THE RELATION BETWEEN POLLED AND HERMAPHRODITIC CHARACTERS IN DAIRY GOATS

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THE problem of the occurrence of hermaphrodites in dairy goats, especially in purebred herds where attention is given to the breeding of polled animals, has led to inquiries regarding the relation between the polled condition and the birth of hermaphrodites. Several observers have noted the fact that horned hermaphrodites are very rare or perhaps do not occur at all. ADDINGTON and CUNNINGHAM (1935), of the New Mexico Station, in a study of the heredity of horns in goats noted that four hermaphrodites, all polled, appeared in matings between animals heterozygous for the polled condition. PAGET (1943) reported that horned hermaphrodites are a very great rarity, known only in occasional instances among British goats. ASDELL (1944) has observed about 200 intersexual goats both in England and in America and found all to be hornless.

These observations and direct inquiries have led to a study of the polled or horned condition of hermaphrodites and normal animals in the UNITED STATES DEPARTMENT OF AGRICULTURE's herd of Saanen and Toggenburg goats at Beltsville, Md.

EXPERIMENTAL DATA

The period included in this study covers 20 years from 1925–1944, inclusive. The data recorded include number of polled and horned animals, number of normal males, females, and hermaphrodites, and the various types of matings. These data are shown separately for Saanens and Toggenburgs in table 1. The horned character of several of the progeny was not recorded, and in a few cases sex was not recorded, the latter being stillbirths and abortions. In some instances the horned character of the dams was not known. These have been indicated in the table by a question mark. The bucks in both herds were polled except one of the Toggenburgs, which sired only 11 kids. One Saanen buck evidently was homozygous for the polled condition, since all of the 66 kids which he sired out of both polled and horned does were polled.

All hermaphrodites produced in the Beltsville herd, and their parents, were polled. Horns in goats are inherited as a simple recessive. Therefore, in matings between animals heterozygous for the polled condition, one quarter of the progeny should have horns. In the Saanens the ratio was 219 polled: 63 horned; and in the Toggenburgs 255: 89. These numbers agree very well with expectation. Chi-square for the two herds combined is 1.203 with a corresponding P value of 0.548. In deriving these values, chi-square is the sum of the chi-squares for each breed calculated separately, and P is caclulated for two degrees of freedom (the sum of one degree of freedom for each breed).

TABLE I

Types of progeny from different types of matings of Saanen and Toggenburg goats. 1925–1944, inclusive.

Saanen

TYPE OF MATING*	NUMBER OF DOES	MALES		FEMALES		HER-MAPHRO-DITES	HORNED CHARACTER UNDETERMINED		SEX UNDE-TER-MINED	TOTAL
		P	p	P	p	P	MALES	FEMALES		
$PP \times Pp$	16	24	—	14	—	12	—	—	—	50
$PP \times pp$	6	10	—	6	—	—	—	—	—	16
$Pp \times Pp$	55	107	27	64	31	31	15	11	5	291
$Pp \times pp$	22	18	15	23	11	—	5	8	2	82
$Pp \times Pp$ (?)	7	9	3	8	2	—	1	1	3	27
Total	106	168	45	115	44	43	21	20	10	466

Toggenburg

$Pp \times Pp$	62	117	42	76	41	36	7	8	2	329
$Pp \times pp$	44	45	52	50	47	—	12	8	2	216
$pp \times pp$	2	—	1	—	2	—	—	—	—	3
$Pp \times Pp$ (?)	7	16	5	10	1	—	1	4	—	37
$Pp \times pp$ (?)	6	4	4	7	10	—	—	2	—	27
Total	121	182	104	143	101	36	20	22	4	612

Saanen Buck × Toggenburg Does

$Pp \times Pp$	1	—	—	1	—	—	—	1	—	2
$Pp \times pp$	3	1	2	3	—	—	2	—	—	8
Grand Total	231	351	151	262	145	79	43	43	14	1088

* PP represents homozygous polled; Pp, heterozygous polled, and pp, horned animals.

