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Genetic basis of prolificacy in Meishan pigs

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Research in France and in the UK confirms the prolificacy of the Chinese Meishan breed to be about three to four piglets greater than that of control Large White females. Crossbreeding studies clearly indicate that this breed difference is due to genes acting in the dam and not in the litter itself. There is high heterosis for litter size in F_1 Meishan × Large White crossbred females, such that their litter size is similar to or greater than that of purebred Meishan females. There is some discrepancy between studies about whether the Meishan female has a higher ovulation rate than does the Large White breed and this can be attributed in large part to the different basis upon which breed comparisons have been made. Nevertheless, there may be real genetic differences between Meishan pigs exported to different countries. In young gilts at comparable numbers of oestrous cycles after puberty, the ovulation rate is similar in Meishan and Large White gilts, but in older gilts, and particularly in multiparous sows, Meishan pigs have a higher ovulation rate in British studies. Once comparisons of prenatal survival between breeds have been adjusted for any breed difference in ovulation rate, the main cause of prolificacy in Meishan pigs can be seen to be an enhanced level of prenatal survival. Crossbreeding studies show that this is controlled by the maternal genotype and not that of the embryos. The advantage in prenatal survival to the Meishan pig is clearly present in the post-attachment period (after day 20 of gestation), but may also be present earlier in gestation. Results from a study presented here suggest that Meishan sows have a higher uterine capacity than do Large White sows and this allows them to maintain their higher number of attached embryos through gestation. F_1 Meishan × Large White crossbred females achieve their high litter size via a different route than do purebred Meishan females. These animals have a lower ovulation rate and fewer attached embryos than do purebred Meishan sows, but a very low level of fetal loss allows them to produce litters of similar size. The low level of fetal loss in F_1 females appears to be due to the higher uterine capacity of F_1 females compared with purebred Meishan sows.

Introduction

The Meishan pig is a member of the Taihu group of breeds from the area around Lake Taihu to the west of Shanghai in the People's Republic of China. The Taihu breeds contain the most prolific pigs known and the breeds are in fact closely related and similar in appearance and performance (Cheng, 1983) and genetically (Oishi *et al.*, 1988). Meishan pigs are of great interest for two main reasons. First, they contain genes that are of potential commercial value in the West. With a litter size three or more piglets greater than those of the best European breeds the Meishan pig contains genes with the potential to enhance the efficiency of production of European breeds. Second, an understanding of the control of prolificacy in Meishan pigs would not only broaden our understanding of the genetic basis of reproductive performance in pigs, but would also provide insight into the important mechanisms in other species.

The export of Meishan pigs, initially to France in 1979 (with later dissemination of some of these animals to the Netherlands) and subsequently to other countries, principally the UK, Japan and the United States, has allowed the study and exploitation of these animals in the West to commence. Much progress has been made, but the problem has proved to be more complex than was originally anticipated by some and we are still far from obtaining a complete and clear picture. The purpose of this paper is to summarize the findings on the genetic basis of prolificacy in Meishan pigs, to report some of our own recent results and to look at future directions for the work.

The Basis of Genetic Comparisons

Breed comparisons

Breed comparisons, such as that between the Meishan and European breeds, play a valuable role in the study of genetic variation, but the results must be interpreted cautiously. It is not always clear whether a physiological difference that might explain a phenotypic difference is in fact causal. It must also be borne in mind that pig breeds are neither genetically homogeneous nor are they unchanging over time. There is substantial genetic variation within breeds for most traits and genetic drift or deliberate selection means that two samples from the same breed are likely to differ genetically to a greater or lesser extent. In the case of the Meishan pig, samples exported to the West come from at least two farms which have been genetically isolated for at least 20 years. The British and French Meishan samples are derived from the same farm, but the small size of the samples (six in total to France and 32 to the UK), their separation in time, and the fact that the Jiadin farm from which they were derived maintains four different and genetically distinct lines, means that even these two samples may differ genetically to some extent. The same considerations apply to the breeds with which the Meishan has been compared – animals from the same nominal breed may differ markedly according to their origin and selection history. Thus, although two samples from the same breed are likely to be broadly similar, with a broadly similar basis to their differences from another breed, there are likely to be differences in detail, and this must be borne in mind when comparing the results of different trials.

The use of crossbreeding

Crossbreeding can provide a powerful tool for studying the genetic basis of breed differences. Embryo transfer studies have often been used to distinguish between maternal and embryonic influences on prenatal survival and thus litter size, but crossbreeding studies can often be more effective. By mating females of two breeds to males of the two breeds, purebred females carrying pure and crossbred embryos can be compared. The effect of the maternal genotype can be determined by comparing purebred females from the two lines that are carrying crossbred embryos of the same genotype (for example, Meishan females carrying F_1 embryos sired by Large White boars and Large White females carrying F_1 embryos sired by Meishan boars). Extending the comparisons to include F_1 females allows determination of whether the maternal genes are additive in their action (if F_1 performance is intermediate between the purebreeds) or dominant in their action (if F_1 performance is similar to one or other purebreed). The effect of the embryo genotype (and the additive and dominant action of the genes it carries) can be measured by comparing the performance of purebred females carrying either purebred or crossbred embryos (e.g. Meishan females carrying either Meishan or F_1 embryos and Large White females carrying either Large White or F_1 embryos). In fact crossbreeding will often be more effective than embryo transfer for distinguishing the effects of embryo and dam on prenatal survival because its simplicity allows much larger trials to be performed, it has none of the technical problems that can potentially affect interpretation of embryo transfer studies and it has no deleterious welfare implications for the animals concerned.

