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Endocrine and follicular studies in Meishan pigs

M. G. Hunter, C. Biggs and L. S. Faillace

Department of Physiology and Environmental Science, University of Nottingham, Sutton Bonington Campus, Loughborough, Leics LE12 5RD, UK

The enhanced early embryonic survival in Chinese Meishan compared with Large-White gilts may be due, in part, to differences in ovarian and endocrine function, particularly during the periovulatory period. The overall patterns of oestradiol, LH and FSH secretion were not different between Meishan and Large-White hybrid controls during this period, although circulating inhibin concentrations were higher in Meishan gilts. Thus, there appeared to be a decreased sensitivity to inhibin feedback on FSH secretion in Meishan gilts. Behavioural oestrus was exhibited earlier relative to the LH surge in Meishan gilts than in Large-White hybrid gilts, but the time interval from the oestradiol peak until the LH surge was similar in both breeds. This finding suggests that Meishan gilts are more sensitive in terms of initiating a behavioural response, but not in terms of positive feedback. Although preovulatory follicular characteristics were as variable in Meishan as in Large-White hybrid gilts, follicles from Meishan gilts were smaller, but contained a higher concentration of oestradiol in the follicular fluid. This was probably due to increased aromatase activity in both granulosa and theca cells of Meishan follicles. The enhanced maturation of the intrafollicular environment in Meishan gilts was reflected in the oocyte population which was at a more advanced stage of development in the period preceding ovulation. In addition to decreasing the time between onset of oestrus and ovulation, advancing the LH surge to coincide with onset of oestrus (via hCG administration) decreased embryo survival at day 30 of gestation. It is concluded that both endocrine and follicular mechanisms have a role in ensuring the prolificacy in the Meishan breed.

Introduction

The precise physiological mechanisms responsible for the enhanced prolificacy in Chinese Meishan pigs are yet to be fully elucidated, although it is known that Meishan pigs benefit from reduced embryonic mortality at a given ovulation rate which leads to larger litters (Haley and Lee, 1990; Wilmut *et al.*, 1992). Cross-breeding studies have indicated that this is the result of genes acting in the mother (Haley and Lee, 1990), which could be effective either through the oocyte or the uterus. Several studies have suggested that variation in the rate of preimplantation embryonic development is a likely cause of the high embryonic loss in European breeds of pig (Anderson, 1978; Pope *et al.*, 1986; Pope *et al.*, 1990) and, furthermore, that this embryonic variation is a direct consequence of heterogeneity in the preovulatory follicular population (Xie *et al.*, 1990a, b). There is considerable evidence that porcine follicles produce factors that influence oocyte maturation, fertilization and early embryonic development (Moor *et al.*, 1990; Yoshida *et al.*, 1990; Ding and Foxcroft, 1992) and it is relevant, therefore, to investigate the characteristics of follicles and oocytes of Meishan pigs in conjunction with the endocrinology and timing of events during the periovulatory period. Current information on the above topics will be reviewed and the implications of the data with regard to the enhanced prolificacy in Meishan pigs will be discussed.

