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Maternal social status and birth sex ratio in domestic pigs: an analysis of mechanisms

MICHAEL MENDEL*, ADROALDO J. ZANELLA†, DONALD M. BROOM‡ &
COLIN T. WHITTEMORE§

*Genetics and Behavioural Sciences Department, Scottish Agricultural College-Edinburgh

†Institut für Tierhygiene, Verhaltenskunde und Tierschutz, Munich

‡Department of Clinical Veterinary Medicine, University of Cambridge

§Institute of Ecology and Resource Management, University of Edinburgh

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Abstract. In support of the Trivers & Willard model of adaptive variation in birth sex ratio, recent research showed that high-ranking female domestic pigs, *Sus scrofa*, gave birth to a greater proportion of sons than low-ranking females. Differences in maternal nutritional status caused by differential access to food of high- and low-ranking females, or differences in adrenal activity as the result of stress experienced during agonistic encounters are two possible mechanisms underlying these findings. This study examined the role that these mechanisms may play, and further investigated the relationship between social status and birth sex ratio in the pig, not only within, but also across pregnancies. The reproductive performance of a group of 37 female pigs was recorded across four pregnancies. Social status and adrenal activity of individuals were assessed during the first and fourth pregnancies. Within each pregnancy, there was no relationship between social status and birth sex ratio. Despite cross-pregnancy consistency in social status, there was no consistency in the sex ratios of the females' consecutive litters. However, high-ranking females produced significantly fewer males across all four pregnancies. There was no linear relationship between a female's social status and adrenal activity, and no evidence that adrenal activity was related to subsequent birth sex ratio. Maternal weight gain during pregnancy (an indicator of nutritional status) was unrelated to birth sex ratio. Data from a study of maternal nutrition in pigs also failed to show a clear relationship between nutritional status and birth sex ratio. Differences between the findings of the present and previous studies are discussed from functional and causal perspectives.

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In support of the Trivers & Willard (1973) model of adaptive variation in offspring birth sex ratio, Meikle et al. (1993) provided evidence that high-ranking female domestic pigs, *Sus scrofa*, give birth to a greater proportion of sons than low-ranking females. They speculated that differences in nutritional status caused by differential access to food of high- and low-ranking females, or differences in adrenal activity as a result of stress

experienced during agonistic encounters, may have been important in mediating the observed effects. However, they were unable to provide evidence to support these speculations.

A number of studies of the effects of maternal social status on offspring birth sex ratio have produced contradictory findings for related species (e.g. primates: rhesus macaques, *Macaca mulatta*: Simpson & Simpson 1982; Meikle et al. 1984; bonnet macaques, *Macaca radiata*: Silk et al. 1981; savannah baboons, *Papio cynocephalus*: Altmann 1980; Wasser & Norton 1993; ungulates: red deer, *Cervus elaphus*: Clutton-Brock et al. 1984; zebra, *Equus zebra zebra*: Lloyd & Rasa 1989). It is therefore important to examine the extent to which the results found by Meikle et al. (1993), the first reported for any *Sus* species, are supported by other studies of domestic pigs.

Correspondence: M. Mendl, Genetics and Behavioural Sciences Department, SAC-Edinburgh, West Mains Road, Edinburgh EH9 3JG, U.K. A. J. Zanella is at the ITVT, Schwere-Reiter Strasse 9, 80797 München, Germany. D. M. Broom is at the Department of Clinical Veterinary Medicine, Madingley Road, Cambridge CB3 0ES, U. K. C. T. Whittemore is at the Institute of Ecology and Resource Management, West Mains Road, Edinburgh EH9 3JG, U.K.

In addition, knowledge about the causal basis of dominance-related variation in birth sex ratio is an important goal for those seeking a full understanding of the phenomenon, and for those advocating a marriage of functional and mechanistic approaches to problems in animal behaviour (see Bateson & Gomendio 1992; Curio 1994). Consequently, it is appropriate to investigate the mechanisms that may underlie the effects of social dominance on birth sex ratio in pigs, including those that Meikle et al. (1993) suggested.