(?) indicates the horned character of the dam was undetermined, but probably was of the character indicated. P and p under males, females, and hermaphrodites, indicate polled and horned, respectively.

EATON and SIMMONS (1939) have reported hermaphrodism to be inherited as a simple recessive. If, however, as has been suggested by ASDELL (1944), only females are affected, matings between heterozygous normals will give 7 normals: 1 hermaphrodite. Divided as to sex, this ratio becomes 4 males: 3 females: 1 hermaphrodite. Matings of homozygous recessive bucks with heterozygous does should give 50 per cent males, 25 per cent females, and 25 per cent hermaphrodites. There was one such male in the Saanen breed. The number of hermaphrodites observed in each breed did not deviate significantly from expectation. More detailed analysis of the data will be given in the next section of this paper.

The sex ratio for goats is usually reported with a high excess of males. In the Saanens there were 130.7 males per 100 females and in the Toggenburgs 115.0.

If the hermaphrodites are considered as females, the sex ratio approaches more nearly the 50:50 usually expected for most animals. The sex ratio for both breeds combined then becomes 103.0 males per 100 females, or expressed in percentage, 50.7 per cent males.

<div align="center">GENETIC ANALYSIS OF DATA</div>

Since all, or most hermaphrodites, are hornless, there is the possibility that the genes for hornless and hermaphrodism may be linked. Working on this theory and on the known heredity of horns, a detailed analysis of the data may be attempted.

If there is linkage between the genes for the characters concerned, it may be assumed that $Ph\ pH$ is the formula for heterozygous animals of both sexes, P denoting polled, p its allele, and h and H hermaphrodism and normal, respectively. Horned animals of either sex would then be $pH\ pH$ and hermaphrodites $Ph\ Ph$. If, however, only females are affected by the h gene, males of the formula $Ph\ Ph$ would be normal. All polled does according to this scheme are heterozygous and capable of producing hermaphrodites when mated with polled bucks.

There are in each breed in the Beltsville herd family lines based on the relationship of the bucks. These lines are shown in figures 1 and 2. In each of these
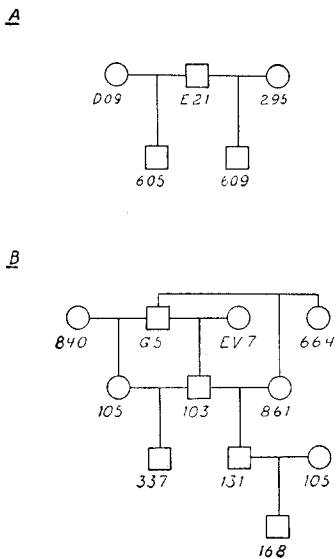

FIG. 1.—Pedigree of two lines of Saanen bucks.—A. Does D09 and 295 were unrelated to E21.—B. 840 was a daughter of 664 and is the only horned doe shown in the pedigree. Neither EV7, 664, nor 840 was related to G5.

lines matings were made to half-sisters, to dams, daughters, and granddaughters of the bucks as well as to unrelated does in an attempt to increase milk production. Only polled bucks were used except in the one case previously mentioned.

The number of progeny from certain bucks or groups of bucks makes possible a rather detailed analysis for the several lines. For convenience in classifying, five classes may be recognized as follows: polled males, horned males, polled females, horned females, and hermaphrodites which are also included in calculating the number of polled animals. For matings between heterozygotes the ratio would be for the five classes named: 3:1:2:1:1. In the case of the homozygous buck in the Saanen breed there would be only three classes, males,
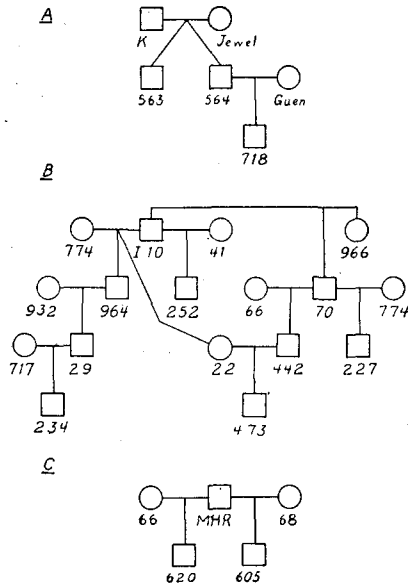