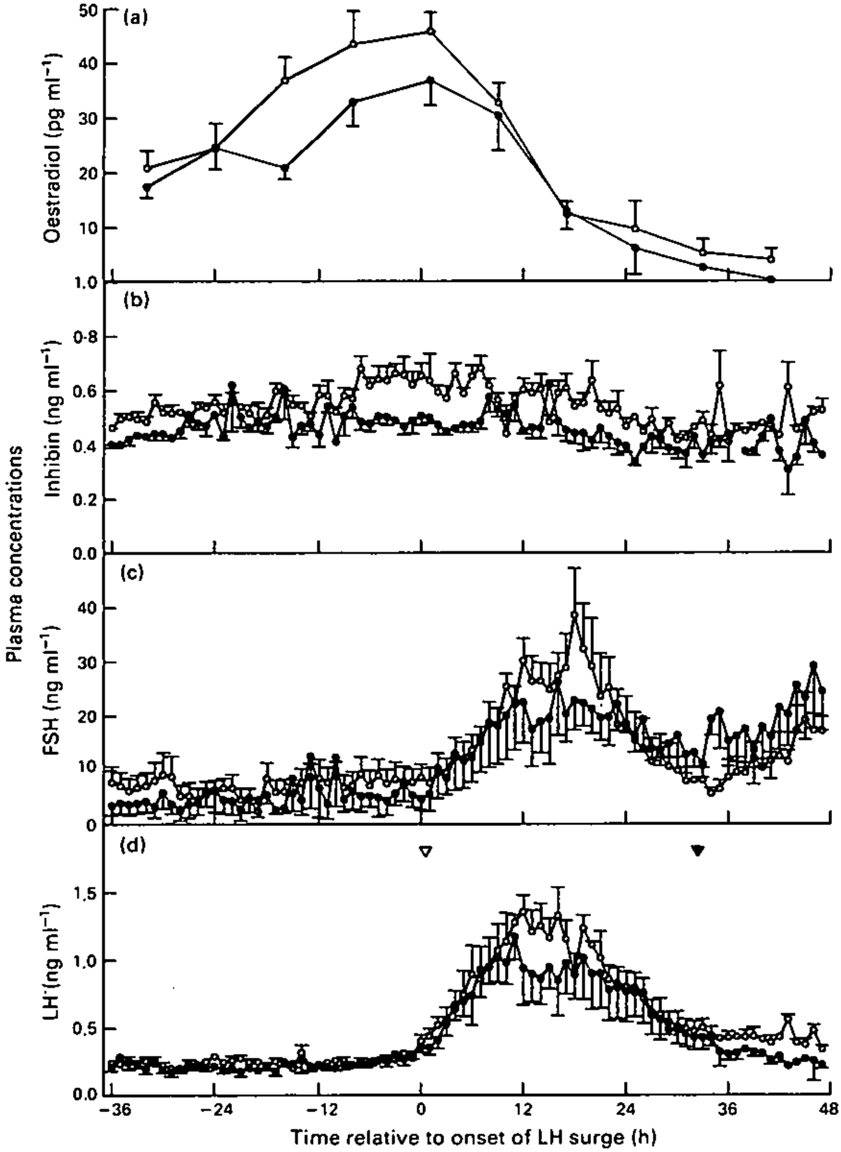

Fig. 1. Endocrine profile showing mean and SEM of plasma (a) oestradiol, (b) inhibin, (c) FSH and (d) LH, synchronized around the onset of the LH surge for Meishan (○, $n = 6$) and Large-White hybrid (●, $n = 5$) gilts. The mean onset of behavioural oestrus is indicated for Meishan (▽) and Large-White hybrid (▼) gilts. (Reproduced from Hunter *et al.*, 1993.)

Endocrinology of the periovulatory period

Preliminary observations by Ellendorff *et al.* (1988) suggested that the LH surge is higher in Meishan pigs than in contemporary European Large-White pigs, but these results were not supported by the more substantial studies of Hunter *et al.* (1993) (Fig. 1). In this experiment, animals of similar reproductive status, that is from third to sixth oestrus, were sampled during 4 days and were also checked each hour for a lordosis response to back pressure. The results were standardized to the time of onset of the LH surge (time 0) and the duration of the preovulatory LH and FSH surges and the interval between the onset of

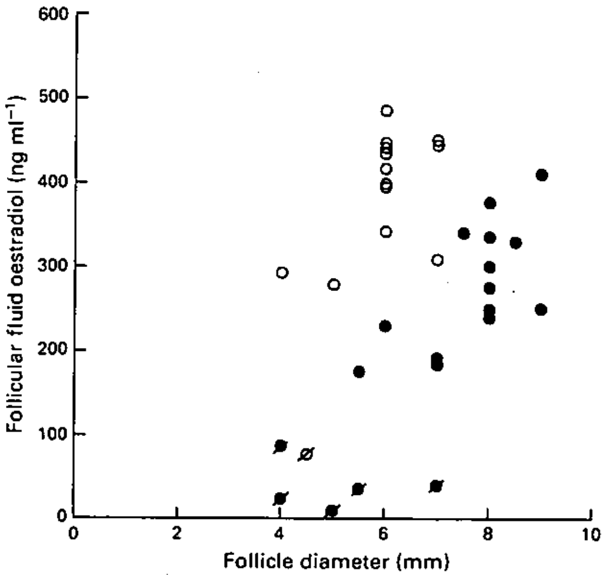

Fig. 2. Follicular fluid oestradiol concentration (ng ml^{-1}) versus follicle diameter (mm) for all follicles ≥ 4 mm diameter recovered from one typical animal from (○) Meishan and (●) Large-White hybrid gilts. The lower points with the line through represent those follicles rejected as not destined to ovulate on the basis of oestradiol concentration.

