crossbred equisition from a line in II and III	I the sire's \mathbf{n} inbred.	s breed is given Angus line. III equisitions from

TABLE 2

435

.

periment to date (through the 1970 calf crop), the foundation cows and their daughters, 120 all told, produced 439 term calves distributed by genotype of sire as shown in table 1. Two of these calves were double-muscled. They resulted from matings of two replacement females (paternal half sibs) to an mm bull. We may eventually prove the sire of these two cows heterozygous (m+), since 12 of his daughters are still in the herd, and we are mating them repeatedly to mm bulls.

Table 2 is a schematic representation of the matings used to produce the experimental calves under study. They were born in the experimental herd during 1968, 1969, and 1970 from matings of known parentage. Most of the dams were straight bred or crossbred representatives of the Angus, Hereford, Red Angus, or Shorthorn breeds. Most of the sires carrying the m gene, either as heterozygotes or homozygotes, were of Angus or Red Angus breeding. Exceptions were one double-muscled (mm)Charolais bull that sired two calves, one double-muscled (mm) Charolais female that produced two calves, and one (m+)Holstein cow that produced one calf.

The double-muscled type

An index, I_2 , (see Appendix) was developed for this study in an attempt to describe and measure in an objective and quantitative way the fullness of the bulging muscles in the shoulder and in the thigh of a double-muscled animal and the almost-circular arc (when viewed from the side) of the animal's outline from just forward of the base of the tail to the lateral aspect of the gaskin. Contour shapes and protuberances of specific muscles are scored. However, whether or not an animal is classified as double-muscled or not depends on the classifier's opinion-not its I_2 value.

Table 3, showing distributions of I_2 values, gives some idea of the variation

TABLE 3

I_2^*	FI	REQU	EN	ICY	D	ISTR	IBUT	IONS	BY
GЕ	NC	TYP	\mathbf{E}^{\dagger}	\mathbf{AN}	D	SEX	FOR	CALV	ES
]	IN	THE	E	XPF	R	IMEN	TAL	HER	D

		I ₂ fre	quency (listribı	tions	
$I_2 \ score$	Male				Female)
	mm	<i>m</i> +	++	mm	m+	++
12 - 16	2	0	0	0	0	0
17 - 21	3	0	0	1	0	0
22 - 26	4	0	0	2	0	0
27-31	1	0	0	3	0	0
32-36	1‡	0	0	1	0	0
37-41	0	0	0	0	0	0
42-46	0	2	0	0	0	0
47-51	0	3	0	0	0	0
52-5 6	0	2	0	0	0	0
57-61	0	2	0	0	0	0
62-66	0	8	0	0	4	0
67-71	0	6	0	0	3	0
72-76	0	0	0	0	4	1
77-81	O	1	0	0	3	0
82-86	0	1	2	0	1	2
87-91	0	1	2	0	8	5
92-96	0	0	3	0	4	1
97-101	0	0	0	0	2	4
102-106	0	0	0	0	0	2

* See Appendix for explanation of I₂. All I₂ scoring was done by one observer.

† An animal is classified as double-muscled (mm)or nondouble-muscled on the basis of its phenotype. A nondouble-muscled animal is classified as m + or + + on the basis of pedigree or progeny test.

‡ A steer.

in muscularity within the doublemuscled and the nondouble-muscled types and the distinctness between the two types.

Descriptions of the postnatal (animals six months or older) double-muscled conformation are numerous in the literature and are similar to the one given in the Introduction of this paper, regardless of the breed or sex of the animal. However, a description of the conformation that identifies a calf as double-muscled within a day or two of

TABLE 4

USEFUL CONFORMATIONAL TRAITS FOR IDENTIFICATION OF THE NEONATAL DOUBLE-MUSCLED CALF

•		
Body part	Double-muscling trait and how to determine it	Rank of importance
Shoulder	Appears wide. Shaggy fur obscures muscles, fullness of triceps brachii can be easily palpated by placing thumb and fingers on either side between the elbow and scapula.	1
Forearm	Carpal extensors bulge out at the top of the forearm. Easily palpated with fingertips.	1
Loin	Although fullness of loin is obscured by shaggy fur, it is easily palpated with an open hand across the back. It is fleshy in the double-muscled calf, whereas in the nondouble-muscled calf it is flat and boney.	1
Gluteus medius	Shaggy fur does not usually conceal the bulges. Can be easily felt with the fingertips.	. 1
Vastus lateralis	Fullness best observed in dorsal view. For better appraisal of relative fullness, palpate with cupped hand or thumb and fingers on either side above the patella.	2
Thigh	Outline from lateral view is a straight or slightly convex curve between the tuber ischii and the Achilles tendon, rather than concave as in normal calf. Fullness can be felt with thumb and fingers placed on lateral and medial sides, respectively.	1
Gaskin	Shaggy fur obscures muscling, but fullness is easily palpated with thumb and fingers on lateral and medial sides, respectively.	1
Hips and rib cage	View back dorsally, and note the difference between the width of the hips and the width of the rib cage. Hold down shaggy fur, which may obscure, with the fingertips.	2
Leg	Easily-observed anomalies may impair both locomotion and stance. Taken separately, following anomalies may not be useful in identifying a double- muscled calf, but together, they are worthy of consideration: Straight and buckled-over pasterns, front and rear, sickle hocks (lateral view); bucked knees (the legs buckle forward at the knees) and turned-out toes in the front legs.	2
Tail and area of attachment.	Angle at which the anterior side of the tail meets the top line is less obtuse in the double-muscled calf than in the nondouble-muscled calf, where this angle approaches 180°. Tail appears to be thinner than in the normal calf.	2
Bone structure	Fineness of bone is easily observed in the metatarsals and the metacarpals, especially when the animal is wet.	2

birth could not be found in the literature by the authors.² An attempt at such a description follows:

In general, a calf identified as neonatally double-muscled on the basis of conformation has a wider body and finer bones than the calf judged to be nondouble-muscled. Fuller muscling is evident in the regions of the shoulder, forearm, loin, thigh, and gaskin, respectively, and the gluteus medius and vastus lateralis muscles, individually. A dorsal view shows a high ratio of the width of the hips to that of the rib cage.