FIG. 2.—Pedigree of three lines of Toggenburg bucks.—A. Neither Jewel nor Guen was related to Buck K.—B. Doe 717 was a full sister to 718 of the previous pedigree. 774 was a daughter of 718×717 of the previous pedigree, and unrelated to I10. 966 was unrelated to I10 and was half-sister to 932. Doe 41 was a daughter of 964×965. 965 was a full sister of 966. 66 was a daughter of I10×717. Does 717, 966, 932, and buck 252 were horned. Buck 227 died and produced no progeny.—C. 66 is the same animal as in pedigree B above. 68 was a daughter of I10×774 in the above pedigree.

females, and hermaphrodites, all polled, in the ratio 2:1:1. The ratio for heterozygous bucks mated with horned does should be 1:1:1:1, there being no hermaphrodites produced. The numbers observed, numbers expected, chi-square and P values for the various lines are shown in table 2. In making these calculations correction to a sex ratio of 50.7 per cent males has been made. For the total value of chi-square, the sums of all the chi-squares were taken, and P was calculated for degrees of freedom equal to the sum of the degrees of freedom for the several groups of similar type matings. P values of 0.05 or higher are considered not significant deviations from the expected class values.

<div align="center">DISCUSSION</div>

The numbers observed in the different classes fit the expected numbers very closely. However, there are a few questions which are not settled. According

TABLE 2

Goodness of fit for observed classes of kids produced by various sires or sire lines in Saanen and Toggenburg goats.

Saanen

	MALES		FEMALES		HERMAPH-RODITES	TOTAL
	POLLED	HORNED	POLLED	HORNED		
E21 line×Polled does						
Observed	22	4	8	3	5	42
Expected	15.97	5.32	10.35	5.18	5.18	42
	D.F.=4	χ^2=4.062	P=0.395			
Male 103×Polled does						
Observed	27	7	10	7	8	59
Expected	22.44	7.48	14.54	7.27	7.27	59
	D.F.=4	χ^2=2.458	P=0.649			
Males 131, 168, and 337 ×Polled does						
Observed	18	7	16	5	5	51
Expected	19.39	6.46	12.57	6.29	6.29	51
	D.F.=4	χ^2=1.610	P=0.857			
Other heterozygous bucks×Polled does						
Observed	49	12	38	18.	13	130
Expected	49.43	16.48	32.05	16.02	16.02	130
	D.F.=4	χ^2=3.140	P=0.532			
Total for 4 groups	D.F.=16	χ^2=11.270	P=0.792			
Homozygous male G5 ×Polled does						
Observed	24	—	14	—	12	50
Expected	25.35	—	12.33	—	12.32	50
	D.F.=2	χ^2=0.306	P=0.858			
Homozygous male G5 ×Horned does						
Observed	10	—	6	—	—	16
Expected	8.11	—	7.89	—	—	16
	D.F.=1	*χ^2=0.483	P=0.489			
Heterozygous males ×Horned does						
Observed	18	15	23	11	—	67
Expected	16.98	16.98	16.52	16.52	—	67
	D.F.=3	χ^2=4.678	P=0.197			

* Yates' "correction for continuity" was used here. It consists in the subtraction of 0.5 from the deviation from expected for each class.