behavioural oestrus and the time of the LH surge and peak oestradiol concentrations were compared for the two breeds. The time of onset of oestrus relative to the onset of the LH surge is also shown; Meishan gilts exhibited oestrus significantly earlier ($P < 0.005$) than did Large-White hybrid females, with a range of -15 to $+14$ h in Meishan gilts and $+14$ to $+40$ h in Large-White hybrid gilts. There were similar differences in the interval between the onset of oestrus and the peak of the preovulatory rise in oestradiol concentrations; however, the interval between peak oestradiol and the LH surge remained constant between the breeds (3.7 ± 5.7 versus 1.2 ± 8.0 h ($P > 0.1$) for Meishan and Large-White hybrid gilts, respectively). Although there were no significant differences in the mean basal concentrations of either LH or FSH in the pre-surge period, in peak surge concentrations of LH and FSH or in the duration of the LH surge, there was a consistent trend for gonadotrophin concentrations to be higher in Meishan gilts than in Large-White hybrid gilts.

Although there was no evidence of a fall in inhibin concentration coincident with the FSH surge as observed by Mukai *et al.* (1989) and Hasegawa *et al.* (1988) in gilts, inhibin concentrations were significantly higher ($P < 0.05$) in Meishan gilts during the preovulatory period. Nevertheless, this was not accompanied by a reduction in circulating FSH concentrations, suggesting a decreased sensitivity to the feedback of inhibin on FSH secretion in Meishan gilts. This conclusion is further supported by the finding that treatment with charcoal-stripped follicular fluid was less effective in reducing FSH in ovariectomized Meishan gilts than in ovariectomized Large-White hybrid gilts (Tilton *et al.*, 1993). There have also been reports of higher circulating concentrations of inhibin in prolific breeds of sheep (Tsonis *et al.*, 1988). This differential sensitivity to inhibin feedback may allow for an increased FSH:LH ratio at critical times in the oestrous cycle of Meishan pigs and may also be associated with the increased ovulation rates in older, parous Meishan sows.

The difference in the timing of onset of oestrus relative to the LH surge provides an endocrine basis for the extended interval between onset of oestrus and ovulation in Meishan gilts and sows reported by Martinat-Botte *et al.* (1989) Faillace *et al.* (1991) and Wilmut *et al.* (1992) and discussed below. This interval was approximately 49 h in Meishan sows compared with 34 h in European controls. As circulating oestradiol concentrations were not different between the breeds, Meishan gilts appear to be more

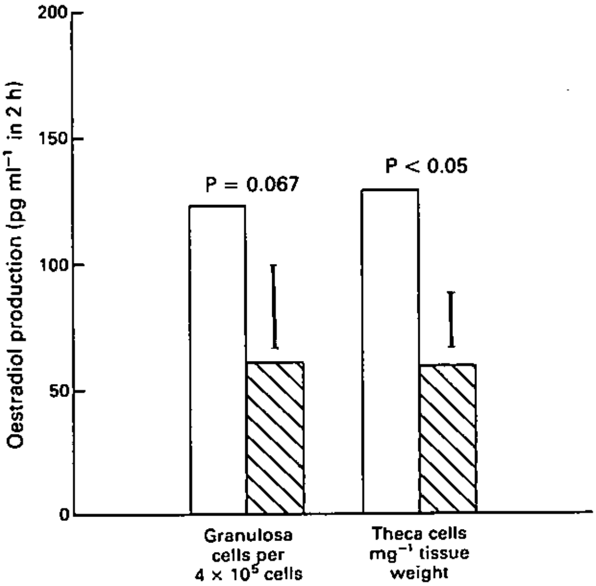

Fig. 3. Mean ± SED of oestradiol production, as a measure of aromatase activity, from granulosa and theca cells of the ten largest preovulatory follicles from (☐) Meishan and (▧) Large-White hybrid gilts (n = 5 per breed). Aromatase activity is expressed for granulosa cells per 4 × 10^5 cells and for theca per mg tissue weight.