Since the neonatal calf often has a shaggy coat, and since it is difficult to get it to stand properly, palpation of muscles, as well as visual observation, is important in judging its conformation. Even so, softness of the muscles at this age tends to blur the intermuscular creases that are visible in the postnatal double-muscled animal.

Table 4 provides a detailed descrip-

³Raimondi (1957), however, observes that although the neonatal muscling of the posterior region in the Piedmont breed is usually not excessively developed, it is easy to observe the crease between the semimembranosus and semitendinosus muscles and some fullness in the gluteus medius muscles.



Fig. 2. Double-muscled Angus bull calf 015B (see table 5): (top and bottom) one day old; (page 439) three months old.





tion of traits useful in identifying the double-muscled neonatal calf and figure 2 shows double-muscled Angus bull calf 015B (see also table 5).

Double-muscled calves born in the experimental herd

In 1968 the first double-muscled calf was born in the experimental herd. During 1968, 1969, and 1970, 31 calves unequivocally judged postnatally to be double-muscled were born (table 5). In addition, two calves of equivocal doublemuscled status were born. On the basis of pedigree, each of these could have an mm or m+ genotype. Their growth and development, and body composition will be analyzed in subsequent papers.

A calf's neonatal double-muscled status was first noted on the day of birth in 26 cases, within two days in three cases, on the fourth day of age in one case, and in the remaining case, no date was recorded, but the calf in question was not classified as unequivocally double-muscled until six months of age.

The neonatal and postnatal doublemuscled status of an animal were each judged by one or more of the authors, as well as by one or more of three herdsmen. If two or more evaluators were not in agreement, the status was recorded as equivocal (E). A calf's status was also recorded as E if one or more of the evaluators so considered it.

Of the 14 calves judged unequivocally double-muscled at birth (Yes in table 5) and living to at least 10 months of age, all were judged unequivocally double-muscled during the remainder of their lives or to the present time, if still alive.

The sex ratio of double-muscled calves born in the experimental herd, 23 bulls (B):8 heifers (H) is significantly different from 1:1 ($X^2 = 7.26$, P < .01). That of nondouble-muscled calves produced in the same experiment,

TABLE 5

ESTIMATED DOUBLE-MUSCLED STATUS OF NEONATAL DOUBLE-MUSCLED CALVES BORN IN THE EXPERIMENTAL HERD AND THEIR DOUBLE-MUSCLING INDEXES AT ONE YEAR OLD*

Calf ID no.†	Birth- weight	Age at first evaluation	Prediction of postnatal double-	Age when unmistak- ably double-	Dou inc	ble-muscl lexes at or year‡	ing ne	Remarks
	_		muscling	muscled	RS	Iı	I_2	
• • • • • • • • • • • • • • • • • • • •	pounds	days						
81H	67	2	No	3 weeks	1.00	9		•••
85 B	80	Birth	Yes	Birth			•••	Stillborn
820B	55	Birth	No	1 week	0.50	9	• • • •	
83 6 H	83	Birth	Yes	Birth	1.00	12		•••
851B	65	Birth	Yes	Birth	0.50	9		•••
870B	74	2	No	2 weeks	1.00	9		
98B	80	Birth	Yes	Birth	•••		•••	Stillborn
930B	75	4	Yes	4 days			• • • •	Died at 10 mos.
932H	66	2	No	1 mo.	1.50	15	33	
949B	56	Birth	Yes	Birth	0.50	6	14	
953H	61	Birth	Yes	Birth	0.75	10	23	
956B	60		No	6 mos.	1.50	15	34	Castrated at 2 mos.
971B	87	Birth	Yes	Birth	0.50	6	21	
01B	54	Birth	No	20 days				Sold at 10 mos.
07H	73	Birth	Yes	Birth				Stillborn
015B	69	Birth	Yes	Birth	0.50	9	20	
021B	55	Birth	Yes	Birth	0.75	10	21	
022B	60	Birth	Yes	Birth	0.75	10	26	
026B	99	Birth	Yes	Birth				Stillborn
029B	70	Birth	Yes	Birth	1.00	12	25	
030H	64	Birth	Yes	Birth	1.00	9	25	
037H	74	Birth	Yes	Birth	1.50	15	30	
040B	67	Birth	Yes	Birth		•••		Stillborn
050B	65	Birth	Equivocal	12 days				Died at 2 mos.
(twin)			-					
064B	65	Birth	Yes	Birth	0.50	6	16	•••
068B	49	Birth	Equivocal	1 week	1.50	15	30	
074B	65	Birth	Yes	Birth		•••		Stillborn
076B	62	Birth	Yes	Birth				Stillborn
090B	65	Birth	Yes	Birth	•••	•••	•••	Died at 2 days (E. coli?)
091B	60	Birth	Yes	Birth			•••	Died at 2 days (E. coli)
092H	78	Birth	Yes	Birth	0.50	9	18	

* Records of calves dying perinatally are included if they were unequivocally judged to be double-muscled at birth. The neonatal and postnatal double-muscled status of an animal were each judged by one or more of the authors and usually (in addition) by one or more of three herdsmen. If two or more evaluators were not in agreement, the status was recorded as equivocal. A calf's status was also recorded as equivocal if one or more of the evaluators considered it so.