Litter Size

Breed comparisons

Results of some representative studies of the number of live births in Meishan compared with European white breeds are shown (Table 1). Comparative studies of litter size in Meishan and European

Table 1. Number of live births (±SEM where reported) in Chinese Meishan and European white pigs

Meishan sample	Parity	White breed used	Number born alive Meishan	White breed	Reference
Chinese	1–2	—	12.9±0.2 (386)[a]	—	Zhang *et al.* (1983)
Chinese	3–10	—	14.8±0.2 (511)	—	Zhang *et al.* (1983)
French	1–3[b]	Large White	13.6±0.3 (93)	10.3±0.5 (44)	Bidanel *et al.* (1989)
French	1–4[c]	Large White	13.6±0.3 (124)	9.7±0.3 (231)	Després *et al.* (1992)
UK	1	Large White	13.2±0.4 (63)	10.0±0.5 (56)	Haley and Lee (1990)
UK	2	Large White	15.0±0.9 (33)	9.8±0.9 (28)	Haley and Lee (1990)
US	1	Yorkshire	11.8±0.6 (21)	7.2±0.7 (20)	McLaren *et al.* (1990)
US	1	—	11.5 (22)	—	Rothschild *et al.* (1990)
US	1	White Synthetic	11.9 (21)	9.5 (61)	Young (1990)

[a]The number of observations is shown in parentheses. Where the original publication gives sizes of litters sired by different breeds, we give weighted means over all sire breeds.
[b]Least squares means over first three parities.
[c]Least squares means over first four parities.

breeds performed both in China (Zhang *et al.*, 1983) and in Europe (for example, Bidanel *et al.*, 1989; Haley and Lee, 1990; Després *et al.*, 1992) indicate mean litter sizes of 13–14 in gilt litters for Meishan pigs and 14 or more in later litters. This is an advantage in prolificacy of three to four piglets born alive compared with the Large White pigs. Results from initial small trials of the Meishan pigs imported into the US suggested lower mean litter sizes in gilt litters (Table 1). The US importation was from a different source from those to the UK and France, but the animals would also be kept under different environmental conditions. It will be necessary to wait for the results of further trials on later parities to determine whether these animals are really less prolific than those imported into Europe.

Crossbreeding studies

Crossbreeding has been used to investigate the genetic control of this prolificacy in two studies (Bidanel *et al.*, 1989; Haley and Lee, 1990). Both studies have used crossbreeding to the Large White breed and, although the sources of the animals in the two trials were different, they gave broadly similar results (Table 2). In essence, both trials led to the conclusion that the breed difference in litter size is under the control of genes in the dam. Thus the litter size depends upon the genotype of the carrying dam, not upon the genotype of the litter she is carrying. In addition, both trials reported maternal heterosis for litter size, estimates of litter size in F_1 females being significantly greater than the mean of the two pure breeds and generally greater (although not significantly so) than those of purebred Meishan females.

Components of Litter Size

A number of different trials have compared the components of litter size – ovulation rate and embryo or prenatal survival – in Meishan and European breeds. Despite the similarity of the litter size results on the French and UK importations, the results of various studies of the components of litter size have not always appeared to be so consistent.

Ovulation Rate

Breed comparisons

Data from breed comparisons of ovulation rate are shown (Table 3). In most studies ovulation rate has been estimated from the number of corpora lutea observed on the surface of ovaries. Dissection of the

Table 2. Genetic estimates from crossbreeding studies of the number of live births in Chinese Meishan pigs

Genes acting in	Effect[a]	Parities 1–4[b]	Parities 1–2[c]
Embryo/fetus	Additive	−0.7 ± 0.8	0.0 ± 0.8
Embryo/fetus	Heterosis	0.9 ± 0.6	−0.5 ± 0.6
Dam (maternal)	Additive	4.2 ± 0.8***[d]	4.9 ± 1.2***
Dam (maternal)	Heterosis	2.6 ± 0.3***	2.3 ± 0.7***
Granddam	Additive	−0.4 ± 0.5	−1.7 ± 0.8*

Values are means ± SEM.
[a]The additive effect is the estimate of the total breed difference due to the additive effect of genes acting at the specified level (i.e. embryo/fetus, dam or granddam). The heterosis effect is the estimated deviation from the mean of the two breeds due to heterosis at the specified level.
[b]Data from Bidanel *et al.* (1989); [c]data from Haley and Lee (1990).
[d]Genetic effects that are significantly different from zero (i.e. have a significant effect on number born alive) are indicated thus: *P: 0.05–0.01; ***$P < 0.001$.

Table 3. Ovulation rate (± SEM where reported) in Chinese Meishan and European white pigs