TABLE 2—*(continued)*

*Goodness of fit for observed classes of kids produced by various
sires or sire lines in Saanen and Toggenburg goats.*

Toggenburg

| | MALES | | FEMALES | | HERMAPH- | |
	POLLED	HORNED	POLLED	HORNED	RODITES	TOTAL
K line×Polled does						
Observed	25	9	20	5	4	63
Expected	23.96	7.99	15.33	7.76	7.76	63
D.F.=4		χ^2=4.263		P=0.369		
Male I10×Polled does						
Observed	28	9	13	9	12	71
Expected	27.00	9.00	17.50	8.75	8.75	71
D.F.=4		χ^2=2.408		P=0.658		
Males 70 and 964 ×Polled does						
Observed	23	10	10	7	7	57
Expected	21.68	7.22	14.05	7.03	7.02	57
D.F.=4		χ^2=2.318		P=0.675		
Males 29, 234, 442, and 473×Polled does						
Observed	16	9	13	4	3	45
Expected	17.11	5.70	11.09	5.55	5.55	45
D.F.=4		χ^2=3.916		P=0.414		
MHR, 605 and 620×Polled does						
Observed	16	4	7	6	4	37
Expected	14.07	4.69	9.12	4.56	4.56	37
D.F.=4		χ^2=1.382		P=0.844		
Other heterozygous bucks×polled does						
Observed	25	6	23	11	6	71
Expected	27.00	9.00	17.50	8.75	8.75	71
D.F.=4		χ^2= 4.319		P=0.362		
Total for 6 groups D.F.=24		χ^2=18.606		P=0.770		
Heterozygous bucks ×horned does						
Observed	49	56	57	57	—	219
Expected	55.52	55.52	53.98	53.98	—	219
D.F.=3		χ^2=1.108		P=0.774		

TABLE 3

Birth data for normal and hermaphrodite kids in the Beltsville
Saanen and Toggenburg goats.

	SAANEN	TOGGENBURG
Number of kids born	466	612
Number of males	234	306
Number of females	179	266
Number of hermaphrodites	43	36
Sex undetermined	10	4
Single hermaphrodites (number of cases)	6	11
Twin hermaphrodites (number of cases)	1*	2*
Male with hermaphrodite (number of cases)	13	10
Two males with hermaphrodite (number of cases)	6	1
Female with hermaphrodite (number of cases)	9	6
Two females with hermaphrodite (number of cases)	2	—
Male and female with hermaphrodite (number of cases)	5	4
Number of births	251	341
Average number of kids per birth	1.86	1.79

* In the Saanan breed this case consisted of two hermaphrodites with a normal female; in the Toggenburgs, one case was twin hermaphrodites; the other, two hermaphrodites with a normal male.

to the theory presented, all polled does are heterozygous and should produce hermaphrodites when mated with heterozygous bucks. There were, however, 35 does in the Saanen and 35 in the Toggenburg breeds which did not produce hermaphrodites. It is evident that some of these which produced only one to three or four kids had not produced enough progeny for a hermaphrodite to appear. The average number of kids per doe among the 54 which produced hermaphrodites was 8.0, while the 70 does which produced none averaged 3.8 kids per doe. If crossing over between the Ph- and the pH-bearing chromosomes takes place, a new arrangement of the genes, PH and ph, will be formed. Polled bucks or does carrying these new combinations (PH/PH or PH/ph) should produce polled kids, none of which would be hermaphrodites. The type $PH\ ph$ is a heterozygote and phenotypically indistinguishable from the $Ph\ pH$ heterozygote, but should breed differently. One-half of the horned progeny from $PH\ ph \times PH\ ph$ matings should be males, the other half horned hermaphrodites, the double recessive combination. Also, horned does of the type $pH\ ph$ mated to $PH\ ph$ or $Ph\ ph$ bucks should produce horned hermaphrodites. Since all the hermaphrodites observed have been invariably polled, not only in the Beltsville herd, but apparently in goats in general, the theory of linkage, except perhaps for absolutely complete linkage, may be ruled out.