† Series 8 was born in 1968, series 9 in 1969, series 0 in 1970. B signifies bull, and H signifies heifer.

‡ Indexes are defined in the Appendix.

TABLE 6 A RESUME FROM THE LITERATURE AND FROM THE CURRENT STUDY OF SEX RATIOS FOR DOUBLE-MUSCLED OFFSPRING (CHI-SQUARED TESTS OF GOODNESS OF FIT TO A 1:1 SEX RATIO)

				Sex ratio	os for do	uble-mus	cled offsr	oring:*		
Study		Double-n	uscled fi	rstborn		Subse	quent to	doubl o -n	nuscled f	irstborn
	В	н	n	H/n	X2	В	н	n	H/n	X2
(1) Hanset (1967b and 1968)	517	447	964	.46	5.08	137	145	282	.51	0.23
(2) Raimondi (1963).	15	10	25	.40	1.00	17	11	28	.39	1.29
(3) Current U.C. study	15	3	18	.17	8.00	8	5	13	.38	0.69
(4) Smith (1949)	2	0	2	.00		3	1	4	.25	
(5) Kidwell et al. (1952)	3	2	5	.40		0	0	0		
Pooled studies (1), (2), and (3)	547	460	1,007	.46	7.52	162	161	323	.50	0.003
Heterogeneity		$X^2 = 6.$	56, .05>.	P> .025	I		X ² =	= 2.21, F	.30 ×	1

* B = bulls; H = heifers.

TABLE 7 SEX RATIOS FOR OFFSPRING OF RECALVERS* (CHI-SQUARED TESTS OF GOODNESS OF FIT TO A 1:1 SEX RATIO)

Study source and calf status	Bţ	H†	n	H/n	Xэ	Р	Heterogeneity of pooled studies
(1) Current U.C. study: double-muscled calves	8	5	13	.38	0.69	> .30	
(2) Current U.C. study: nondouble-muscled calves	6	10	16	.62	1.00	> .30	
(3) Hanset (1968): double-muscled calves	137	145	282	.51	0.23	> .50	
(4) Hanset (1968): nondouble-muscled calves	376	347	723	.48	1.16	<u>≃</u> .20	
Pooled studies:							
(1) & (2)	14	15	29	.52	0.34	> .50	$X^2=1.35~P\simeq .25$
(3) & (4)	513	492	1005	.49	0.44	<u>≃</u> .50	$X^2 = 0.95 P > .30$
$(1), (2), (3) \& (4) \ldots$	527	507	1034	.49	0.39	> .50	$X^2 = 2.69 (3D.F.) P > .30$

* Recalver is Hanset's (1967b) term for a nondouble-muscled cow that has previously had a double-muscled calf. $\dagger B =$ bulls; H = heifers.

81B:95H, is not significantly different from a 1:1 ratio $(X^2 = 1.11, P > .25)$.

These sex ratios considered jointly imply one of two alternatives: (1) There is greater prenatal selection against double-muscled females than against double-muscled males; or (2) the two sexes have different modes of inheritance of the double-muscling trait.

Our experimental evidence as well as that found in the literature favor alternative(1). Hanset (1967b and 1968) reported the following sex ratios for double-muscled calves:

Type 1, for heifers or parous cows having a first double-muscled calf, 517B:447H, significantly different from a 1:1 ratio ($X^2 = 5.08$, P < .025), Type 2, for cows having second and subse-

Matin	ng type		Frequenci	ies, genotypes	, and phene	otypes of res	ulting calves	
Sire	Dam	D	ouble-muscle (mm)	əd	No: (ndouble-muse $m+$ or $++$	cled)	Total
		В*	H*	Total	В	н	Total	1
mm	m+	5	2	7	6	8	14	21
m+	mm	1	0	1	0	1	1	2
m+	m+	0	2	2	0	2	2	4
TO	TAL	6	4	10	6	11	17	27

 TABLE 8

 U.C. DATA AMENABLE TO MENDELIAN ANALYSIS

* B = bulls, H = heifers.

			T.	ABLE	9				
CHI-SQUARI	ED TESTS	S OF G	OODNESS	\mathbf{OF}	\mathbf{FIT}	\mathbf{OF}	U.C.	EXPERIMENTAL	HERD
DATA (TA	BLE 8) 7	TO AN	AUTOSOM	[AL]	REC	ESS	IVE	MONOHYBRID M	DAL

	в*	H*	B and H
n = number of calves observed	12	15.0	27.0
O_1 = observed frequency of double-muscled calves	6	4.0	10.0
$E_1 =$ expected frequency of double-muscled calves	6	6.5	12.5
O_2 = observed frequency of nondouble-muscled calves	6	11.0	17.0
$E_2 =$ expected frequency of nondouble-muscled calves	6	8.5	14.5
X ²	0	1.7	0.92
P		≅.2	> .80

* B = bulls, H = heifers.

quent double-muscled calves, 137B: 145H, not significantly different from $1:1 (X^2 = 0.23, P > .50).$

Partitioning the U.C. experimental herd data in a similar fashion yields 15B:3H for type 1 calvings and 8B:5H for type 2. The former is significantly different from 1:1 ($X^2 = 8.00, P \approx .005$) while the latter is not ($X^2 = 0.69, P > .30$).

Tables 6 and 7 present sex ratio data and tests of goodness of fit to a 1:1 ratio for the experimental herd data and those of several studies reported in the literature. For the most part, these data indicate a difference in sex ratios of double-muscled calves resulting from type 1 and type 2 matings as just defined, viz., fewer females than males resulting from type 1 and no apparent deviation from a 1:1 ratio in type 2. Furthermore, for the type 2 mating chisquared tests of sex ratios of doublemuscled and of nondouble-muscled calves separately and jointly fail to reject the 1:1 hypothesis.