In this paper, we use data from two recent studies of female domestic pigs (Yang et al. 1989; Mendl et al. 1992) to address the above issues. First, we provide further information about the relationship between social status and birth sex ratio, both within and across consecutive pregnancies. Second, we investigate the role that nutrition and adrenal activity may play in affecting birth sex ratios, by examining whether either the nutritional status or stress-related adrenal activity of individuals during pregnancy is related to subsequent birth sex ratios. These factors are known to play a role in sex-ratio determination in other species (e.g. golden hamster, *Mesocricetus auratus*: Pratt & Lisk 1990; mule deer, *Odocoileus hemionus*: Kucera 1991), and it is important to examine the generality of their effects across species.

METHODS

Full details of methods are given in Mendl et al. (1992). A summary description is provided here together with relevant information not presented in Mendl et al. (1992). For the sake of clarity, a brief description of the design of Yang et al.'s (1989) experiment is given at the appropriate point in the Results.

Subjects, Housing and Care

The subjects were 37 female Large White \times Landrace pigs housed in a large indoor pen comprising a strawed lying area (11.4 \times 5.5 m), and an unstrawed dunging area (5.1 \times 5.5 m), part of which was occupied by an electronic sow feeder unit in which pigs were fed one at a time. Individuals were fed 2.2 kg per day and each daily feed cycle started at 1500 hours. Water was provided ad libitum from four drinker points in the dunging area. The dunging area was cleaned daily and straw was added to the lying area at regular intervals.

Experimental Protocol

All pigs were individually identifiable by ear tattoos and tags. The pigs were introduced into the pen when they were about 9 months old and in the seventh week of their first pregnancy. For practical reasons, pigs were introduced in four batches, each batch being separated from the next by between 4 and 6 weeks. For every pig, including those in the first batch, introduction to the pen involved mixing with unfamiliar animals. The pigs remained in the same pen for their first four pregnancies, except during birth and lactation, at which time each pig would leave the pen for about 6 weeks. Throughout the study, no new pigs were added to the group.

The behaviour of each batch of pigs was observed for 3 days during the first week following introduction to the pen in the first pregnancy, and for 2 days during the third week. During the fifth week (11th–12th week of pregnancy), each individual was subjected to an adrenocorticotrophic hormone (ACTH) challenge test to examine pituitary-adrenal activity.

Further behavioural observations were carried out during the third and fourth pregnancies. By this time, pigs that had been synchronized for stage of gestation in the original four batches were now no longer in synchrony. Consequently, it was not practicable to watch all animals at the same stage of gestation. Instead, three separate 5-day watches were carried out during the period at which most sows were in their fourth pregnancy. During each of these watches, at least 60% (23 or more) of the pigs were present in the pen. Thirteen pigs were subjected to an ACTH challenge test during the 10th–11th week of their fourth pregnancy. Eleven of these pigs were amongst the 27 observed during the fourth pregnancy, and represented animals of a wide range of social status (social status index (see below): ranks 1, 3, 5, 8, 11, 15, 18, 20, 23, 24, 25).

Social Status Measurements

For observation purposes, a number was sprayed on the back and flanks of each pig. On each observation day, the pigs were watched four times, once in each of the following time periods: 0830–1000 hours; 1130–1300 hours; 1400–1530 hours; 1600–1730 hours. The observation procedure was as described in Mendl et al. (1992). All

agonistic interactions were recorded. This was possible since nearly all of these interactions were accompanied by vocalizations or rapid locomotor movements which could be detected easily by the observer. Agonistic interactions were those in which one or both pigs performed knocking, biting, threatening or chasing behaviour, or avoidance without contact, or in which both pigs engaged in a prolonged fight. In all agonistic encounters, a note was made of which, if either, of the pigs was displaced by the other. Displacements were recorded when a pig moved away from another individual who was either knocking, biting, threatening or chasing it, or who was not directing any behaviour at it (an active avoidance by the displaced pig). For each observation period, an index of each individual's ability to displace other pigs in agonistic interactions (an index of social status: see Mendl et al. 1992) was calculated as follows

$$\frac{\text{no. of pigs that an individual is able to displace}}{\text{no. of pigs that an individual is able to displace} + \text{no. of pigs that are able to displace the individual}} \times 100$$

In smaller groups where it is possible to construct a dominance hierarchy based upon an $N \times N$ matrix in which the number of rank reversals is minimized (cf. Meikle et al. 1993), the social status index correlates strongly with this hierarchy (e.g. M. Mendl, unpublished data: $r_s=0.918$, $N=15$, $P<0.001$).