Meishan sample	Parity	White breed used	Ovulation rate: Meishan	Ovulation rate: White breed	Reference
French	1[a]	LW	14.1 ± 1.2 (8)[b]	18.5 ± 1.2 (7)	Bazer *et al.* (1988)
French	1[c]	LW	14.6 ± 1.7 (7)	14.0 ± 1.8 (26)	Terqui *et al.* (1992)
French	1 (1st oestrus)	LW	9.2 ± 0.8 (13)	13.7 ± 0.7 (15)	Bolet *et al.* (1986)
French	1 (3rd oestrus)	LW	11.7 ± 0.6 (15)	14.4 ± 0.6 (12)	Bolet *et al.* (1986)
French	1–8[d]	LW	17.2 ± 1.2 (4)	17.6 ± 0.8 (4)	Bolet *et al.* (1986)
French	> 1	LW	22 (19)	19 (18)	Terqui *et al.* (1992)
French	—[e]	LW	20.3 (38)	19.1 (19)	Bidanel *et al.* (1990a)
UK	1	C	21.7 ± 0.6 (30)	17.1 ± 0.9 (32)	Ashworth *et al.* (1990)
UK	1 (4th oestrus)	LW	14.1 (18)	14.1 (19)	Hunter *et al.* (1991)
UK	1	C	20.2 ± 0.8 (19)	15.4 ± 0.9 (14)	Ashworth *et al.* (1992)
UK	1	LW	19.0 ± 0.4 (63)	14.9 ± 0.4 (56)	Haley and Lee (1990)
UK	2	LW	22.1 ± 0.9 (33)	17.0 ± 0.9 (28)	Haley and Lee (1990)
UK	3	LW	26.2 ± 1.0 (23)	18.3 ± 1.1 (20)	Wilmut *et al.* (1992)
UK	3	LW	27.8 ± 1.1 (14)	20.7 ± 0.9 (20)	Galvin *et al.* (1993)
US	1	C	14.5 ± 0.5 (20)	17.3 ± 0.8 (17)	Anderson *et al.* (1992)
US	2/3[f]	C	24.9 ± 1.1 (14)	15.2 ± 0.7 (15)	Anderson *et al.* (1992)
US	2	Y	22.7 (19)	16.3 (12)	White *et al.* (1991)

LW: Large White; C: crossbreed; Y: Yorkshire.
[a]Animals all in at least third oestrous cycle.
[b]The number of observations is shown in parentheses.
[c]All animals at their second oestrus.
[d]One to 11 animals per parity, means are least squares estimates over parities.
[e]A mixture of gilts and sows, means are least squares estimates over parities.
[f]Meishan sows were third parity, whereas crossbred sows were second parity.

ovaries would give a slightly more accurate estimate of the number of corpora lutea but estimates from the two methods are very highly correlated (e.g. Haley *et al.*, 1990; J. M. Galvin and C. S. Haley, unpublished results) and so the conclusions of the studies would not be affected by the measurement method used. Comparisons of ovulation rate on the French Meishan sample are generally consistent in finding no difference or a greater ovulation rate in Large White sows. The one exception is the trial of Terqui *et al.* (1992) which reports a significantly higher ovulation rate in multiparous Meishan sows than in multiparous Large White sows. In contrast, all of the comparisons but one on the UK sample found significantly higher ovulation rates in the Meishan than in white pigs. Trials in the US found a significantly higher ovulation rate in multiparous Meishan sows than in multiparous white sows, but Meishan gilts do not always have a higher ovulation rate than do white gilts (Table 3).

One component of the discrepancy between trials in whether a breed difference in ovulation rate is observed is highlighted by the study of Hunter *et al.* (1991) on the UK sample and the comprehensive survey of Christenson (1992) on the US sample. That is, when Meishan gilts are compared with European gilts at a fixed number of cycles after puberty – at which time the Meishan females will be around three months younger and considerably smaller – the ovulation rates are similar. At a similar age, when the Meishan sows have experienced more oestrous cycles, they have a higher ovulation rate, and the difference between the breeds seems to increase as the sows get older. This conclusion is also consistent with data from China (summarized by Cheng, 1983) in which the ovulation rate in the Meishan and other Taihu breeds is low in the period just after puberty, but increases to high values in older sows. This pattern is reported by Christenson (this supplement). This may not be the entire reason for the difference between the results from France and those from elsewhere, because both the study of Bolet *et al.* (1986) and that of Bidanel *et al.* (1990a) included sows of higher parity and found no breed difference in ovulation rate, although their use of least squares means over all parities makes comparison with other studies more difficult.

Crossbreeding studies

We are aware of only three published crossbreeding studies in which ovulation rate has been measured (Bidanel *et al.*, 1990a; Haley and Lee, 1990; Galvin *et al.*, 1993). Although the breed difference in ovulation rate was not the same in these studies, they are consistent in that none of them find any evidence of heterosis for ovulation rate, i.e. the inheritance of ovulation rate is additive, and F_1 females have ovulation rates that are approximately intermediate between those of the two pure breeds. These results are consistent with reports of ovulation rate in studies of crossbreeding between European breeds, in which breed differences in ovulation rate are inherited in an additive fashion (e.g. Blasco *et al.*, 1993).

Conclusions

In conclusion, there appears to be a discrepancy between studies as to whether the Meishan breed has an increased ovulation rate compared with European white breeds. A part of this discrepancy may be due to whether comparisons were carried out with animals of a similar age or of similar number of oestrous cycles after puberty. None the less, there is good evidence that, at least in sows, the ovulation rate in all the Meishan samples is high compared with that in control animals of European white breeds. However, the magnitude of the breed difference may vary according to the Meishan sample in question and it seems likely that there are real genotypic differences between the Meishan samples and between the European white pigs with which they have been compared.

Prenatal Survival

Breed comparisons

Results from breed comparisons of prenatal survival are shown (Table 4). Prenatal survival is defined as the percentage of ova (estimated by the number of corpora lutea) represented as either conceptuses or piglets. At first sight, different studies of prenatal survival are as variable as are those of ovulation rate.

