

314. Mendl, M., Zanella, A.J., Broom, D.M. and Whittemore, C.T. 1997. Studying birth sex ratio in domestic pigs. *Anim. Behav.*, 53, 432-435.

Studying birth sex ratio in domestic pigs

MICHAEL MENDEL*, ADROALDO J. ZANELLA†, DONALD M. BROOM‡ & COLIN T. WHITTEMORE§ *Genetics and Behavioural Sciences Department, Scottish Agricultural College-Edinburgh †Department of Animal Science, Michigan State University ‡Department of Clinical Veterinary Medicine, University of Cambridge §Institute of Ecology and Resource Management, University of Edinburgh.

In their commentary, Meikle et al. (1997) point out that if social status exerts its effects on birth sex ratio in the domestic pig, *Sus scrofa*, via stress-related changes in adrenal activity prior to or around implantation (days 12–14 post-mating), our (Mendl et al. 1995) study would have failed to detect this. We agree, and made exactly this point in our original paper (page 1369). Meikle et al. (1997) conclude from this that the design of our (Mendl et al. 1992) study was inappropriate for ‘a reasonable test of any model of sex-ratio variation’ in pigs. This we do not agree with. Our analysis was able to examine whether the effect of social status on birth sex ratio reported by Meikle et al. (1993) may have occurred by sex-specific embryo mortality during the post-implantation period of pregnancy. At the outset of our analysis, we did not feel that we should dismiss this possibility a priori, without examining the available empirical evidence. We had a number of reasons for taking this view.

(1) A variety of candidate mechanisms may underlie sex-ratio adjustment in mammalian species. These include sperm selection, the degree of synchronization between uterine and embryo activity, and sex-specific embryo and fetal mortality (see Krackow 1995). Presently, we lack a full understanding of these mechanisms and their relative importance. As Krackow (1995, page 274) stated, ‘convincing evidence of a physiological mechanism of sex ratio adjustment is completely lacking’. Furthermore, it is possible that more than one mechanism is involved in any one species. For example, Meikle & Drickamer (1986) suggested that pre-fertilization sperm selection affects sex ratio in house mice, *Mus musculus*, while Krackow (1990) provided evidence that sex-specific post-implantation embryo mortality can influence sex ratio in the same species. Given this current state of knowledge and the fact that we were presenting the first attempt to examine mechanisms underlying sex-ratio variation in the pig, we felt that there was no case for ruling out one possible mechanism (sex-specific post-implantation embryo mortality) without at least attempting to investigate it.

(2) Meikle et al. (1997, page 429) argue against the occurrence of post-implantation adjustment of sex ratio in pigs, by speculating that this should result in litters of different sex ratio also being of different size, something that they (Meikle et al. 1993) did not find. However, Hornig & McClintock (1996) showed that the lack of a relationship between sex ratio and litter size at birth does not rule out the possibility that pre-birth adjustments to the sex ratio occur via offspring losses after implantation. In their study, post-implantation sex-ratio biasing occurred when uterine horns were overcrowded. Some offspring loss was inevitable as litter size decreased to that which the uterus could effectively sustain. Sex-ratio biases were achieved through selective loss of these offspring, and litter sizes at birth were similar in both male- and female-biased litters.

(3) In pigs, although embryo mortality occurs prior to and around implantation time, there is

evidence that it also occurs later on in pregnancy. Surveying 26 studies, Pope & First (1985) proposed that embryo mortality in pigs occurred in two phases: between conception and day 40 (ca 30%), and from day 40 to term (ca 10–20%). They emphasized the importance of limited uterine and nutritional resources as a cause of fetal mortality in later stages of gestation. Chen & Dziuk (1993) showed that significant fetal losses occurred between days 29 and 35 (well after implantation) in gilts where uterine space per fetus was below 25 cm (ca 50% of embryos develop under these conditions). In addition, they noted that there may be sex-specific effects of limited uterine space on fetal growth and survival during the later stages of pregnancy.

If there is an adaptive basis to sex-ratio variation (evidence for this is lacking, Clutton-Brock & Iason 1986; Krackow 1995), selection might favour parental manipulations of sex ratio that occurred when the parent had accurate information about the environmental conditions in which lactation, probably the most energetically costly part of parental investment (at least twice as costly per day as gestation in the pig, AFRC 1990), would take place. In other words, manipulations might be expected to occur close to the time of birth. Obviously, there would also be selection against the costly loss of well-developed young. As pig fetuses double their length during the last 25 days of a 116 day gestation (Altman & Ditmer 1962), selection against fetal loss would be especially strong during this period.