For the second kind of evidence, let us turn to tables 8 and 9. The doublemuscled calves, bulls and heifers, involved in the tests of goodness of fit to the Mendelian ratios for a monohybrid autosomal recessive type of inheritance are all from type 2 matings. Neither the test for the bulls nor that for the heifers rejects the hypothesis. The heterogeneity chi-square test upon pooling bulls and heifers yields a nonsignificant chisquare $(X^2 = 0.78, P > .30)$.

Goodness of fit to Mendelian ratios

An animal is considered mm on the basis of its phenotype or if it results from an $mm \times mm$ mating. It is considered m+ if its phenotype is nondoublemuscled and if one parent was mm or the animal, itself, is the parent of an mm animal. Six $mm \times mm$ matings have yielded term calves. All of these calves had a double-muscled phenotype.

Twenty-seven calves have been born from matings of the types shown in table 8. For the data in table 8, chisquare tests for goodness of fit, assuming an autosomal recessive monohybrid type of inheritance, indicate good agreement between the observed and expected frequencies of double-muscled and nondouble-muscled calves (see table 9). The question of incomplete recessiveness, that is, the extent to which the m+ phenotype is distinguishable from the ++ phenotype, is not of primary concern in this paper. Substantial evidence for incomplete recessiveness exists in our data (see the distributions of I_2 values, table 3).

Results of matings of the type shown in table 8 that first identified a parent as m+ (when the pedigree information was lacking or was indefinite on the point) are not included in table 8 (nor are results prior to such a mating), since these data would bias the results towards an excess of double-muscled calves.

Note that in a diallel cross of a double-muscled Angus and a doublemuscled Charolais bull with a doublemuscled Angus and a double-muscled Charolais cow, all four of the resulting calves had double-muscled phenotypes. These formal test results are consistent with informal observations made in the experimental herd and others reported in the literature: that one and the same gene appears to be responsible for double-muscling in the breeds in which this condition has been reported. Also of interest here is that a nondoublemuscled cow, when mated to a doublemuscled bull, produced twin calvesone of which was a double-muscled male and the other a nondouble-muscled female.

DISCUSSION

Wreidt (1929), Weber and Ibsen (1934), Paci (1935), Smith (1949), Kidwell *et al.* (1952), Raimondi (1957 and 1963), and Logeay and Vissac (1970) present data that support an autosomal monohybrid mode of inheritance for double-muscling (table 10).

Kronacher (1934), on the other hand, presents data from a German herd that lead him to reject the monohybrid model in favor of a trihybrid one involving epistasis (one gene triggering the action of the other two). Lauvergne *et al.* (1963), in commenting on Kronacher's position, point out the paucity of his data for formulation of such a precise hypothesis and state themselves in favor of a monohybrid explanation involving incomplete penetrance.

Kronacher's rejection of the monohybrid model is largely based on six successive progeny produced by the cow Bärbel which, allegedly, showed no signs of double-muscling. Her record follows:

- 1. Mated to three different sires in 1926, 1927 and 1928; produced three double-muscled female calves which died at birth.
- 2. Mated to Baldur in 1929; produced a double-muscled female calf (butchered).
- 3. Mated to Burggarf in 1930 and in 1931; produced a double-muscled female calf (slaughtered) and a double-muscled male calf (died during parturition).

Kronacher states that the five different sires to which Bärbel was mated were certainly not all carriers of doublemuscling. Given the frequency of double-muscling reported in German herds of the time, this statement is open to question.

					ТА	BLE 10			
REPORTS	\mathbf{IN}	THE	LITERA	ATURE	THAT	SUPPORT	\mathbf{AN}	AUTOSOMAL	MONOHYBRID
		MO	DE OF	INHER	ITANC	E FOR DO	UBL	E-MUSCLING	

Author	Breed studied	Scope of study
Wreidt (1929)	Danish Shorthorn	A genetic analysis of a three-generation pedigree network in a herd produc- ing double-muscled animals.
Weber and Ibsen (1934)	Hereford	Four consecutive years of records in a herd having used a double-muscled sire followed by a double-muscled son.
Paci (1935)	Piedmont	A phenotypic classification of: (i) 77 animals from double-muscled X double- muscled matings; (ii) 154 from double-muscled (male) X normal (females); (iii) five from reciprocal crosses to (ii). (iv) 51 from normal X normal matings.
Smith (1949)	Angus	Thirteen years of records in an experiment station herd linebred to a double- muscled female.
Kidwell, <i>et al.</i> (1952)	$Angus \times Africander$	A genetic analysis of a five-generation pedigree network in an experiment station herd that produced five double-muscled calves.
Raimondi (1957)	Piedmont	A phenotypic classification of 28 offspring resulting from mating a double- muscled male to heterozygous females.
Raimondi (1963)	Piedmont	A phenotypic classification of the offspring of 53 pregnancies resulting from double-muscled \times double-muscled matings.
Logeay and Vissac (1970)	Charolais	A phenotypic classification in an experiment station herd of: (i) 24 animals from double-muscled \times double-muscled matings. (ii) 20 from double-muscled (males) \times normal (females). (iii) 21 from reciprocal crosses to (ii). (iv) 18 from normal \times normal.

On the other hand, if one allows that not all of the calves were mm, some being m+, then the data could fit a monohybrid hypothesis without requiring that all of the sires carried the mgene.

Kronacher makes the somewhat puzzling statement with reference to the herd in question: "A similar case has come to the author's attention very recently." Since Kronacher's paper was published in 1934, and the last cited calf of Bärbel's was born in 1932 and died during parturition, it appears (from his statement) that Kronacher, himself, may not have seen the breeding animals or calves about which he wrote.