Table 4. Prenatal survival (±SEM if reported) in Chinese Meishan and European white pigs

Meishan sample	Day of gestation	White breed used	Prenatal survival (%) Meishan	Prenatal survival (%) White breed	Regression on OR	PS adjusted for OR Meishan	PS adjusted for OR White breed	F_1	Reference
French	8–11	LW	90 (10)[a]	73 (12)	—	—	—	—	Bazer *et al.* (1988)
French	30	LW	89 (8)	55 (7)	—	—	—	—	Bazer *et al.* (1988)
French	30	LW	92 (36)	70 (28)	—	—	—	—	Terqui *et al.* (1992)
French	30–50	LW	78 (38)	67 (19)	—	78	66	81	Bidanel *et al.* (1990a)
French	Term	LW	84 ± 9 (37)	74 ± 7 (38)	−2.5 ± 0.7	79 ± 4	68 ± 4	—	Bolet *et al.* (1986)
UK	1–3	LW	94 ± 4 (9)	86 ± 4 (13)	0.0 ± 0.6	94 ± 4	86 ± 4	—	Wilmut *et al.* (1992)
UK	2–4	LW	103 ± 4 (15)	92 ± 4 (17)	−0.1 ± 0.9	100 ± 4	88 ± 4	—	Wilmut *et al.* (1992)
UK	6–9	LW	74 ± 5 (14)	77 ± 6 (7)	−1.6 ± 0.9	79 ± 5	67 ± 6	—	Wilmut *et al.* (1992)
UK	20–22	LW	84 ± 4 (14)	74 ± 4 (20)	−1.3 ± 0.4	90 ± 5	71 ± 4	80 ± 2	Galvin *et al.* (1993)
UK	27–31[b]	C	80 ± 6 (10)	72 ± 8 (6)	−0.9 ± 1.0	82 ± 6	69 ± 8	—	Ashworth *et al.* (1992)
UK	Term	LW	68 ± 2 (96)	64 ± 2 (84)	−2.4 ± 0.4	73 ± 2	59 ± 2	77 ± 2	Haley and Lee (1990)
US	9	C	95 ± 2 (14)	96 ± 3 (15)	—	—	—	—	Anderson *et al.* (1992)
US	9–11	C	75 ± 4 (20)	72 ± 10 (17)	—	—	—	—	Anderson *et al.* (1992)
US	27–32	C	73 ± 4 (24)	81 ± 4 (17)	—	—	—	—	Christenson (1992)

LW: Large White; C: crossbreed; PS: prenatal survival; OR: ovulation rate.
[a]The number of observations is shown in parentheses.
[b]Data from control animals only.

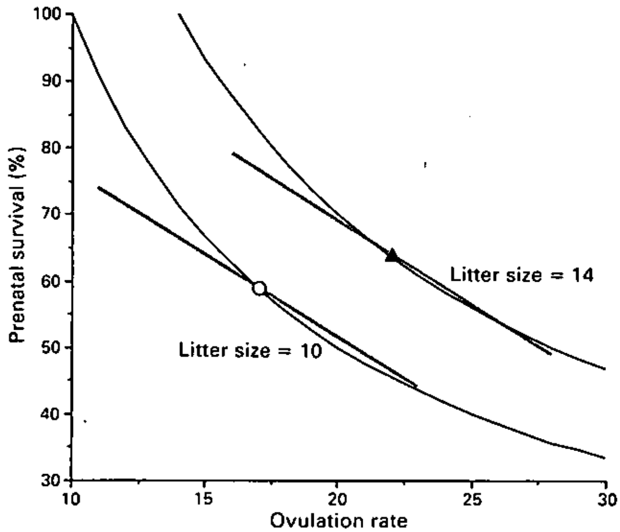

Fig. 1. The relationship between ovulation rate, prenatal survival and litter size in British Meishan versus Large White sows. The two curves (solid lines) connect points that have the same litter size, either 10 or 14 piglets. The Meishan sows have approximately four extra piglets per litter and a higher mean ovulation rate. Within both breeds there is a negative relationship between prenatal survival and ovulation rate, with a decline of around 2.5% in survival for each extra ovum. At the same ovulation rate, Meishan has an advantage of around 15% in prenatal survival and this is the main cause of its prolificacy. The mean for (▲) Meishan and (O) Large White sows are shown and the straight dashed lines represent the average within breed relationships between the ovulation rate and the mean prenatal survival, with their length representing the approximate spread (± 2 SD) within the breed.

However, differences in ovulation rate between trials complicate comparisons of prenatal survival, because there is a negative phenotypic association within breeds between prenatal survival and ovulation rate (Wrathall, 1971). Thus, if the same negative association exists between breeds, a difference in their ovulation rate could either lead to an apparent difference in prenatal survival where none exists, or reduce a difference that actually exists.

In studies of prenatal survival in the UK in which ovulation rate has differed between breeds, we have included a regression of prenatal survival on ovulation rate and adjusted to a common mean ovulation rate (see Table 4). We have found no significant difference between breeds or parities in the relationship of prenatal survival with ovulation rate and the relationship does not differ significantly from linearity. Our results are consistent with other studies within European breeds (for example Wrathall, 1971) in showing a decline in prenatal survival to term of about 2.5% for each ovum increase in ovulation rate. Before adjustment for breed differences in ovulation rate, observed differences in prenatal survival to term between the Meishan and the Large White breeds are small in the UK studies; however, once adjusted to a common ovulation rate, the difference is about 14% (Haley and Lee, 1990; Table 4). This is very similar to the breed difference in survival to term at a constant ovulation rate in the two studies of the French Meishan sample that have been reported (Bolet *et al.*, 1986; Bidanel *et al.*, 1990a; Table 4). A summary of the relationship between prenatal survival and ovulation rate and the difference between Meishan and Large White breeds obtained from studies in the UK is shown (Fig. 1).