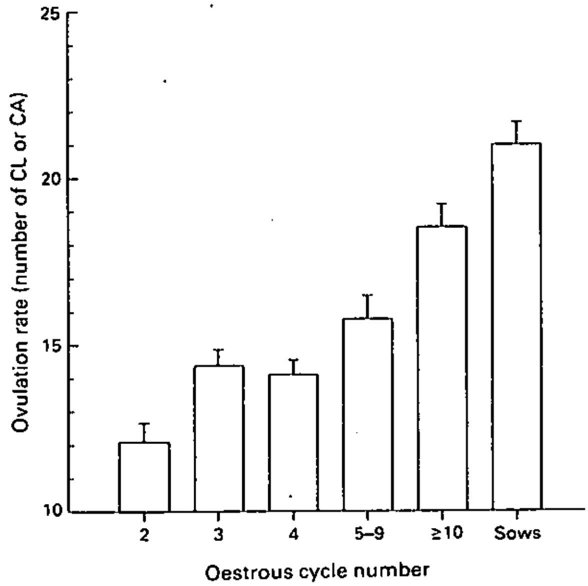

Fig. 4. Means and SEM for ovulation rate (number of corpora lutea (CL) or corpora albicantia (CA)) in Meishan gilts at 2nd (n = 22), 3rd (n = 24), 4th (n = 18), 5th to 9th (n = 9) and 10th to 21st (n = 12) oestrous cycle or in primiparous sows (n = 12) (L. S. Faillace, C. Biggs and M. G. Hunter, unpublished observations).

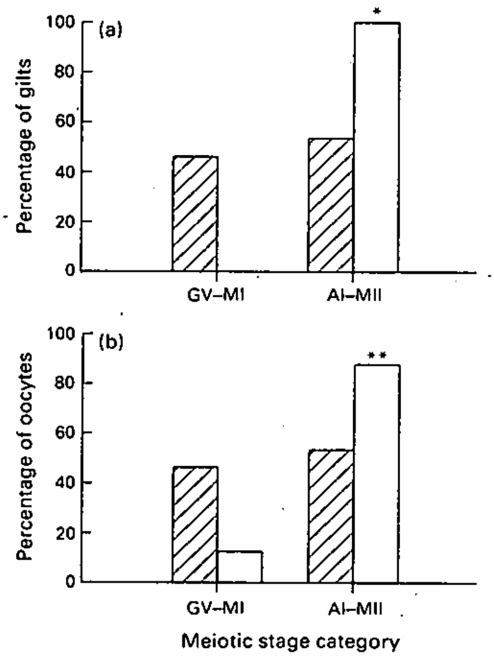

Fig. 5. Percentage of (▨) Large-White hybrid and (□) Meishan (a) gilts (Large-White, n = 13; Meishan, n = 16) that had a majority of their oocytes in one of two meiotic stage categories and (b) total oocytes (Large-White hybrid, n = 176; Meishan, n = 207) that fell into each of the same two categories. The GV–MI category included germinal vesicle, prometaphase and metaphase I and the AI–MII category included anaphase I, telophase I and metaphase II. The proportions of gilts and oocytes were compared between breeds using χ^2 analysis. A greater proportion of *Meishan gilts ($P < 0.03$) and **Meishan oocytes ($P < 0.001$) were in the more advanced category (AI–MII) than were Large-White hybrid gilts and oocytes.

sensitive in terms of initiating a behavioural response, but not in terms of positive feedback, as the time interval from peak oestradiol to the onset of the LH surge was similar in both breeds. An increased interval between onset of oestrus and the LH surge was reported in prolific breeds of sheep (Land *et al.*, 1973) and this may have arisen from different oestradiol secretion patterns or from differential sensitivity to feedback control. In the Meishan breed, this longer period of oestrous behaviour would result in earlier and more frequent mating, which may provide benefits in terms of sperm transport and capacitation (Claus, 1990) or result in a faster fertilization process (Terqui *et al.*, 1992) and therefore contribute to the prolificacy in Meishan pigs.