If one assumes Bärbel and each of the five sires to which she was mated to have been m+ and the six calves each to have been mm, then the probability of such an event (i.e., six mm calves in succession) is $(\frac{1}{4})^{\circ}$. If one alters the above assumptions to allow that Bärbel was in fact mm (lack of penetrance of the mm genotype) the probability, $(\frac{1}{2})^{\circ}$, is still rather low.

If, on the other hand, one assumes that some of the five sires to which Bärbel was mated were m+ or mm and the remainder ++ and that some of the resulting calves were m+ and the remainder mm, then there are numerous hypothetical combinations of these data that could comfortably fit a monohybrid model, if one invokes lack of penetrance of the mm genotype in the case of Bärbel.

The possibility of confusing mm with m+ animals on the basis of conformation does not seem farfetched, given the evidence for varying expressivity of m+ or mm animals when nutrition- and agerelated effects are not adequately controlled, Mackellar (1960), Lauvergne, Vissac, and Perramon (1963), Logeay and Vissac (1970), and the authors of the present paper (unpublished data).

Hanset's work

Hanset (1967a) reports on a body of

TABLE 11 PROGENY TEST RESULTS OF AI SIRES MATED TO m+ COWS (HANSET, 1968; TABLE 5)

Name of sire	Number of offspring	Number of double- muscled offspring	Percentage of double- muscled offspring
Dodal	70	31	44.29
Bijou	64	27	42.19
Emin	48	17	35.42
Patrick	95	31	32.63
Dare-Dare	31	10	32.26
Surcouf	30	9	30.00
Renard	48	13	27.08
Baiser	25	6	24.00
Gaillard	55	13	23.64
Marquis	44	10	22.73
Jasmin	32	7	21.87
Idéal	50	9	18.00
Farceur	47	8	17.02
Désiré	41	5	12.20
Jacob	31	2	6.45

data that leads him to question the monohybrid model. These data consist of the percentages of double-muscled calves among the offspring (resulting from artificial insemination) of individual bulls in one of the big studs of Belgium. The animals involved are members of the Moyene and Haute Belgique (MHB) breed.

In subsequent reports by Hanset (1967b and 1968), the progeny test data are for AI bulls in the same stud as referred to in his 1967a study. The data in table 11 are taken from table 5 in Hanset's (1968) report. Its progeny test results involve the offspring of nondouble-muscled dams, each of which had previously produced a double-muscled calf, and, therefore, on the basis of the monohybrid model, are m+.

If these progeny test data conform to a monohybrid model, one should be able to assign the sires to one of the three genotypes mm, m+, or ++. Chisquared tests of homogeneity of progeny test results within assigned genotype of sire, and the goodness of fit of the pooled values within such sire groupings to expected Mendelian ratios, should indicate to what extent the data do or do not support a monohybrid model.

The following groupings of the sires are examined in the manner just described. Firstly, Jacob will be considered ++, the two alleged double-muscled calves attributed to him (6.45 per cent) being considered misclassifications. As Hanset (1967*a*) explains, the calves are classified as double-muscled or nondouble-muscled by the breeder neonatally on the farm; errors of classification may run as high as 10 per cent.

Let us classify Dodol through Surcouf as mm and make the required chisquare tests, as shown in table 12. Now let us classify Renard through Désiré as m+ (table 13).

As shown in tables 12 and 13, heterogeneity chi-square values for each of two sire groupings, mm or m+, do not reject the hypothesis that, within groups, the individual sires are compatible with the same rate of transmission of the m gene. However, in the pooled data for each group the observed number of double-muscled calves falls below that expected for a monohybrid model, extremely so in the case of the mm sires, and at border-line statistical significance in the case of the m+ sires.

The monohybrid model

Following are the biological possibilities of an hypothesis that brings these data into agreement with a monohybrid model:

Suppose there were a net exchange in early pregnancy of 20 per cent of double-muscled (mm) embryos for nondouble-muscled (m+ or ++). ("Exchange" occurs when a dam loses a double-muscled embryo and upon being rebred conceives a nondouble-muscled embryo (or vice versa), which is carried to term.) We should then adjust

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TABLE 12 CHI-SQUARE TESTS OF HETEROGENEITY AND GOODNESS OF FIT FOR AI SIRES CLASSIFIED AS mm

	Number of offspring	Observed number of double-muscled offspring	Goodness of fit to a 1 double-muscled: 1 nondouble-muscled ratio	
Sires			Expected number of double-muscled offspring	X2
Dodol	70	31	35.0	0.91
Bijou	64	27	32.0	1.56
Emin	48	17	24.0	4.08
Patrick	95	31	47.5	11.46
Dare-Dare	31	10	15.5	3.90
Surcouf	30	9	15.0	4.80
(Pooled)	338	125	169	22.91 P < .001
Heterogeneity $X^2 = 26.71 - 22.91 = 3.80 (5D.F.)$				P > .50

TABLE 13 CHI-SQUARE TESTS OF HETEROGENEITY AND OF GOODNESS OF FIT FOR AI SIRES CLASSIFIED AS m_+

	Number of offspring	Observed number of double-muscled offspring	Goodness of fit to a 1 double-muscled: 3 nondouble-muscled ratio	
Sires			Expected number of double-muscled offspring	<u>X</u> 2
Renard	48	13	12.00	0.11
Baiser	25	6	6.25	0.01
Gaillard	55	13	13.75	0.05
Marquis	44	10	11.00	0.12
Jasmin	32	7	8.00	0.17
Idéal	50	9	12.50	1.31
Farceur	47	8	11.75	1.60
Désiré	41	5	10.25	3.58
(Pooled)	342	71	85.50	3.28 .10 > P > .05
Heterogeneity $X^2 = 6.9$	5-8.28 = 3.67 (7D)	. F .)		P <u>≃</u> .80

 O_1 values in tables 12 and 13 to $O_1' = O_1 + E_1/5$.