The social status indices calculated for the 37 animals during the first week after introduction into the pen in the first pregnancy were highly positively correlated with those calculated for the third week ($r_s=0.714$, $N=37$, $P<0.001$). Therefore, an overall index was calculated for each pig over this 3-week period (see Mendl et al. 1992). Social status indices calculated from each of the three observation periods during the fourth pregnancy were also positively correlated with each other (correlations for all combinations of observation periods: $r_s=0.650$, $N=17$, $P=0.005$; $r_s=0.696$, $N=21$, $P<0.001$; $r_s=0.645$, $N=21$, $P=0.002$). Data from the observation period during the fourth pregnancy in which most animals ($N=27$) were present in the pen are used in the subsequent analyses. Long-term stability of social status is indicated by the high positive correlation between the first and fourth

pregnancy social status indices ($r_s=0.751$, $N=27$, $P<0.001$).

Tests of Adrenal Activity

The responsiveness of pigs' adrenal glands to an ACTH challenge test was used as an indicator of adrenal activity. This test is of use in assessing the functional state of the pituitary-adrenal system which may, in turn, reflect the psychological state and experiences of the individual during the preceding few days or weeks. A high maximal cortisol response to ACTH is often seen in individuals who have recently been exposed to certain types of chronic stress, especially socially induced stress (Sassenrath 1970; Meunier-Salaun et al. 1987; see Mendl et al. 1992). The tests were carried out in situ in the pens and started at about 1330 hours. The tests differed slightly in the first and fourth pregnancies, but followed the same basic protocol. An initial sample was collected. An injection of dexamethasone (DXM, a synthetic glucocorticoid) was then given (Merck, Sharp & Dohme, Hoddesdon, U.K.; 1st parity: 0.02 mg/kg intra-venous. 4th parity: 0.1 mg/kg intra-venous). This brought the animal's own corticosteroids down to a low level prior to the ACTH injection. Two hours later, the ACTH injection ('Synacthen', CIBA, Horsham, U.K.) was given (1st pregnancy: 4 µg/kg intra-muscular; 4th pregnancy: 5 µg/kg intra-venous). Samples were collected for 2 h following this injection (1st pregnancy: 1 per h; 4th pregnancy: 1 per 20 min). During the first pregnancy, saliva samples were collected by getting the pigs to chew on a veterinary cotton bud for 15–20 s. Between 0.5 and 1 ml was obtained from most pigs. Salivary cortisol was measured using an enzyme-linked immunosorbent assay (Cooper et al. 1989). In the fourth pregnancy, plasma samples were collected using temporary ear catheters (Zanella & Mendl 1992), and plasma cortisol was measured using a radioimmunoassay technique. The response to the ACTH challenge was measured as the area under the cortisol curve during the 2 h following ACTH injection (see Friend et al. 1977).

Measures of Weight and Reproduction

All pigs were weighed before each conception and each birth. The number and total weight of

Table 1. The relationship between high- and low-ranking halves of the group and litter sex ratio

	Number of female-biased litters	Number of unbiased litters	Number of male-biased litters
First pregnancy			
High rank	9	1	6
Low rank	4	3	9
Fourth pregnancy			
High rank	5	3	5
Low rank	4	3	7

piglets born alive, number born dead, and number of live born males and females were recorded at each of the four pregnancies.

Statistical Analyses

In all our analyses, birth sex ratio was calculated as: males/(males+females). We used correlational analyses to examine the relationships between social status, measures of adrenal activity and nutritional status, birth sex ratio, and other measures of reproduction. In their analysis, Meikle et al. (1993) divided pigs into the low- and high-ranking halves of the group. They then used chi-squared tests to analyse the frequency distribution of male-biased litters (those containing more males than females), unbiased litters and female-biased litters in relation to a mother's position in the low- or high-ranking half of the group. Where appropriate, we present the results of this sort of analysis in addition to the results of our correlational analysis.