Follicular Development in Meishan gilts

Comparisons were made between characteristics of preovulatory follicles recovered from Meishan and Large-White hybrid gilts in the late follicular phase preceding their fifth oestrous cycle to determine whether there is an ovarian basis for the enhanced prolificacy in Meishan gilts. A total of 177 follicles per breed were classified as preovulatory on the basis of oestradiol concentrations in follicular fluid and follicles of Meishan pigs were found to be smaller (6.5 versus 7.2 mm; $P < 0.06$), contain less follicular fluid (157 versus 109 µl; $P < 0.005$), but contain a similar amount of DNA in the granulosa cell layer ($P > 0.1$) compared with Large-White hybrid gilts (Biggs *et al.*, 1993). In a study of follicles recovered during the late follicular phase both before and after an hCG injection Downey and Driancourt (1992) also reported a smaller size of the Meishan follicles. Again, it is interesting to note that prolific breeds of sheep have smaller follicles than do nonprolific breeds (Driancourt *et al.*, 1991; Webb and Gauld, 1985; McNatty *et al.*, 1986).

Another important finding was that Meishan follicles, although smaller than follicles of Large-White hybrid gilts, contained a similar amount of oestradiol such that the actual concentration in the fluid was higher (319 versus 234 ng ml^{-1} for Meishan and Large-White hybrid gilts, respectively, $P < 0.06$; Biggs *et al.*, 1993). Data from individual follicles from one representative animal of each breed are shown (Fig. 2). The higher oestradiol concentration in the Meishan follicles of gilts indicates that follicles were at a more advanced stage of development in terms of the intrafollicular environment than follicles in Large-White hybrid gilts and the implications of this are discussed below. Concentrations of inhibin in follicular fluid were similar in both breeds ($P > 0.1$) which resulted in a trend ($P = 0.06$) towards less inhibin in Meishan follicles. A similar reduction in inhibin secretion by individual preovulatory follicles has been reported for prolific ewes (Driancourt *et al.*, 1991). Guthrie *et al.* (1992) reported increased expression of inhibin mRNAs in porcine follicles selected to ovulate and there is now considerable evidence that inhibin and related proteins have a paracrine role in ovarian function (Findlay *et al.*, 1991). The higher concentration of circulating inhibin in Meishan gilts reported above suggests that non-ovarian sources of inhibin (Knight, 1991) make a significant contribution to circulating concentrations.

There was, however, no evidence for reduced variability in any of the follicular characteristics investigated (diameter, follicular fluid volume, DNA content of the granulosa cells, oestradiol, testosterone and inhibin in the follicular fluid, hCG binding to granulosa cells), suggesting that there is no increase in synchrony of Meishan follicles at this stage of development.

The higher oestradiol concentration in the Meishan follicles may be due to earlier activation of aromatase activity in Meishan follicles, increased androgen substrate availability or simply oestradiol being secreted into a smaller volume of fluid. These possibilities were investigated in two separate experiments using follicles recovered either during the early (day 16) or late (day 20) follicular phase from Meishan and Large-White hybrid gilts. Aromatase activity in granulosa cells recovered from alternate follicles $\geqslant 3$ mm was higher in follicles from Meishan than from Large-White gilts ($P < 0.05$) and was enhanced most in Meishan follicles from the larger size classes when expressed either on a per follicle basis or per µg DNA (M. G. Hunter, A. R. Pickard and L. S. Faillace, unpublished observations). This finding suggests that even during the early follicular phase, aromatase activity was enhanced in Meishan follicles. In the second experiment, aromatase activity was assessed in both granulosa and theca tissue of preovulatory follicles and was significantly higher in the theca tissue when expressed per mg of tissue ($P < 0.05$) and tended ($P = 0.06$) to be higher in the granulosa when expressed on a per cell basis (Fig. 3). There was no difference between the breeds in secretion of testosterone by the theca tissue during incubation, although presumably more was converted to oestradiol by the Meishan theca tissue. The use of a specific aromatase inhibitor would enable the measurement of total androgen production and this area needs further evaluation. Nevertheless, aromatase activity was higher in the Meishan granulosa cells which were provided with the same concentration of androgen substrate (100 ng ml^{-1}) as those from Large-White hybrids. Together, these experiments show increased aromatase activity in follicles of Meishan gilts during both the early and late follicular phase and suggest that this is the basis for the higher oestradiol concentration in the follicles of Meishan gilts. The mechanism by which the Meishan gilt gains the increased aromatase activity is uncertain. Circulating FSH concentrations were similar during the late follicular phase (see above); however, nothing is known about circulating concentrations during the early follicular phase. It is also possible that an increased sensitivity to FSH in the follicles of Meishan gilts resulted in the higher follicular oestradiol concentration. Aromatase activity has been shown to be high in granulosa cells from follicles of particular sizes in prolific breeds of sheep (McNatty *et al.*, 1986) and peak values are achieved in ewes by smaller follicles than those in nonprolific breeds. This additional similarity between the characteristics observed in prolific pigs and sheep raises the possibility that similar mechanisms may operate to increase fecundity in both species.