This leads then to the consideration that a single gene may be responsible for both the polled and hermaphroditic characters. Hermaphrodites are supposed to be due to excessive or delayed hormone secretions during or immediately prior to sexual differentiation. It may be assumed that horn growth or development is inhibited by the same hormone concerned with sexual differentiation. While horns are not manifest at this early period, their anlagen could well be determined. Since P determines the polled condition, it could also be as-

sumed that a single dose of P is not sufficient to disturb normal sexual develop-
ment, but a double dose of P, (PP), modifies sexual differentiation as well as
inhibits horn development. By this theory, the same ratios are derived as by
the two-factor theory. The difference is that two seemingly unrelated charac-
ters, one dominant, the other apparently recessive, are produced by a single
dominant gene which has a recessive effect in regard to one character, her-
maphrodism.

Another question concerns the fertility of homozygous bucks. Why should
not these bucks be so modified sexually that they are infertile or physically
incapable of breeding the same as similar females? ASDELL (1944) proposed
that sex modification in mammals is almost always from female to male. This
is due presumably to an excess of male hormone secreted, either by the devel-
oping embryo or by the dam, during the period of sexual differentiation of the
embryo. GREEN (1942) has shown that an excess of androgen (male hormones)
has little effect on the male rat embryo. The effect is manifested by an acceler-
ation in the development of the prostate and seminal vesicles and an increase
in the size of the penis. These changes would not seem great enough to affect
the fertility of a buck or his ability to perform the sexual act. OTT (1937), how-
ever, believed that infertility in bucks in Bavaria was related to hermaphro-
dism. He reported several cases where the infertile bucks were full brothers to
hermaphrodites. He did not state if these were born in the same season, but
from the number of cases cited it seems obvious that some of them were not.
There are no records in the Beltsville herd to indicate that brothers or sisters
of hermaphrodites were infertile.

There were some cases in the Beltsville herd which were questionable. In an
earlier report EATON (1943) considered them as grades of the intersexual con-
dition. In the present report, however, they have been regarded as males, since
they possessed none of the distinctly female structures found in other cases.
There were three such cases which have not been counted as hermaphrodites
in this paper. Two of them, cases 20 and 27 of the above mentioned report,
were distinctly cryptorchids, with one or both testes undescended, apparently
normal males in every other respect. Case 2, which had difficulty in unsheath-
ing and erecting the penis and had small testicles, though pendant in the
scrotum, probably should be considered a normal male so far as the gene
for intersexuality is concerned. Case 19 which had the unicorn uterus and the
structure reported as an ovotestis, is doubtful. This animal was horned and
was out of a horned doe. She appeared externally like a normal female, and it
was only through dissection for another purpose that the abnormal sex organs
were found. The structure called an ovotestis was very unlike the structures
terminating the uterine horn in any of the other cases examined, being much
smaller and showing none of the characteristics of a testis externally such as
globus major, glogus minor, and the vas epididymis. Sections of other testes
uniformly showed the presence of seminiferous and efferent tubules. None of
these were present in sections of case 19. What was interpreted as rete canals
might have been only loose vascular tissue. The location of the follicle was in

the cortical portion of the organ, agreeing with the location in two other observed cases of ovotestes where seminiferous tubules were present also. This case was considered a female in the present paper.

By the injection of estrogen into the pregnant rat, GREENE (1942) produced hypospadiac males and females and also males with undescended testes. The latter, however, possessed other abnormalities of the male sex organs as well as certain female organs which were present. These facts suggest that hypospadias, cryptorchidism, and hermaphrodism may be effects of the same gene. Experimental results with rats seem to indicate that two separate hormones are involved. However, the gene that controls the excessive secretion of androgens might also control an excessive secretion of estrogens, if excessive secretions of these substances are involved. It is probably necessary to take a time factor into consideration also.