RESULTS

Social Status and Birth Sex Ratio within Pregnancies

We found no correlation between social status index and birth sex ratio during either the first ($r_s = -0.222$, $N=32$, $P=0.223$) or fourth ($r_s = -0.193$, $N=27$, $P=0.334$) pregnancies. When we divided pigs into the low- and high-ranking halves of the group (following Meikle et al. 1993), the two halves of the group did not differ in the number of male-biased litters, unbiased litters, and female-biased litters they gave birth to (first pregnancy: $\chi^2=3.52$, $df=2$, $P=0.172$; fourth pregnancy: $\chi^2=0.41$, $df=2$, $P=0.815$; Table

1). At neither pregnancy was social status index significantly correlated with any other measures of reproduction, although high-ranking sows tended to give birth to fewer males during the fourth pregnancy ($r_s = -0.350$, $N=27$, $P=0.074$).

Our data allowed us to investigate reproduction of the same individuals across four pregnancies and therefore to get a better approximation of lifetime reproductive success in relation to social status. As mentioned earlier, social status scores for pigs recorded during both the first and fourth pregnancies were positively correlated ($r_s=0.751$, $N=27$, $P<0.001$). This suggests a high degree of stability in social status across all four pregnancies. For each pig, we calculated a mean social status index rank based upon its rank in the first and fourth pregnancies, and used this as an indicator of its social status across all four pregnancies (high social status is indicated by a high rank score). We then examined whether there was any relationship between this mean rank order and reproduction during the second and third pregnancies. At neither pregnancy was mean rank correlated with birth sex ratio (second pregnancy: $r_s = -0.006$, $N=26$, $P=0.975$; third pregnancy: $r_s = -0.249$, $N=27$, $P=0.209$), or any other measure of reproduction except for the number of males born during the third pregnancy. Pigs with a higher mean rank gave birth to fewer males at this time ($r_s = -0.440$, $N=27$, $P=0.022$). Pigs assigned to the high- and low-ranking halves of the group on the basis of their mean rank did not differ in the number of male-biased, unbiased and female-biased litters they produced during the second pregnancy ($\chi^2=0.88$, $df=2$, $P=0.645$), although there was a non-significant tendency for low-ranking pigs to produce more male-biased litters during the third pregnancy ($\chi^2=4.98$, $df=2$, $P=0.083$).

Table II. A summary of significant cross-pregnancy correlations in measures of reproduction

Reproduction measure	Pregnancies in which rank ordering of females for each reproduction measure was positively correlated at $P < 0.05$
No. piglets born alive	1-3, 2-4
No. piglets born dead	2-3
Total weight of live born piglets	2-3, 2-4
Mean piglet birth weight	1-2, 3-4
No. live born males	1-2, 2-4
No. live born females	2-4, 3-4
Litter sex ratio	—

Social Status and Birth Sex Ratio across all Four Pregnancies

Given that social status appeared to remain fairly constant, it might be expected that any consistent but subtle effect of social status on sex ratio at each pregnancy would become magnified across all four pregnancies. In other words, a tendency to produce more offspring of one sex than the other would become evident when analysed across several pregnancies (e.g. Clutton-Brock et al. 1984). To investigate this possibility, we first examined whether individual reproductive performance across pregnancies was consistent. Significant correlations between reproductive outcomes of successive pregnancies in our study were all positive (Table II). This suggests that there was some consistency in each female's reproductive output at each pregnancy. However, sex ratio was the only variable to show no significant cross-pregnancy correlations.

We then examined the relationship between each individual's mean social status rank across all four pregnancies and cumulative measures of her reproductive performance. For each pig, we summed the total number of piglets born alive or dead and the total number of live born males and females across all four pregnancies. There was a non-significant tendency for pigs who had high mean ranks (were consistently successful in agonistic interactions) to have a more female-biased overall sex ratio ($r_s = -0.377$, $N=22$, $P=0.08$; Fig. 1a) and to produce fewer live born piglets ($r_s = -0.356$, $N=27$, $P=0.07$; Fig. 1b) than lower ranking animals. They also produced significantly fewer males across all four pregnancies ($r_s = -0.710$, $N=22$, $P < 0.001$; Fig. 1c).