Ovulatory Characteristics

Oestrogenic follicles are more likely to respond rapidly and synchronously to the preovulatory LH surge, and Downey and Driancourt (1992) noted that progesterone production by follicles of Meishan gilts was higher after hCG administration (to mimic the endogenous LH surge) than by similar follicles from Large-White hybrids, suggesting more efficient luteinization in the Meishan gilts. Furthermore, Ashworth *et al.* (1991) showed that the rise in circulating plasma progesterone concentrations between days 0 and 15 occurred earlier and reached a maximum sooner in Meishan than in Large-White hybrid gilts, which is consistent with more rapid luteinization. Characterizing the chronology of events during oestrus in the Meishan gilt is crucial for the study of the prolificacy of this breed, as many experiments depend on the accurate prediction of the time of ovulation and subsequent fertilization. As previously mentioned, the interval from the onset of behavioural oestrus to ovulation is substantially longer in Meishan gilts (Faillace *et al.*, 1991; Terqui *et al.*, 1990) and sows (Wilmut *et al.*, 1992) than in European breeds (Signoret *et al.*, 1972; Terqui *et al.*, 1990; Wilmut *et al.*, 1992) and results from breed differences in the timing of the LH surge relative to the onset of behavioural oestrus (Hunter *et al.*, 1993). This conclusion has been further substantiated by more recent findings (Faillace *et al.*, 1991): advancing the LH surge to coincide with onset of oestrus in Meishan gilts (by administering hCG at first observed onset of oestrus) significantly shortened the interval from onset of oestrus to ovulation (44.2 and 48.7 h for hCG-treated and control gilts, respectively; $P < 0.05$). Furthermore, this treatment resulted in a similar interval from hCG to ovulation to that observed in European gilts (Dziuk and Baker, 1962; Baker *et al.*, 1969), as well as an earlier increase in circulating progesterone concentration compared with untreated Meishan gilts (L. S. Faillace, H. M. Picton and M. G. Hunter, unpublished observations). More importantly, shortening the interval from onset of oestrus to ovulation in Meishan gilts had no influence on ovulation rate, but tended to decrease both the number of live embryos (17.2 versus 12.8; $P < 0.08$) and embryonic survival rate (92.1 versus 75.8%; $P = 0.10$) at day 30 of gestation (L. S. Faillace, H. M. Picton and M. G. Hunter, unpublished observations). In European breeds, advancing the LH surge in cyclic gilts and induction of ovulation in prepubertal gilts has no detrimental effects on either the ovulatory process (Pope *et al.*, 1988) or embryo survival by day 35 of gestation (van der Lende and Shoenmaker, 1990). Considered collectively with the fact that naturally cyclic Meishan gilts have preovulatory oocytes at more advanced stages of maturation before ovulation (Faillace *et al.*, 1992) and ovulate during a shorter interval than European gilts (Terqui *et al.*, 1990), this evidence suggests that the chronology of events within the oestrous period may be critical to the prolificacy of Meishan pigs.