Although differences in ovulation rate in Meishan and Large White females are found in the UK sample, the main cause of the difference in litter size is the difference in prenatal survival. This can be shown by including a regression on ovulation rate in the analysis of litter size and adjusting to a constant ovulation rate. When this is done, the breed difference in litter size at a constant ovulation rate is similar to that obtained without adjustment for differences in ovulation rate (Haley and Lee, 1990). This can be visualized by reference to Fig. 1, where it can be seen that increasing ovulation rate in Large White females to the level observed in the Meishan female would increase litter size only slightly. The remainder of the increase in litter size in the Meishan comes from an increase in prenatal survival. Thus the results of the studies of the UK and French Meishan samples are consistent in concluding that a difference in prenatal survival is the main cause of the prolificacy of the Meishan breed.

Studies in the UK (see Table 4) are consistent with previous studies (e.g. Wrathall, 1971) in showing a tendency for the regression of prenatal survival on ovulation rate to become more negative as gestation progresses. Not all studies show a significant difference in prenatal survival in early gestation between the Meishan and white breeds, even after adjustment for ovulation rate differences. This is not very surprising given the small size of some of the trials and the magnitude of the experimental variation. There is, however, a relatively clear consensus between the trials performed in the UK and France that, after adjustment to a common ovulation rate, there is a difference in embryo survival that can be observed in the post-attachment period (days 20–50 of gestation). The advantage to the Meishan breed in the 20–50 day period of gestation ranged from 11 to 34% in the studies performed in France (with no adjustment for breed differences in ovulation rate, but these were small or in favour of the Large White in these studies) and was 13% and 19% (after adjustment to a common ovulation rate) in the two studies performed in the UK. Some evidence of a breed difference in embryo survival in the pre-attachment period is shown (Table 4), although the trials have been limited in both size and number.

Studies on the US importation of Meishan pigs (Anderson *et al.*, 1992; Christenson, 1992) have yet to demonstrate an advantage in prenatal survival compared with European breeds (Table 4). The reported breed comparisons have not, however, been adjusted for the breed differences in ovulation rate that are found in the US studies (Table 3). Furthermore, the early studies of the US importation of Meishan pigs do not show that it has any large advantage in litter size (Table 1) and so it is perhaps not surprising that no differences in prenatal survival have been reported.

Crossbreeding studies

Three crossbreeding studies of prenatal survival have been performed, but prenatal survival has been measured at different times in each (Table 4). The study of Haley and Lee (1990) found marked heterosis for prenatal survival to term, such that F_1 females had about 10% higher prenatal survival than did purebred Meishan females before adjustment for differences in ovulation rate. After adjustment for differences in ovulation rate, prenatal survival in F_1 females is higher than in purebred females, but not significantly so. In the study of Bidanel *et al.* (1990a), performed at 30–50 days of gestation, F_1 females also showed marked heterosis for prenatal survival, with levels slightly greater than in Meishan females. Galvin *et al.* (1993) found no evidence for heterosis in embryo survival at 20–22 days of gestation; however, F_1 females had levels intermediate between those of the two pure breeds. If these latter results are confirmed, it suggests that heterosis evolves in the later part of gestation. Thus, although the Meishan and F_1 females have similar litter sizes, the mechanisms underlying these may differ, with the F_1 female having a lower ovulation rate (at least in the UK animals), a lower number of attached fetuses at day 20–22 of gestation, but a very low level of fetal loss compared with Meishan females. It may then be this low level of fetal loss, and not a particularly low level of embryonic loss, that causes heterosis for overall prenatal survival, and thus for litter size, in F_1 females.

All of the crossbreeding studies of prenatal survival are consistent in that none of them find any contribution of the genotype of the embryo to its own survival; differences in survival seem to be solely determined by the genotype of the dam. Given that differences in litter size seem to be controlled by the genes of the dam, this last result is not surprising.

Conclusions

In summary, once differences in ovulation rate and their associated effect on prenatal survival have been accounted for, there are clear differences in prenatal survival between Meishan and European white

Table 5. Ovulation rate, number of live births and embryo survival (±SEM) in unilaterally ovariectomized–hysterectomized Meishan, Large White and F_1 crossbred pigs

Characteristic	Genotype of female Meishan	Large White	F_1 crossbreed
Number of records	26	32	28
Ovulation rate (OR)	19.4 ± 0.7^{a}	15.0 ± 0.7^{b}	18.6 ± 0.7^{a}
Number of live births	7.0 ± 0.6^{ab}	6.0 ± 0.6^{a}	8.2 ± 0.6^{b}
Prenatal survival (%)	37.6 ± 4.0^{a}	41.2 ± 3.8^{a}	47.6 ± 4.4^{a}
Prenatal survival adjusted for OR	42.0 ± 3.8^{ab}	36.8 ± 3.6^{a}	49.2 ± 3.9^{b}

A restricted maximum likelihood analysis of first and second parity data was performed. Within rows, means with different superscripts are significantly different ($P < 0.05$).

pigs and these are the main cause of the prolificacy of the Meishan breed. These differences are controlled by genes expressed in the dam and not those of the embryo. The breed difference in prenatal survival to term is about 15% and this difference appears fully established by 20 days of gestation and is possibly present earlier. High levels of heterosis for prenatal survival are observed in F_1 females and this seems to be due to a low level of fetal loss, rather than a particularly high level of survival in early gestation.