Adrenal Activity and Birth Sex Ratio

Meikle et al. (1993) suggested that adrenal activity, related to the stress of agonistic encounters, may have influenced birth sex ratios in their study. The hypothesis has two parts: (1) low-ranking animals have higher levels of stress-related adrenal activity and (2) high levels of adrenal activity result in termination of disproportionately more male than female embryos (see Meikle et al. 1984; Pratt & Lisk 1990). We investigated these possibilities by first examining whether social status was correlated with measures of adrenal function. We found no significant correlation between rank and response to the ACTH challenge test during either the first ($r_s = 0.038$, $N=35$, $P=0.83$) or the fourth ($r_s = 0.527$, $N=11$, $P=0.10$) pregnancy. Thus, low-ranking animals did not have higher adrenal activity in our study.

These data suggest that in our study, there was no simple linear relationship between social status and a measure of adrenal function. However, this does not rule out the possibility that high levels of adrenal activity during pregnancy are related to the production of female-biased litters. We examined this second part of the hypothesis and found that, in both the first and fourth pregnancies, the cortisol response to ACTH injection was not related to the subsequent birth sex ratio (first pregnancy: $r_s = -0.196$, $N=31$, $P=0.292$; fourth pregnancy: $r_s = -0.099$, $N=13$, $P=0.748$) or any other reproduction measure.

Nutritional Status and Birth Sex Ratio

An alternative hypothesis put forward by Meikle et al. (1993) to explain their results is that

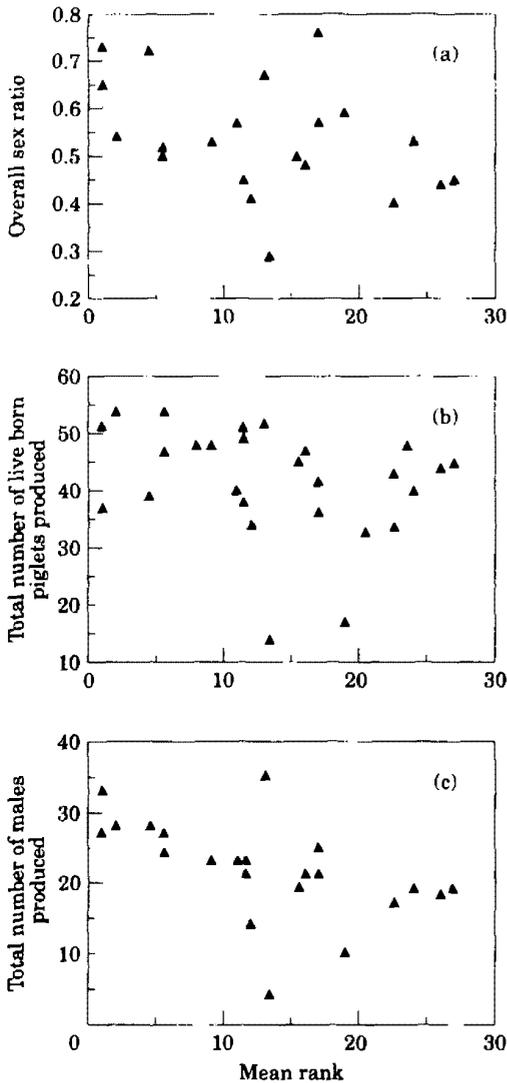


Figure 1. The relationship between a female pig's mean social status index rank (1 = low rank) and (a) her overall birth sex ratio, (b) the total number of live born piglets she produced, and (c) the total number of male piglets she produced, across all four pregnancies.

high-ranking females were able to monopolize food resources and so had a superior nutritional status to lower ranking animals. The better-fed mothers then gave birth to male-biased litters (see also Labov et al. 1986; Meikle & Drickamer 1986). In our study all pigs received the same amount of food each day in an enclosed electronic sow feeder unit. However, it is possible that high-ranking animals, by vocalizing and banging

the feeder unit, were able to intimidate lower ranking animals to leave the feeder before they had finished eating their ration. Thus, although food intake was, in theory, independent of social status, it is possible that dominance rank could have exerted some minor effect on nutritional status which, in turn, could have affected birth sex ratio. We had no direct information on the nutritional status of our animals. However, we did have data on the weight gain of females across each pregnancy (an indirect indicator of nutritional status). There was no relationship between social status and weight gain during the first pregnancy ($r_s = -0.061$, $N=33$, $P=0.736$), but there was a significant correlation during the fourth pregnancy ($r_s=0.510$, $N=27$, $P=0.007$). However, maternal weight gain during pregnancy and weight prior to parturition were unrelated to subsequent birth sex ratio for any of the four pregnancies (Spearman rank correlations, $P>0.10$). This may have been because these weight measures were influenced by factors such as litter size and piglet weight, and did not provide a very accurate indicator of maternal nutritional status.