Doing so gives $X^{*} = 1.21$ (P > .25) and $X^{*} = 0.11$ (P > .70) in tests of goodness of fit to expected Mendelian ratios for the pooled adjusted data for mm and m+ sires, respectively.

That a substantial amount of embryonic and foetal loss in cattle populations occurs during the first 60 days or so of pregnancy is attested to by reports in the literature based on both experimental and survey type data, Winters, Green, and Comstock (1942), Tanabe and Casida (1949), Casida (1953), Salisbury and VanDemark (1961), and Wijeratne (1971).

Hanset (1968) reports that the nonreturn rate to first service in the MHB breed is 62.7 per cent as compared to

Source of data	Unadjusted data*	Adjusted data*		
(1) Experimental herd	n = 27 $O_1 = 10$ $E_1 = 12.5$ $O_2 = 17$ $E_2 = 14.5$ $X^2 = 0.92 P > .30$	n = 27 $O_1' = 12.5$ $E_1 = 12.5$ $O_2' = 14.5$ $E_2 = 14.5$ $X^2 = 0$		
(2) Smith (1949)	n = 13 $O_1 = 5$ $E_1 = 5.5$ $O_2 = 8$ $E_2 = 7.5$ $X^2 = 0.08 P > .70$	n = 13 $O_1' = 6.1$ $B_1 = 5.5$ $O_2' = 6.9$ $B_2 = 7.5$ $X^2 = 0.11$ P > .70		
(1) and (2) pooled	n = 40 $O_1 = 15$ $E_1 = 18$ $O_2 = 25$ $E_2 = 22$ $X^2 = 0.91 P > .30$	n = 40 $0_1' = 18.6$ $E_1 = 18$ $0_2' = 21.4$ $E_2 = 22$ $X^2 = 0.04 P > .80$		

TABLE 14 CHI-SQUARE TESTS OF GOODNESS OF FIT OF EXPERIMENTAL HERD AND SMITH (1949) UNADJUSTED AND ADJUSTED DATA TO EXPECTED MENDELIAN RATIOS

* n = number of calves observed; $O_1 =$ observed number of double-muscled calves; $E_1 =$ expected number of double-muscled calves; $O_2 =$ observed number of nondouble-muscled calves; $E_2 =$ expected number of nondouble-muscled calves; $D_2 =$ expected number of nondouble-muscled calves; $D_1 = O_1 + E_1/5$; $O_2' = n - O_1'$.

69.02 per cent in the Pie Noire, a Belgian breed with a relatively low occurrence of double-muscling.

In the section, Double-muscled Calves Born in the Experimental Herd, we discussed evidence for a heifer-to-bull sex ratio at birth of less than one for double-muscled calves. This phenomenon may be an indication of prenatal selection against double-muscled (mm) embryos.

Wreidt (1929) in reviewing an 1888 paper by Kaiser writes, "Kaiser said that people believed that it was firstcalf heifers that gave double-muscled calves." (Our translation.) This observation in conjunction with the evidence we have just discussed may imply less prenatal selection against male doublemuscled embryos than against female double-muscled embryos, until a dam has conceived her second double-muscled embryo—the net result being less prenatal selection against double-muscled embryos carried by young dams than by older ones. In table 14 chi-square tests of goodness of fit to Mendelian ratios are presented for the experimental herd data and for the data of Smith (1949) using the actually observed number of double-muscled calves (O_1) on the one hand and the adjusted number (O_1') on the other. (The adjustment was the same as that applied to Hanset's data.) These results indicate no incompatability of the experimental-herd data or the Smith data with the hypothesis under discussion of prenatal selection against mm embryos.

Hanset (1967*a*, fig. 11) presents progeny test data for AI bulls mated to nondouble-muscled females of unknown genotype (m+ or ++, but not mmsince Hanset describes them as dairy type cows). Let us focus our attention on the 15 bulls tested in 1965. It is likely that some or most of these sires were included in the set of 15 he reported on in his 1968 paper, which we have just discussed.

In table 15 these 15 sires are listed

in descending order of percentage of double-muscled offspring, as A, B, C, and so forth, based on their 1965 record. Where available, their 1964 records are also given.

After a genetic analysis of the 1965 progeny, Hanset concluded:

In order to make our observations coincide with a monofactorial type, we must take into account:

- 1) A weak penetrance of the gene, at the heterozygous state (.08), and incomplete penetrance of the gene, at the homozygous state (.60).
- 2) The existence of modifiers possessing a high amplitude of action.

With such qualifications, Hanset's suggestion that the monohybrid model loses much of its meaning appears reasonable.

Hanset defines penetrance of the mutant gene in the heterozygous genotype as leading to "full character expression." This seems inconsistent with his statement that the gene is "incompletely recessive."

Rieger, Michaelis and Green (1968) define penetrance as:

The frequency (in per cent) with which a (dominant or homozygous recessive) gene or gene combination manifests itself in the ... phenotype of the carriers.... P. [penetrance] is complete when all the homozygous recessives show one phenotype, when all of the homozygous dominant show another phenotype, and when all of the heterozygotes are alike....

They do not define "incomplete recessive," but following is their definition of semi-dominance:

Semidominance (= Partial dominance; incomplete dominance): the phenotype of the heterozygous form (Aa) lies between that of AA and aa, i.e., it is "intermediate"; ...