Uterine Capacity

The advantage of the Meishan over European white breeds in terms of prenatal survival is fully established in early gestation and yet it seems unlikely that this is the sole basis of its prolificacy. European breeds subject to an increased number of attached embryos, either via superovulation or via embryo transfer, tend to lose them after day 30 of gestation, presumably because of the effects of uterine crowding (Wrathall, 1971). Thus it seems likely that Meishan sows have mechanisms that allow them to overcome the effects of uterine crowding in the latter part of pregnancy to complement their high level of embryo survival and maintain their fetuses to term. As already suggested, F_1 females seem to cope even better and have very low levels of fetal loss.

The measurement of 'uterine capacity', as such an ability has been termed, is not easy in pigs. In normal gilts or sows, variation in both ovulation rate and embryonic survival means that uterine capacity may not be challenged in many individual pregnancies (i.e. there may be fewer embryos than the number of fetuses that the animal can carry to term). Christenson *et al.* (1987) have argued that the use of unilateral hysterectomy–ovariectomy provides an effective measure of uterine capacity. In unilateral hysterectomy–ovariectomy, hypertrophy of the remaining ovary results in approximately the usual number of ova being crowded into a single uterine horn. Thus the number of viable embryos is likely to exceed the uterine capacity in all females and twice the resulting litter size may provide a measure of uterine capacity in normal intact females.

We have recently used the unilateral hysterectomy–ovariectomy method in a small trial comparing uterine capacity in Meishan, Large White and F_1 (progeny of Large White males × Meishan females) females (C. S. Haley, G. J. Lee, I. Wilmut, A. MacDonald, M. Ritchie and M. Thompson, unpublished). The means of the results from the first two parities are shown (Table 5). The ovulation rates in the remaining ovary in this study were similar to those we have previously observed in intact females and the breed difference between Meishan and Large White females was maintained. The litter sizes observed in this study support the hypothesis that the Meishan sow has a higher uterine capacity than the Large White sow and that the uterine capacity of F_1 females is higher still. If it is assumed that doubling the observed litter sizes provides an estimate of uterine capacity, the uterine capacity of the Large White females would have been greater (at 12) than their normal average litter size, as has been observed previously (e.g. Christenson *et al.*, 1987), whereas that of the Meishan females would have been close to their normal litter size (at 14.0). On the basis of these results, F_1 females would have had a uterine capacity for two more piglets (at 16.4) than would the Meishan. These results, taken together with those of Galvin *et al.* (1993), suggest that in some normal intact Meishan females litter size could be limited by uterine capacity, as a high ovulation rate and embryo survival in this genotype may result in more attached embryos than the uterine capacity. However, under normal conditions, the litter size of F_1 females may be limited by their ovulation rate and level of embryo survival, as fewer embryos may attach than the female can support to term.

Potential Factors Affecting Prenatal Survival

Embryo survival

There is reasonable evidence that differences in survival in early gestation contribute to the prolificacy of Meishan pigs, but as yet there is no clear mechanism for this. One possibility that has been explored is that differences in the rate and homogeneity of embryonic development may contribute. Bazer *et al.* (1988) concluded that Meishan embryos were both more rapidly developing and more homogeneous than those from the Large White in the period up to elongation (about 8–12 days after mating). Terqui *et al.* (1992) reported that Meishan embryos were more advanced than Large White embryos at about days 1–4 of gestation. However, Wilmut *et al.* (1992) found no difference in the rate of development between breeds in the period from day 1 to day 10 of gestation and Anderson *et al.* (1992) reported less developed embryos in the Meishan than in white crossbred sows at days 9–12 of gestation. In addition, neither of these latter studies found evidence of much greater homogeneity in embryos developing in Meishan females compared with those in white females. Thus the role played by rate and homogeneity of development in the high embryonic survival of Meishan sows is uncertain.

Other breed differences that could contribute to the advantage of the Meishan in embryo survival have been observed (e.g. Bazer *et al.*, 1991). It is, however, difficult to determine the role that these differences have and this will remain a major challenge for future work. In addition, although the cross-breeding studies of litter size and its components suggest that it is the maternal, rather than the embryonic, genotype which leads to enhanced embryo survival, it is not yet clear whether this is achieved by the dam producing 'better quality' oocytes or by providing a better environment for the developing embryo. Identifying the relative importance of these two factors would be valuable in allowing future studies aimed at identifying potential mechanisms to be more accurately focused.

Fetal survival

The results reported here support the view that a component of prolificacy in Meishan sows is a high 'uterine capacity'. This is unlikely to be associated with uterine size *per se* as several studies report that Meishan sows have uteri similar in size or smaller than those of the Large White sows (Bazer *et al.*, 1988; Bidanel *et al.*, 1990b; Galvin *et al.*, 1993). The control of fetal growth in such a way as to ameliorate the effects of fetal crowding may be a factor. At birth, piglets born to Meishan dams are about 20–25% lighter than those born to Large White dams, and this difference is largely controlled by the maternal genotype (Bidanel *et al.*, 1990c; Haley and Lee, 1990). The differences in fetal weight that precede those in birth weight are beginning to become apparent by day 30 of gestation, at which time they are also largely under the control of the maternal genotype (Ashworth *et al.*, 1990, 1992). These differences are not a simple effect of crowding, as adjustment for breed differences in litter size has little effect on breed differences in fetal weight at day 30 of gestation (Ashworth *et al.*, 1990, 1992) or birth weight (Bidanel *et al.*, 1990c; Haley *et al.*, 1992). It is possible that the ability of Meishan sows to produce and maintain smaller fetuses is central to its ability to support greater litter sizes in later pregnancy.