On the basis of the above, it is clear that sex-ratio changes can take place in pigs in the post-implantation period that we (Mendl et al. 1992) studied and, from an adaptive perspective, that they might be as likely to occur then as earlier on in pregnancy.

(4) Meikle et al. (1993) measured dominance rank in sow groups on days 1–5 after group formation, and days 30, 60 and 90 after mating, but not during the period when females were mated (days 5–15 after group formation) and implantation took place. Apparently, they made no measurement of dominance rank for the first 30 days following insemination, the period in which they (Meikle et al. 1997) suggest that dominance status affects sex ratio. During this period, sows were in oestrus. It is known that the activity of sows increases during oestrus (Signoret 1970). They investigate, push and mount other sows

(Schenk 1967), and are likely to receive more aggressive and sexual responses. Thus, it is likely that social activity and organization in groups changed during the period (possibly as long as 10 days) in which different group members were in oestrus in the Meikle et al. (1993) study. Consequently, it is impossible to be sure that dominance relations and each sow's experience of 'social stress' during this period were the same as those measured by Meikle et al. before and after this time. As Meikle et al. (1993) were only able to relate sex ratio to pre-mating and post-implantation measures of dominance, it was not unreasonable to speculate that dominance ranks post-implantation could have been responsible for the observed effects.

For the above reasons we could not rule out the possibility that sex-specific post-implantation embryo mortality played a role in sex-ratio variation in Meikle et al.'s (1993) study. As we had access to data that could be used to test this possibility, we felt it worthwhile to analyse and present these data. Furthermore, unlike Meikle et al. (1993), information was available for the same sows across several pregnancies, breed and parity effects were controlled for, and we had access to physiological data that are needed to address hypotheses about underlying mechanisms of sex-ratio variation.

We therefore disagree with Meikle et al.'s (1997) assertion that our data did not allow 'a reasonable test of any model of sex-ratio variation'. There were logical reasons for using our data in this context, and the negative results of our analysis cannot be used retrospectively to invalidate the study.

Meikle et al. (1997) make two other points which we should like to address here to reiterate and clarify our position. First, they (page 429) assert that we (Mendl et al. 1995) rejected the hypothesis that there may be an adrenal-mediated mechanism for sex-ratio variation, with low-ranking females producing larger amounts of adrenocortical hormones than high-rankers. This misrepresents our conclusions. In our analysis, we failed to find a simple linear relationship between rank and adrenal activity (cf. Krackow 1995; Mendl & Deag 1995; Creel et al. 1996). Although Meikle et al. (1997, page 429) suggest that such a relationship was found in the Mendl et al. (1992) study, they omit to mention that, in this study, the lowest ranking 'No Success' pigs had similar

adrenal activity to the highest-ranking 'High Success' pigs (i.e. we observed an inverted U-shaped relationship between adrenal activity and rank). In our (Mendl et al. 1995, page 1369) discussion of this issue, we pointed out that there might be quite different relationships between rank and adrenal activity in different social groupings. Thus, we did not reject the possibility that a linear relationship may occur, but suggested that it might only be found in certain sorts of group structure, for example in small groups.

More generally, it may be that different forms of relationship between an animal's social status and its adrenal function could explain the different findings of studies investigating the association between rank and birth sex ratio. To examine this possibility, such studies should proceed via two steps; first, an examination of how rank is related to adrenal activity, and hence how rank may relate to 'social stress'; and second, an analysis of how adrenal activity is related to birth sex ratio (see Mendl et al. 1995, page 1365).

Meikle et al. (1997) attack our suggestion that our data lend some support to the Local Resource Competition model in pigs. We were careful not to over interpret our analysis in this respect. We emphasized that the most parsimonious interpretation of our findings was that they showed little evidence of a strong relationship between maternal social status and birth sex ratio but, if considered in terms of the Trivers & Willard (1973) and Local Resource Competition models, they tended to provide some support for the latter. In particular, our analysis of the nutritional study by Yang et al. (1989) suggested that poor nutritional state throughout pregnancy (including around the implantation period) did not result in the female-biased sex ratio predicted by Trivers & Willard. In fact, undernourished mothers produced significantly more males than females during one pregnancy. Since nutritional state is a good indicator of an animal's condition, this at least raises a question mark over the relevance of the Trivers & Willard model to pigs.