To explore this issue further, we reanalysed data from a study of the effects of maternal nutrition on reproduction in pigs (Yang et al. 1989) where information on litter sex ratios was available to us. In this experiment, singly housed Large White \times Landrace pigs in their first pregnancy were fed so as to achieve two different back fat levels (a good indicator of energy stored). Fat pigs (F) had 20–24 mm of backfat by the time of their first litter while thin pigs (T) had 10–14 mm of backfat. From birth of the first litter onwards, the pigs were subdivided into eight groups according to three criteria: (1) fat versus thin; (2) high fed (up to 7 kg/day) during lactation (H) versus low fed (3 kg/day) during lactation (L); (3) litters adjusted to six offspring (6) versus litter adjusted to 10 offspring (10). The groups were, in order of increasing nutritional deprivation: FH6, FH10, FL6, FL10, TH6, TH10, TL6, TL10. Data on 11 F animals and 11 T animals during the first pregnancy, with numbers dropping to 7 F and 8 T animals by the fourth pregnancy, were available for our analysis.

F and T animals did not differ in the number of male-biased, unbiased and female-biased litters they gave birth to during any of the four pregnancies studied (chi-squared tests, $P>0.10$). In

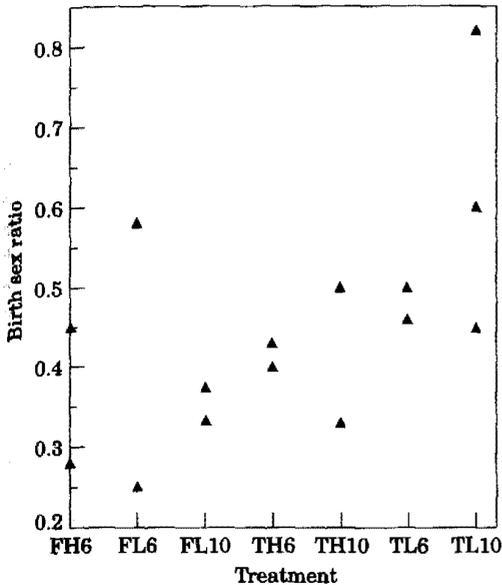


Figure 2. The relationship between the degree of nutritional deprivation experienced (plotted from low severity (FH6) to high severity (TL10); see text for details) and birth sex ratio for female pigs in their third pregnancy in Yang et al.'s (1989) study.

addition, as for our study, there was no indication that females were consistent in the sex-bias of their litters across the four pregnancies (Spearman rank correlations, $P > 0.50$ for all combinations of pregnancies). For the last three pregnancies in Yang et al.'s study, we correlated birth sex ratio with treatment type arranged in order of increasing nutritional deprivation. In the third pregnancy, litter sex ratios increased (became more male-biased) with increasing nutritional deprivation ($r_s = 0.735$, $N = 15$, $P = 0.002$; Fig. 2). Although this is a small data sample, it comes from an experiment that imposed major manipulations of nutritional state on animals throughout each pregnancy. As such, it indicates that low nutritional state during pregnancy is not related to the production of female-biased litters in domestic pigs.

DISCUSSION

Social Status and Birth Sex Ratio

In contrast to the findings of Meikle et al. (1993), our data provided no evidence that high-ranking female pigs gave birth to a greater

proportion of sons than low-ranking females. Rank and litter sex ratio were unrelated on a within-pregnancy basis. Furthermore, although each pig's social status remained reasonably stable across the four pregnancies studied, the sex ratio of her litters did not.