Another factor that may reduce the effects of uterine crowding is suggested by Galvin *et al.* (1993), who report that there is less variation in spacing between embryonic attachment sites in Meishan than in

Large White sows. This could have the effect of equalizing competition between adjacent fetuses such that the chance of an individual fetus suffering unduly and dying owing to the effect of crowding is reduced.

Galvin *et al.* (1993) report significant heterosis in F_1 sows for uterine weight and length at days 20–22 of gestation. The same study also found significant heterosis for increased embryonic growth and reduced variation between embryos within a sow in measures of growth and reduced variation in spacing between attachment sites. Thus uterine size and control of embryonic growth and spacing could play a role in the low fetal mortality and high uterine capacity of the F_1 sows.

Evidence for a Major Gene

The breed comparisons and crossbreeding studies that have been performed have shown that the main factor underlying the difference in litter size is improved prenatal survival and that this is due to genes expressed in the dam, not in the embryo. One hypothesis is that a single major gene (rather than many genes of small effect) that is fixed for alternative alleles in the Meishan and European breeds is responsible for this difference. The studies of mean differences between genotypes cannot throw light on the number of genes that control the breed difference – one gene or many genes could produce the same pattern of genotypic differences.

If a major gene were responsible for the breed difference, in theory its presence could be detected in backcross or F_2 generations from a cross between the Meishan and European breed. In these generations the gene would be segregating, i.e. there would be females of two (in the backcrosses) or three (in the F_2) genotypes, and thus there should be increased variation in litter size in these generations compared with the pure breeds or the F_1 generation. Mandonnet *et al.* (1992) have investigated the possibility of a major gene by using data on litters born to females in the purebred, F_1, backcross and F_2 generations. These authors found very little evidence for a single gene being responsible for the breed difference in litter size. It is, however, possible that there are several genes of important effect, each perhaps contributing to a different component of the reproductive performance of the Meishan pigs (e.g. ovulation rate, embryo survival, fetal survival).

Conclusions

Studies in Meishan pigs suggest that the genetic control of prolificacy is complex. Ovulation rate differences are very clear in some comparisons of the Meishan with European breeds, but their role in the prolificacy of Meishan pigs is relatively minor. The key to the prolificacy of Meishan pigs is enhanced prenatal survival and genetic studies have shown that this is controlled by the genotype of the dam and not that of the embryo/fetus. Enhanced prenatal survival in Meishan pigs seems to require both increased survival during the embryonic period and increased fetal survival. Both of these areas merit further study. It is not yet clear whether the enhanced embryonic survival is due to improved 'quality' of ova produced by the Meishan female or to the provision of an improved environment for the developing embryo. Factors affecting uterine capacity in Meishan and F_1 females need to be determined and the potential role of the control of fetal growth assessed. For genetic studies powerful new tools are being provided by the mapping of the pig genome (Haley and Archibald, 1992). The use of molecular genetic markers from such maps may allow some of the genes contributing to the prolificacy to be mapped and perhaps ultimately cloned and studies have identified some of the traits on which the mapping efforts can be concentrated. The Meishan pig provides one of the few models in which prenatal survival is clearly enhanced and will continue to provide fascinating research material.

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References

Anderson LH, Christenson LK, Christenson RK and Ford SP (1992) Investigations into the control of litter size: comparisons of Chinese (Meishan) and American pigs. In *Proceedings of the International Symposium on Chinese Pig Breeds*, pp 86–90 Ed. C. Runsheng. Northeast Forestry University Press, Harbin

Ashworth CJ, Haley CS, Aitken RP and Wilmut I (1990) Embryo survival and fetal growth following reciprocal embryo transfer between Chinese Meishan and Large White gilts. *Journal of Reproduction and Fertility* **90** 595–603

Ashworth CJ, Haley CS and Wilmut I (1992) Effect of regumate on ovulation rate, embryo survival and conceptus growth in Meishan and Landrace × Large White gilts *Theriogenology* **37** 433–443

Bazer FW, Thatcher WW, Martinat-Botte F and Terqui M (1988) Conceptus development in Large White and prolific Chinese Meishan pigs *Journal of Reproduction and Fertility* **84** 37–42

Bazer FW, Thatcher WW, Martinat-Botte F, Terqui M, Lacroix MC, Bernard S, Ravault JP and Dubois DH (1991) Conceptus–endometrial interactions affecting composition of uterine flushings from Large White and prolific Chinese Meishan gilts *Reproduction, Fertility and Development* **3** 51–60

Bidanel JP, Caritez JC and Legault C (1989) Estimation of crossbreeding parameters between Large White and Meishan porcine breeds. I. Reproductive performance *Génétique, Sélection, Evolution* **21** 507–526

Bidanel JP, Caritez JC and Lagant H (1990a) Ovulation rate and embryonic survival in gilts and sows with variable proportions of Meishan (MS) and Large White (LW) genes. Mean performance and crossbreeding parameters between MS and LW breeds. In *Symposium sur le Porc Chinois* pp 109–110 Eds M Molenat and C Legault. INRA, Paris

Bidanel JP, Caritez JC and Lagant H (1990b) Characteristics of the reproductive organs of gilts and sows with variable proportions of Meishan (MS) and Large White (LW) genes. In *Symposium sur le Porc Chinois* pp 107–108 Eds M Molenat and C Legault. INRA, Paris

Bidanel JP, Caritez JC and Legault C (1990c) Estimation of crossbreeding parameters between Large White and Meishan porcine breeds. II. Growth before weaning and growth of females during the growing and reproductive periods. *Génétique, Sélection, Evolution* **22** 431–455