Their definition seems to be equivalent to "incomplete recessive" as used by Hanset. It seems that semantic as well

TABLE 15 1964 AND 1965 PROGENY TEST RESULTS OF 15 AI SIRES (TAKEN FROM FIGURE 11, HANSET (1967a))

Q:	Percentage of double-muscled offspring		
Sires	1965	1964	
A	10.1	8.4	
в	9.1	9.1	
Ø	8.3	8.1	
D	7.8	not listed	
\mathbf{E}	7.7	5.6	
F	7.5	5.8	
G	6.5	5.7	
н	6.3	6.0	
I	6.2	5.2	
J	5.4	4.7	
K	5.0	3.9	
\mathbf{L}	4.7	3.6	
М	4.5	5.3	
Ν	1.5	1.4	
0	1.3	0.9	

as biological complications encumber Hanset's analysis.

Partial dominance

The position we take in this paper is that the modal value of the heterozygote is intermediate to those of the two homozygotes (partial dominance). There is variation around these modal values but not to the extent of invalidating the concept.

In our analysis of the progeny test results in Hanset's 1967a and 1968reports, we find it simpler and more effective to think of the double-muscled offspring as mm and nondouble-muscled as m+ or ++, with an m+ or ++animal classified as double-muscled or an mm animal classified as nondoublemuscled considered as errors of classification, rather than as examples of penetrance or of its lack.

Given the evidence in the literature and our own unpublished results, suggesting variation in the degrees of expressivity and penetrance of the mmgenotype and of the m gene in the m+ =

mm sires:

m + sires:

A and B averaged

K and L averaged in 1964....

L and M averaged in 1965

Average

OF NONDOUBLE-MUSCLED COWS FROM WHICH ALLOTMENTS OF MATES FOR AI SIRES WERE DRAWN				
	1964 results		1965 results	
Sires*	Percentage of double-muscled (mm) offspring	Estimated per- centage of $m+$ cows in the cow population [†]	Percentage of double-muscled (mm) offspring	Estimated per- centage of $m+$ cows in the cow population [†]

17.6

15.2

16.4

TABLE 16 ESTIMATION OF THE PERCENTAGE OF m+ COWS IN THE POPULATION

* Two sires at each extreme of the distributions in table 13 are chosen to "assure" mm and m+ genotypes, respectively, and, hopefully, to cancel out some of the sampling variation in the proportion of m+ cows in sires" allotments of mates. † Twice the value in the column to the left for mm sires and four times the value for m+ sires.

8.8

3.8

genotype due to breed, sex, age, condition of health, feeding regime, and the like, we find the phrase "lack of penetrance," without some qualifying remarks as to possible cause, abstract and somewhat empty of meaning.

Hanset was attempting to accommodate within the framework of the monohybrid hypothesis the lack of a sharp discontinuity in the progeny test results of the carrier bulls A through M. With respect to this continuity, the distributions of results in table 15 are similar to that of table 11. On the hypothesis we put forward, the carrier bulls were satisfactorily separated into mm or m+ classes (table 11), despite the apparent continuity of their progeny test results and without the postulation of low-level penetrance of the mm genotype.

The results in table 15 compared to those in table 11 have an additional source of variation: the proportion of m+ cows among those cows to which a bull was mated. In order to estimate the magnitude of this component of variation, we need to know the proportion of m+ cows in the population of cows from which the matings of all bulls were drawn.

If we assume that sires A and B in

table 15 are mm, and L and M in 1965 and K and L in 1964 are m+ sires, (the rationale for which is explained in table 16) we then obtain estimates of the proportion of m+ cows in the nondouble-muscled cow population. For 1964 and 1965, respectively, they are 16.4 per cent and 18.8 per cent. The estimated increase of 2.4 per cent of m+ animals in the cow population from 1964 to 1965 accords well with Hanset's figure 10, in which the annual rate of increase in frequency of double-muscled calves for the period 1957 to 1965 among the descendents of AI bulls in the population under discussion was estimated to be .88 per cent.

9.6

4.6

However, Hanset offers no explanation of how cows were assigned to a bull, and the 2.4 per cent increase per annum in m+ cows suggests that variation in the age distribution of cows mated to a bull could contribute to a nonrandom sample with respect to the proportion of m+ cows in the lot assigned to a bull.

Another possible source of error in the progeny test results applies to the data of table 11, as well as to those of table 15. Hanset mentions that verified errors of misclassification of offspring as double-muscled or nondouble-muscled as high as 10 per cent were not

19.2

18.4

18.8

important to his analysis in view of the amount of data available (about 1,000 or more offspring per bull per year). However, when dealing with effective numbers of 150 or 200 offspring per bull per year (offspring of m + cows) such errors would be increasingly important. For example, the 1 per cent to 1.5 per cent listing of double-muscled offspring of sires N and O, the noncarrier bulls, in table 15 (if related to the proportion of m + cows) becomes about 6 per cent, similar to the figure for Jacob, the noncarrier bull listed in table 11. This latter figure indicates to some extent the magnitude of the error of calling a nondouble-muscled (m+ or++) calf double-muscled (mm). Let us call this a type A error. What about the error of calling a double-muscled (mm) calf nondouble-muscled (m+ or ++)? Let us call this a type B error. According to Hanset, as mentioned previously, the offspring in these progeny tests were classified neonatally on the farm by the breeder.

Table 5 shows that, for the experimental herd data, 36 per cent of the calves that lived two months or longer and were unequivocally judged to be double-muscled were classified as nondouble-muscled during the first week of life. If stillborn calves and those dying within a few days but judged to be double-muscled are included, the percentage becomes 26. According to a private communication from Hanset (in \cdot 1969) most double-muscled calves of the MHB breed exhibit a doublemuscled conformation neonatally.

To the extent that type B errors exceed type A, the postulated percentage of net exchange of double-muscled (mm) for nondouble-muscled (m+) embryos in our hypothesis of prenatal selection against mm embryos would be lowered.

