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James (1998) argues that research on sub-binomial variation in the distribution of sex ratios in litters of pigs, *Sus scrofa*, and other polytocous mammals, can provide a solution to the question of how social status may affect birth sex ratio in pigs. The logic used to link sub-binomial variation with social status effects relies on a number of assumptions which we examine here. James' argument begins with a statistical explanation for how sub-binomial variation of birth sex ratio might be achieved (Edwards 1960). The explanation that the probability of a zygote being male, P_{male} , varies from one zygote to the next with a mean of 0.5 during the period of conception certainly works but it is not the only theoretical possibility. Krackow (1995a, 1997) has postulated a post-conception mechanism based on sex differences in embryo development rate and within-sex competitive effects on developmental rate, which can also account for sub-binomial variation of sex ratio. On the basis of current knowledge, for example, that pig blastocysts do indeed show sex differences in developmental rate (Cassar et al. 1994), this explanation would seem a plausible alternative to that offered by James and would focus attention on the post-conception period rather than the conception period which is at the crux of James' arguments.

Nevertheless, following his line of reasoning, James then suggests that fluctuations in hormones (androgens, oestrogen, gonadotrophins, progesterone;

James 1996, 1998) may underlie variation in P_{male} during the period of conception. While there is evidence from other species to support this hypothesis, it is worth noting that limited availability of sperm at the fertilization site, as seems to be the case in rats, *Rattus norvegicus*, and hamsters, *Mesocricetus auratus*, may also lead to variations in P_{male} which result in sub-binomial variation of sex ratios. In other words, the hormonal fluctuation hypothesis may not be necessary to explain sub-binomial variation, and is not supported in a recent study of rats (see Hornig & McClintock 1997). In any case, the physiological processes whereby hormones may exert such an effect remain unclear (Krackow 1995a, b) and, as James acknowledges, there is no direct supportive evidence for such effects in pigs.

James then argues that if hormone levels at conception can explain the phenomenon of sub-binomial variation in pig litter sex ratios, they may also underlie the phenomenon of social status effects on birth sex ratio observed by Melkle et al. (1993, 1996; but see Mendl et al. 1995). A specific explanation for how this might be achieved is not given. However, there seem to be two possibilities. First, assuming that hormones are responsible for the supposed U-shaped regression of P_{male} on time during the conception period, if high-ranking sows mate early or late during this period and low-ranking sows mate in the middle of this period, litters of high-ranking sows should be male-biased and those of low-ranking sows female-biased (cf. Paul & Kuester 1987). However, in practice it is difficult to see how this control over mating time could be achieved by domestic sows whose mating choices are largely determined by their human caretakers, for example by artificial insemination or temporary removal from a group and introduction to a boar

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(as in Meikle et al. 1993, 1996, who nevertheless found a relationship between maternal dominance and birth sex ratio).

The second possibility is that high-ranking sows have hormone profiles that act to increase their mean P_{male} above 0.5, thus resulting in male-biased litters. In this case, it is interesting to note that if P_{male} of these sows remains above 0.5 during the conception period (i.e. the lowest point on the regression of P_{male} on time is elevated to above 0.5) and P_{male} of low-ranking sows remains below 0.5 during the conception period, a population of these high- and low-ranking sows would actually produce a surplus of unisexual litters as contrasted with the binomial expectation. Thus, in the case of this not implausible scenario, a single mechanism underlying P_{male} variation (e.g. hormonal fluctuations) can explain the effects of social status on birth sex ratio but, because more rather than fewer unisexual litters are produced, it cannot explain the occurrence of a sub-binomial variance of litter sex ratios. Under these circumstances, the unifying nature of James' hypothesis is lost.

Therefore, we are not convinced by James' assertion that previous research into the phenomenon of sub-binomial variation in pig sex ratios offers a better explanation for the effects of social status on birth sex ratios, than the post-conception mechanisms considered by Meikle et al. (1997), Mendl et al. (1995, 1997) and others (Krackow 1995a, 1997). Post-conception adjustment of sex ratio remains a strong candidate mechanism given that many more embryos are conceived than are born in the pig, with losses of 30–40% occurring after conception during the periods leading up to and following implantation (Perry & Rowlands 1962; Pope & First 1985; van der Lende et al. 1994; Roberts et al. 1996). It is possible that deaths at these stages are random with respect to the sex of the embryo or blastocyst. However, sex differences in the rate of blastocyst development (males develop faster; Cassar et al. 1994) may render one or the other sex more vulnerable to death when faced with a limited time window for successful implantation (the developmental asynchrony hypothesis; Krackow 1995a, 1997), or limited resources for growth. Indeed, there is evidence in pigs for sex-specific fetal mortality resulting from limited uterine space later in pregnancy (Chen & Dziuk 1993), and there is even a mechanism whereby