Blasco A, Bidanel JP, Bolet G, Haley CS and Santacreu MA The genetics of prenatal survival in pigs and rabbits: a review *Livestock Production Science* (in press)

Bolet G, Martinat Botte F, Locatelli A, Gruand J, Terqui M and Berthelot F (1986) Components of prolificacy in hyperprolific Large White sows compared with the Meishan and Large White breeds *Génétique, Sélection, Evolution* **18** 333–342

Cheng P-L (1983) A highly prolific pig breed of China – the Taihu pig *Pig News and Information* **4** 407–425

Christenson RK (1992) Ovulation rate and embryo survival in Chinese Meishan and Occidental crossbred females. In *Proceedings of the International Symposium on Chinese Pig Breeds* pp 91–98 Ed. C Runsheng. Northeast Forestry University Press, Harbin

Christenson RK, Leymaster KA and Young LD (1987) Justification of unilateral hysterectomy–ovariectomy as a model to evaluate uterine capacity in swine *Journal of Animal Science* **65** 738–744

Després P, Martinat-Botte F, Lagant H, Terqui M and Legault C (1992) Comparaison des performances de reproduction des truies appartenant à trois génotypes: Large White (LW), Large White «hyperprolifique» (LWh), Meishan (MS) *Journées Recherche Porcine en France* **24** 345–350

Galvin JM, Wilmut I, Day BN, Ritchie M, Thomson M and Haley CS (1993) Reproductive performance in relation to uterine and embryonic traits during early gestation in Meishan, Large White and crossbred sows *Journal of Reproduction and Fertility* **98** 377–384

Haley CS and Archibald AL (1992) Porcine genome analysis. In *Genome Analysis Vol 4. Strategies for Physical Mapping* pp 99–129 Eds KE Davies and SE Tilghman. Cold Spring Harbor Laboratory Press, New York

Haley CS and Lee GJ (1990) Genetic components of litter size in Meishan and Large White pigs and their crosses. In *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production* XV pp 458–481 Eds WG Hill, R Thompson and JA Woolliams. Organising Committee, Edinburgh

Haley CS, Ashworth CJ, Lee GJ, Wilmut I, Aitken RP and Ritchie W (1990) British studies of the genetics of prolificacy in the Meishan pig. In *Symposium sur le Porc Chinois* pp 85–97 Eds M Molenat and C Legault. INRA, Paris

Haley CS, D'Agaro E and Ellis M (1992) Genetic components of growth and ultrasonic fat depth traits in Meishan and Large White pigs and their reciprocal crosses *Animal Production* **54** 105–115

Hunter MG, Biggs C, Ashworth CJ and Haley CS (1991) Ovarian function in Chinese Meishan pigs *Biology of Reproduction* **44** Supplement 1 145 (Abstract)

McLaren DG, White BR, Wheeler MB, Hurley WL, Clamp HW, Gonyou HW, McKeith FK, Novakofski J, Mackie RI, Schook LB, Dziuk PJ and Gianola D (1990) Evaluation of Chinese swine breeds: early results at the University of Illinois and research plans. In *Symposium sur le Porc Chinois* pp 115–116 (Abstract) Eds M Molénat and C Legault. INRA, Jouy-en-Josas

Mandonnet N, Le Roy P, Caritez JC, Elsen JM, Legault C and Bidanel JP (1992) Existe-t-il un gène à effet majeur expliquant la prolificité exceptionelle de la race Meishan? *Journées Recherche Porcine en France* **24** 25–30

Oishi T, Tanaka K, Otani T and Tamada S (1988) Genetic variations of blood groups and biochemical polymorphisms in Meishan pigs *Bulletin of the National Institute of the Animal Industries (Japan)* **48** 1–10

Rothschild MF, Christian LL, Hsieh CY, Whipp SC, Michaels RD, Evans LE, Gueniat NM, Hoganson D, Jacobson C, Paul P, Sell J, Nissen S, Ewan R, Roth JA, Goff B, Kunesh J and Ross RF (1990) Evaluation of Chinese breeds: research plans and early results at Iowa State University. In *Symposium sur le Porc Chinois* pp 117–118 (Abstract) Eds M Molénat and C Legault. INRA, Jouy-en-Josas

Terqui M, Bazer FW and Martinat-Botte F (1992) Hyperprolificité de la truie Meishan: le point sur les méchanismes en jeu au début de la gestation *Journées Recherche Porcine en France* **24** 351–356

White BR, McLaren DG, Dziuk PJ and Wheeler MB (1991) Attainment of puberty and the mechanism of large litter size in Chinese Meishan females versus Yorkshire females *Biology of Reproduction* **44** Supplement 1 160 (Abstract)

Wilmut I, Ritchie W, Haley CS, Ashworth CJ and Aitken RP (1992) A comparison of rate and uniformity of embryo development in Meishan and Large White pigs *Journal of Reproduction and Fertility* **95** 45–56

Wrathall AE (1971) *Prenatal Survival in Pigs. Part 1. Ovulation Rate and its Influence on Prenatal Survival and Litter Size in Pigs.* Commonwealth Agricultural Bureaux, Farnham Royal

Young LD (1990) Evaluation of Chinese breeds: research plans and early results from the US Meat Animal Research Center. In *Symposium sur le Porc Chinois* pp 119–120 (Abstract) Eds M Molénat and C Legault. INRA, Jouy-en-Josas

Zhang W-C, Wu J-S and Rempel WE (1983) Some performance characteristics of prolific breeds of pigs in China *Livestock Performance Science* **10** 59–68