It is possible that, despite the lack of a within-pregnancy relationship between rank and birth sex ratio, animals of different rank did produce different proportions of males and females across several pregnancies. This might occur if, for example, random effects within each pregnancy, or carry-over effects from one pregnancy to another, adversely affected the condition of high-rankers or elevated the condition of low-rankers such that any within-pregnancy relationship between rank and sex ratio was temporarily obscured. This may be the case in female red deer where there is no obvious relationship between the sex of consecutive offspring (Clutton-Brock & Albon 1982). Nevertheless, despite this lack of consistency from pregnancy to pregnancy, high-ranking females do produce a larger proportion of male offspring than low-ranking females across their lifetime (Clutton-Brock et al. 1984).

Our data suggest that if there was any relationship between social status and birth sex ratio, it was a weak one which only became evident (and did not reach significance) when the outcomes of all four pregnancies were considered together. This relationship went in the opposite direction to that found by Meikle et al. (1993); higher ranking females tended to have an overall female-bias to the sex ratio of piglets produced across all four pregnancies. They also tended to produce fewer live born piglets, and these two tendencies together were reflected in the significantly lower total number of males they produced in comparison to lower-ranking animals.

The most parsimonious interpretation of these data is that they show little evidence of a strong relationship between maternal social status and birth sex ratio (see Fig. 1). However, when considered in terms of the Trivers & Willard (1973) and local resource competition (Clark 1978) hypotheses of adaptive variation in birth sex ratio, it could be argued that the data, together with the finding from Yang et al.'s (1989) study that undernourished mothers produced more males than females during one pregnancy, tend to support the latter hypothesis. Given that this contradicts the findings of Meikle et al. (1993), it is worth briefly

considering how relevant each of these hypotheses is to the domestic pig.

Meikle et al. (1993) speculated that the polygynous mating system of wild boar and feral domestic pigs (e.g. Wood & Brennehan 1980; Mauget 1981) results in males having greater variation in lifetime reproductive success than females. Thus, following Trivers & Willard (1973), and in accordance with their findings, they suggested that high-ranking mothers in good condition should invest preferentially in male rather than female offspring, because a high-quality male offspring is likely to have a particularly high level of reproductive success. While this may be so, the ability of high-ranking mothers to influence the reproductive success of their sons, a crucial part of the prediction, remains open to debate in view of the lack of direct evidence on this issue, and the fact that males usually emigrate from their natal group and thus leave their mother's sphere of influence prior to reproducing. It could be argued that, since females often remain close to their mothers as they grow up (e.g. Mauget 1981), they may inherit their social rank. Therefore, mothers may actually be better able to influence the reproductive success of their daughters than their sons. If this is the case, then the predictions of the local resource competition model are likely to be more relevant for domestic pigs. High-ranking mothers should produce more females because they can support them effectively in competition for resources and thus help them to reproduce successfully. Low-ranking mothers, on the other hand, will benefit from producing more males who emigrate from the home group. Our data provide some support for these predictions.

The main point here is that until we have detailed data on how the social organization of wild boar and feral domestic pigs influences the reproductive abilities of male and female offspring, it is difficult to distinguish between the relevance of the two hypotheses for pigs, and to make sense of conflicting results from a functional perspective. Thus, we agree with Meikle et al. (1993) that to determine the appropriateness of the Trivers & Willard or local resource competition hypotheses in pigs, we need to measure lifetime reproductive success of males and females born to mothers of different social or nutritional status, and to acquire a better understanding of pig social organization.

Mechanisms underlying Variation in Birth Sex Ratio

In trying to explain the fact that, in contrast to Meikle et al. (1993), we found no strong effects of maternal social status on birth sex ratio, it may be informative to shift away from functional explanations, and to consider the mechanisms by which maternal social status may affect offspring birth sex ratio. Meikle et al. (1993) proposed two possible mechanisms to explain their results. First, they suggested that, in their experiments, dominant pigs were able to monopolize food resources during feeding competition, and that the consequent food restriction imposed upon subordinates may have resulted in these lower-ranking individuals producing female-biased litters (e.g. Rivers & Crawford 1974; Clutton-Brock & Albon 1982; Clutton-Brock & Jason 1986; Labov et al. 1986; Meikle & Drickamer 1986). This mechanism is unlikely to have been important in our (Mendl et al. 1992) study where all pigs were fed individually in an enclosed feeder unit. Therefore, in Meikle et al.'s study, dominance rank could have affected nutritional status which, in turn, could have affected birth sex ratio, whereas in our study food intake was largely independent of social status. This difference in the studies is thus a potential explanation for their different results. However, analyses of indirect indicators of nutritional status (pig weight) in Mendl et al.'s (1992) study, and of the nutritional study carried out by Yang et al. (1989), do not support the hypothesis that low nutritional status during pregnancy is related to a female-biased birth sex ratio in the domestic pig. In fact, the one significant finding from Yang et al.'s study goes in the opposite direction (see above).