The number of ova shed at ovulation is an important component of litter size in swine. In European breeds ovulation rate increases both with increasing number of oestrous cycles experienced and parity (Kirkwood and Aherne, 1985; Anderson, 1987). There has been considerable discrepancy in reports of ovulation rate in the Meishan sows owing to several confounding factors such as chronological age, reproductive age, genetics and environmental factors. Although multiparous Meishan sows clearly have a high ovulation rate (Cheng, 1983; Haley and Lee, 1990; Anderson *et al.*, 1992; Christenson, 1992), the situation in gilts is more obscure. Most reports of ovulation rate in Meishan gilts exported from China found that ovulation rates remained low (Bazer *et al.*, 1988; Terqui *et al.*, 1990; Anderson *et al.*, 1992), even when observed in gilts of 280 days of age (Christenson, 1992). Our own findings show that the number of ova shed by Meishan gilts increased with reproductive age and approached that of first parity Meishan sows only when they experienced ≥ 10 cycles (Fig. 4). In contrast, one investigation reported that young gilts (2–3 oestrous cycles) of the same genetic foundation as our own pigs had a high ovulation rate (Ashworth *et al.*, 1992).

Oocyte Maturation and Fertilization

The highly oestrogenic nature of the follicles of Meishan gilts may provide the key to the prolificacy of this breed by providing a more suitable environment for oocyte maturation and subsequent fertilization.

It is possible that the more oestrogenic follicles will produce more viable ova (Hunter and Wiesak, 1990) which are better prepared to survive the early stages of gestation and this was investigated in subsequent experiments. Comparisons were made between characteristics of follicles recovered from Meishan and Large-White hybrid gilts in the immediate preovulatory period (within 8 h of ovulation) to determine whether differences in the process of oocyte maturation could account for the enhanced early embryonic survival in the Meishan breed. A total of 447 preovulatory follicles was examined from the two breeds and follicles from Meishan gilts were once again found to be smaller and have less follicular fluid but had similar follicular fluid progesterone contents. However, classification of the oocytes from these follicles into discrete stages of meiotic development showed that oocytes of Meishan gilts were more mature than those of Large-White gilts. For most Meishan gilts (15 of 16) examined during this period, the majority of their oocytes were in the final stages of maturation, whereas for almost half (6 of 13) of the Large-White hybrid gilts the majority of their oocytes were in the less developed stages of maturation (Fig. 5). Analysis of all preovulatory oocytes from the two breeds (regardless of the gilts from which they were derived) showed that, overall, more oocytes from Meishan gilts were in the more advanced categories (Fig. 5, $P < 0.001$).

As embryonic development of Meishan pigs is more advanced initially (Terqui *et al.*, 1992) and more uniform at subsequent stages (Bazer *et al.*, 1988) and as there is a greater rate of embryo survival in Meishan pigs, it is not surprising that this breed benefits from ovarian processes that lead to a more mature population of oocytes. Studies of European gilts have shown that there is a skewed population of oocytes in the immediate preovulatory period and that most oocytes are at more advanced stages of maturation (Xie *et al.*, 1990b). Furthermore, the less advanced oocytes in the population were found to give rise to the less advanced embryos and it is these less developed embryos that are thought to be the victims of early mortality (Pope *et al.*, 1990).

Conclusions

As the Meishan oocyte population is more mature before ovulation (Faillace *et al.*, 1992) and as ovulation occurs later in oestrus and is of a shorter duration (Terqui *et al.*, 1990) compared with European breeds, a hypothesis can be developed in which preovulatory follicles of Meishan gilts gain enhanced maturity early in oestrus (before the LH surge) and, therefore, are better able to respond to the subsequent LH surge. This results in more efficient luteinization (Downey and Driancourt, 1992) and an earlier rise in circulating progesterone concentrations (Ashworth *et al.*, 1991). A mature population of ooyctes ovulated over a short time would ensure synchronous fertilization and embryo development with relatively few embryos succumbing to primary mortality. Our recent finding of reduced embryo survival in Meishan gilts that had their LH surge advanced to coincide with the onset of oestrus supports this hypothesis. Current studies are investigating oocyte maturation and follicular endocrinology of preovulatory follicles under conditions *in vitro* to investigate breed differences in the response of such follicles to gonadotrophic stimuli.

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