In summary, the lack of precise knowledge of the numbers of m+ females to which each individual bull was mated to produce the progeny test results presented in table 15 makes these results less valuable, despite the greater volume of data involved, than those of table 11 in elucidating the mode of genetic transmission of doublemuscling in the MHB breed.

Sopeña Quesada and Blanco Cachafeiro (1970b) have reported a study of double-muscling in several breeds of Spanish cattle in Asturias and Galicia. They postulate an autosomal dihybrid mode of inheritance for the trait, with the nine possible genotypes expressed in four phenotypic classes as follows (taken from page 514 of their publication):

- Tipo 1: AABB (homozigotes A y B). Fenotipo culón (C).
- Tipo 2: AABb (homozigote A y heterozigote B). Fenotipo semiculón (C₁).
- Tipo 5: AaBb (heterozigote A y B). normal (N).
- Tipo 4: AaBB (heterozigote A y homozigote B). Fenotipo culón (C).
- Tipo 5: AaBb (heterozigote A y B). Fenotipo semiculón (C_1) .
- Tipo 6: Aabb (heterozigote A y homozigote b). Fenotipo normal (N).
- Tipo 7: aaBB (homozigote B). Fenotipo aculonado (C_2) .
- Tipo 8: aaBb (heterozigote B). Fenotipo aculonado (C_2) .
- Tipo 9: aabb (homozigote a y b). Fenotipo normal (N).

The term *culón* designates the unequivocal double-muscled type. Speaking in terms of modal values, if one were to divide the phenotypic distance between *culón* and *normal* in half, *semiculón* would lie on the *culón* side of the division point and *aculonado* on the *normal* side.

The authors have reported the phenotypic classifications of approximately 675 offspring resulting from matings involving members of the four phenotypic classes. These data were mostly gathered from the routine records and remarks of private breeders. (The authors state that they are currently engaged in supervising some test matings.) Of the above-mentioned observations, 446 were used to establish 13 concordances with expected (theoretical) results from matings of parents with stated genotypes.

These concordances support the dihybrid hypothesis in the sense that theoretically impossible observations occurred only in one case (the authors offer phenotypic misclassification by a breeder as a possible explanation). These concordances, however, are weakened by the fact that in most cases the genotypes of the parents are not known precisely (e.g., σ (AABb or AaBb) \times φ (aaBB or aaBb)). Furthermore, the hypothesis itself was elaborated on the basis of these data, hence they do not serve as an independent verification of it.

The basis for establishing aculonado as a new (i.e., not previously reported in the literature) and fourth phenotypic class appears questionable, since little or no mention is made of the age at which or the environmental circumstances under which animals were phenotypically classified—this, despite the following warning by the authors (1970a) on page 492: Without question it is easy to confuse ... aculonados with normals since many factors hide or enhance this trait [conformation and appearance generally]. Thus, the level of feeding, syndromes associated with [nutritional (?)] deficiencies, sex, the existence or not of parturitions, age, etc. can lead to error [of classification]...²

The case for four phenotypic classes would be strengthened if data collected under adequately controlled conditions and fitting a quadrimodal phenotypic distribution were to become available.

The reported data have limitations in regard to completeness of phenotypic and genotypic information. For example, some progeny groups are reported as composed of "culón [or] semiculón" or of "aculonado [or] normal," and the given phenotype of some parents is questionable and of some others lacking in specificity.

Bearing such limitations in mind, if one relates the four phenotypic classes to genotypes as follows (using our genetic notation)—Culón = mm, semiculón = m+, aculonado = m+ or ++ (an overlap area), and normal = ++—then the data are not incompatible with an autosomal monohybrid mode of inheritance.

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³ Our translation.

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APPENDIX

The I₂ Index

Around one year of age, certain specific muscles of an animal are scored (on the basis of visual observation) for fullness, to the nearest one-half unit as follows:

Score	1	2	3	4
	Very	Full	Slightly	Flat
	full		full	

Occasionally, a double-muscled animal will receive a muscle score as low as 0.5, the modal double-muscled animal receiving a score of 1.0.

To insure accuracy, the animal being observed should stand correctly and have a well shed-off or clipped coat. The following muscles are scored as indicated:

Muscles	Weighting factor
Shoulder region	
Deltoid (D) Triceps brachii	2
Long head (T. Long)	4
Lateral head (T. Lat).	4
Thigh region	
Vastus laterals (VL)	4
Semitendinosus (ST)	2
Semimembranosus (SM) .	4
Biceps femoris (BF)	4

For each of these two anatomical regions an animal's composite score, to be used in the index, is arrived at as follows:

$$\begin{split} \mathrm{S(shoulder)} = 2(\mathrm{D}) + 4(\mathrm{T},\mathrm{Long}) \\ + 4(\mathrm{T},\mathrm{Lat}) \\ \mathrm{T(thigh)} = 4(\mathrm{VL}) + 2(\mathrm{ST}) \\ + 4(\mathrm{SM}) + 4(\mathrm{BF}) \end{split}$$

The I_2 is a linear function of properly weighted values of S, T, and a third score, rump shape (RS). RS is the degree of circularity of an arc extending from just forward of the base of the tail to the lateral aspect of the gaskin (when the animal is viewed from the side).

An animal's RS score is obtained with a device called the rump gage (appendix fig. 1). By moving the rump gage from close to the viewer's eye to full arm's length, some position can be found at which one or two of the outlines approximately coincide visually with the animal's rump shape. If an animal's rump shape conformed to outline 1, for example, the animal's RS score would be 1.0. If the animal's outline fell between outlines 1 and 2 but was closer to 2, then its RS score would be 1.75; it would score 1.5 if it fell midway between 1 and 2.

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