Studies of other ungulate species also give conflicting findings. Some suggest that maternal nutritional status is positively correlated with the proportion of males born in a litter (e.g. Thomas et al. 1989; Kucera 1991), as Trivers & Willard's (1973) hypothesis predicts, while others suggest no relationship or even a negative relationship (Verme 1969; Robinette et al. 1973; Skogland 1986). Meikle & Drickamer (1986) found that female house mice subjected to food deprivation for 1 week before mating gave birth to fewer male young than non-deprived animals, but that this effect disappeared if the mice were deprived for 2 weeks before mating. The authors suggested that

females were initially stressed (see below) by the food deprivation, but were able to recover during the second week. Although their study did not involve depriving the animals during pregnancy, it suggests that animals may be able to adapt to changes in food availability across longer periods of time, thereby preventing any effects on birth sex ratios occurring. Even during the energetically expensive process of lactation, there is evidence that nutritionally deprived mothers are able to buffer their offspring from the effects of food restriction (e.g. Bateson et al. 1990). It is thus possible that a similar form of adaptation occurs in pigs, and therefore long-term food deprivation during pregnancy, if it is not too severe, has no strong or consistent effect on birth sex ratio.

The second mechanism suggested by Meikle et al. (1993) as a possible link between social rank and birth sex ratio relates to the activity of the adrenocortical system. They hypothesized that lower-ranking mothers had higher stress-related adrenocortical activity, as a result of the process of subordination and receipt of aggression from others, and that this difference in physiological state resulted in the rank-related difference in birth sex ratios. The hypothesis can be split in half. First, a negative linear relationship between social rank and adrenal activity is predicted. In our study, however, this did not appear to be the case. One explanation for this may be that the relationship between social rank and adrenal function varies according to group size. In our study of a large group of pigs, there appeared to be an inverted U-shaped relationship between social status and a measure of adrenal activity during the first pregnancy (Mendl et al. 1992; see also Fokkema 1985), and no clear relationship at all during the fourth pregnancy. It is possible that, in large groups, individuals who are classified as low in social status are able to adopt a non-aggressive strategy and avoid confrontations, and hence minimize stress-related activation of the adrenal cortex. In smaller groups, such as those studied by Meikle et al. (1993), in which individuals are likely to encounter each other frequently, it may be much more difficult for them to adopt this non-aggressive strategy, and a negative linear relationship between social status and stress is more likely (e.g. Eberhart et al. 1983).

The second half of the hypothesis predicts that high levels of adrenal activity result in the production of litters with female-biased birth sex ratios,

irrespective of the cause of the elevated adrenal activity. In support of this hypothesis, it is known that elevated levels of adrenocortical activity are implicated in the loss of male fetuses during gestation in subordinate hamsters (Pratt & Lisk 1989, 1990). However, our data do not support the hypothesis in pigs. In both the first and fourth pregnancies, our measures of adrenal activity were unrelated to subsequent birth sex ratios or any other reproduction measure. Nevertheless, our data do not rule out the possibility that adrenal activity could play an important role during early pregnancy in determining subsequent birth sex ratio in pigs. For management reasons, our pigs were never mixed together into the large group until at least 1 week after implantation (ca 12–14 days post-mating), whereas Meikle et al.'s animals were kept together nearly all the time from prior to mating to just before parturition. If social status exerted its effects on sex ratio in Meikle et al.'s study via stress-related changes in adrenal activity around the implantation period, our study would have failed to detect this. Therefore, we suggest that further investigation of the role of adrenal activity should focus on this period of pregnancy in the pig.

In conclusion, the analysis of mechanisms involved in birth sex ratio adjustment may identify possible reasons why different studies produce different findings. More generally, the combination of causal and functional approaches in this way can be a powerful way of making sense of apparently contradictory data, and directing future research.

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