We used these findings to emphasize, as others have done (Clutton-Brock & Iason 1986; Krackow 1995), how important it is to assess critical assumptions underlying theories of adaptive variation in secondary sex ratio. In the pig, as in other species, arguments for or against the appropriateness of the two competing theories are based on speculation and will continue to be so

until it can be demonstrated that parents do enhance their fitness by biasing the sex ratio.

Studies of the effects of maternal social status on birth sex ratio in the pig, and the mechanisms underlying such effects, are at an early stage. We feel that both Meikle et al. (1993) and Mendl et al. (1995) have provided valuable information in this area. As we have argued, we do not agree that Mendl et al.'s (1995) analysis was unable to address this research topic. We look forward to further information from forthcoming work by Meikle and colleagues.

M.M. is grateful for support from the Scottish Office Agriculture Environment and Fisheries Department.

REFERENCES

- AFRC 1990. *Nutrient Requirements of Sows and Boars*. Reading: HGM Publications.
- Altman, P. L. & Ditmer, D. S. 1962 (Eds). *Growth Including Reproduction and Morphological Development*. Washington D.C.: Federation of American Societies for Experimental Biology.
- Chen, Z.-Y. & Dziuk, P. J. 1993. Influence of initial length of uterus per embryo and gestation stage on prenatal survival, development, and sex ratio in the pig. *J. Anim. Sci.*, **71**, 1895-1901.
- Clutton-Brock, T. H. & Iason, G. R. 1986. Sex ratio variation in mammals. *Q. Rev. Biol.*, **61**, 339-374.
- Creel, S., Creel, N. M. & Monfort, S. L. 1996. Social stress and dominance. *Nature, Lond.*, **379**, 212.
- Hornig, L. E. & McClintock, M. K. 1996. Male sexual rest affects litter sex ratio of newborn Norway rats. *Anim. Behav.*, **51**, 991-1005.
- Krackow, S. 1990. Sex-specific embryonic mortality during concurrent pregnancy and lactation in house mice. *J. exp. Zool.*, **256**, 106-112.
- Krackow, S. 1995. The developmental asynchrony hypothesis for sex ratio manipulation. *J. theor. Biol.*, **176**, 273-280.
- Meikle, D. B. & Drickamer, L. C. 1986. Food availability and secondary sex ratio variation in wild and laboratory house mice (*Mus musculus*). *J. Reprod. Fert.*, **78**, 587-591.
- Meikle, D. B., Drickamer, L. C., Vessey, S. H., Rosenthal, T. L. & Fitzgerald, K. S. 1993. Maternal dominance rank and secondary sex ratio in swine. *Anim. Behav.*, **46**, 79-85.
- Meikle, D. B., Vessey, S. H. & Drickamer, L. C. 1997. Testing models of adaptive adjustment of secondary sex ratio in domestic swine. *Anim. Behav.*, **53**, 428-431.
- Mendl, M. & Deag, J. M. 1995. How useful are the concepts of alternative strategy and coping strategy in applied studies of social behaviour? *Appl. Anim. Behav. Sci.*, **44**, 119-137.

- Mendl, M., Zanella, A. J. & Broom, D. M. 1992. Physiological and reproductive correlates of behavioural strategies in female domestic pigs. *Anim. Behav.*, **44**, 1107–1121.
- Mendl, M., Zanella, A. J., Broom, D. M. & Whitemore, C. T. 1995. Maternal social status and birth sex ratio in domestic pigs: an analysis of mechanisms. *Anim. Behav.*, **50**, 1361–1370.
- Pope, W. F. & First, N. L. 1985. Factors affecting the survival of pig embryos. *Theriogenology*, **23**, 91–105.
- Schenk, P. M. 1967. An investigation into the oestrous symptoms and behaviour of sows. *Z. Tierz. Züchtungsbiol.*, **83**, 87–110.
- Signoret, J. P. 1970. Reproductive behaviour of pigs. *J. Reprod. Fert. suppl.*, **11**, 105–117.
- Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**, 90–92.
- Yang, H., Eastman, P. R., Phillips, P. & Whitemore, C. T. 1989. Reproductive performance, body weight and body condition of breeding sows with differing body fatness at parturition, differing nutrition during lactation, and differing litter size. *Anim. Prod.*, **48**, 181–201.