The heredity of cryptorchidism in Angora goats seems to resemble somewhat the heredity of hermaphrodism. LUSH, JONES, and DAMERON (1930) reported aberrant sex ratios of 93.8 males per 100 females among 2,358 Angora goats. When 63 cryptorchids were included, the ratio became 99.2:100. Among progeny of cryptorchid sires the sex ratio was 76.6:100 for 807 animals. When the cryptorchids were inculded, the sex ratio was 104.8 per 100. The above-named authors and WARWICK (1934) proposed a two-factor recessive for the heredity of cryptorchidism, but the number of cryptorchid progeny from cryptorchid bucks was 13.75 per cent, which differs only slightly from the 12.5 per cent expected for hermaphrodites from heterozygous bucks and does. If the three abnormalities, hypospadias, cryptorchidism, and hermaphrodism, are closely related as suggested by experiments with rats, some homozygous males should be incapable of reproduction, either because of infertility due to cryptorchidism in case both testes are involved, or because of mechanical inability to perform the sexual act through the hypospadiac modification of the penis. However, the cryptorchids found in goats, horses, swine, dogs, and other animals may be due to other genes than those concerned in the production of hermaphrodites, since other abnormalities of the reproductive organs are not usually reported in conjunction with them.

The sex ratio for goats is usually reported with a high preponderance of males. HOWLAND (1924) gave the ratio as 139 males per 100 females, while ADDINGTON and CUNNINGHAM (1935) reported 115 males per 100 females. PAGET's data (1943) gave a ratio of 184 per 100. Omitting the hermaphrodites, the ratio for the Beltsville herd was 121.1 per 100 females. By considering the hermaphrodites as females, the sex ratio approached more closely the theoretical 50:50 and agrees fairly well with the sex ratio for other farm animals. In PAGET's data, however, the sex ratio remained high (123:100), even when the hermaphrodites were counted as females. The results, however, suggest that a large proportion of the hermaphrodites must be females genetically.

PAGET (1943) found in his data that there were no cases of single, twin, or triplet hermaphrodites, but they occurred with a normal male, a normal female, or with both. In the Beltsville data there were 17 cases of single her-

maphrodities and three cases where two were born together, one case of twins, one of two hermaphrodites with a normal female, the other two hermaphrodites with a normal male. The data for the Beltsville herd is given in table 3.

The matings in the Beltsville goat herd were made solely on the basis of milk production records. The occurrence of horns and hermaphrodites was merely incidental, except that polled bucks from high-producing dams were selected for the herd sires. The close agreement of the observed number of horned and hermaphrodite animals with those expected by the linkage theory proposed, leads one to believe that we are on the right road to an understanding of the heredity of these characters and the relation between them. It is possible that there may be a low percentage of crossing over to account for some does which appear not to produce hermaphrodites and to explain the very rare occurrence of horned hermaphrodites if they occur at all. If the proposed genetic theory is correct, it should be fairly easy to eliminate hermaphrodism from the goat herd. Matings of polledXpolled will produce hermaphrodites unless some of the animals are crossovers. Mating polledXhorned of either sex will give no hermaphrodites, but one-half of the progeny will be polled and one-half horned. Matings of horned by horned should give no hermaphrodites, but all the progeny will be horned. Only in the case of crossovers will hermaphrodites appear from matings in which one or both parents are horned. From the data presented and the observations of others, such a probability is extremely small. Goat breeders, then should not focus their attention on the elimination of horns from the herd if they desire to eliminate the more undesirable character, hermaphrodism.

SUMMARY

Data are presented which show the frequency of the occurrence of horns and hermaphrodites in goats of the Saanen and Toggenburg breeds.

The data, and observations of others, suggest linkage between the genes for polled and hermaphrodism.

The formula Ph pH is proposed for heterozygous animals of both sexes. A horned animal would be pH pH. P designates the polled character; h, hermaphrodism. An alternate theory of a single dominant gene with recessive effect as regards hermaphrodism is proposed.

The large excess of males reported for goats suggests that a large proportion of the hermaphrodites must be females genetically. When hermaphrodites were counted as females in the data presented, the sex ratio was 103.0 males per 100 females.

Based on the theories suggested, matings between heterozygous polled animals should produce a ratio of 3 polled males: 1 horned male: 2 polled does: 1 horned doe: 1 polled hermaphrodite. The observed numbers agreed well with the expected.

It is suggested that in order to eliminate hermaphrodism from goat herds, matings should be made between a polled and a horned animal, thus giving one-half of the progeny horned, but with no hermaphrodism appearing.

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