high levels of maternal oestrogen (which may occur in dominant sows) around days 11–12 of pregnancy may lead to selective death of slower developing (female) conceptuses (Roberts et al. 1996; S. Krackow, personal communication). Therefore, it seems likely that at least some of the sex-ratio variation in pigs can be accounted for by events occurring after conception, and the combined findings of Meikle et al. (1993, 1996) and Mendl et al. (1995) would indicate that such events, if they happen at all, are likely to happen around the implantation period. Furthermore, post-conception mechanisms can also, in theory, account for sub-binomial variation in litter sex ratios (Krackow 1997).

A final technical point is that James explains why Meikle et al. (1993) found sow social status to affect birth sex ratio and Mendl et al. (1995) did not, by noting that Mendl et al. (1995) did not measure social status very early in pregnancy, the time when he predicts sex-ratio variation to occur. For this argument to be fully supported, it follows that Meikle et al. (1993) must have measured social status at this point. In fact, they did not. They measured dominance rank on days 1–5 after sow group formation, and days 30, 60 and 90 after mating. As mating took place on days 5–15 after group formation, no measures of dominance were made during the first 30 days following insemination. As we (Mendl et al. 1997) argued previously, social organization and dominance status in groups of pigs may alter during the period of conception when sows are in oestrus and showing changes in activity and social behaviour (Schenk 1967; Signoret 1970). Consequently, measures of social status during oestrus and the conception period may be particularly difficult to predict from measures made at other times of the reproductive cycle, which do appear to show some stability (Meikle et al. 1993, 1996; Mendl et al. 1995). Strictly speaking, therefore, the studies investigated the relationship between pre-mating and post-implantation measures of dominance and birth sex ratio. Whether these measures reflect the situation at conception, hence allowing the studies to be interpreted in terms of social effects on pig sex ratio at conception, remains an empirical question.

To conclude, James' (1986, 1996, 1998) hypothesis that hormonal fluctuations at conception influence the sex ratio of zygotes provides another possible explanation for the putative effects of

social status on birth sex ratio in pigs. However, given the above arguments and the unanswered questions that James freely admits the hypothesis raises, we feel that his explanation is unlikely to be the unifying solution that he suggests. If social status does affect sex ratio in pigs as Meikle et al. (1993, 1996) report, it is quite possible that several mechanisms may be involved. For example, hormonal status at birth may influence primary sex ratio which may then be altered at implantation perhaps as a result of the effects of differential uterine and blastocyst synchrony. Further adjustments may occur as a result of subsequent embryonic loss owing to limited uterine resources and space.

We feel that the current discussion has been useful in highlighting the variety of candidate mechanisms that exist in this area. James' contribution is particularly constructive in this sense, identifying specific questions that need to be answered to confirm or refute his ideas. Similar questions can be asked about post-conception mechanisms. For example, are levels of 'stress hormones' (e.g. cortisol) in the sow at the time of implantation related to subsequent birth sex ratio (cf. Pratt & Lisk 1990)? How does social status influence stress hormone levels at this time (cf. Mendl et al. 1992)? Such questions may be tackled by a correlational approach, but ultimately experimental studies will be needed to pin down precise mechanisms. Indeed, the apparent lack of even simple correlational information about these possible physiological mechanisms in the pig was the spur to our claim to be making the first attempt to examine mechanisms underlying sex-ratio variation in this species (Mendl et al. 1997). While this was in some senses an overstatement, James' commentary makes it clear that, when it comes to hormonal influences on birth sex ratio in the pig, there is little hard empirical data to draw on. Thus, although there is no shortage of ideas for mechanisms that may underlie sex-ratio variation in mammalian species, the experimental data to determine the relative contribution that these make is generally lacking (see Krackow 1995b; Hornig & McClintock 1997). For progress to be made, we need more experimental data to support or refute the abundant hypotheses, especially if the final story turns out to be complex (Krackow 1997).

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