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Prenatal influences on reproductive life history strategies

Mertice M. Clark and Bennett G. Galef, Jr

Exposure to hormones before birth can profoundly influence the life history strategies of many vertebrates. Such prenatal effects on reproductive phenotype can have far-reaching consequences and may help to explain the physiological bases of biases in sex ratios, differences in adult competitive abilities and alternative reproductive tactics that are of interest to evolutionary and behavioural ecologists^{1–3}.

The rodent model

In many litter-bearing rodent species, such as the house mouse (*Mus musculus*), the intra-uterine position (IUP) that a male or female foetus occupies relative to siblings of the same or the opposite sex influences the hormonal milieu in which it matures. For example, the testosterone level within a male or female foetus is affected by adjacent foetuses. Male foetuses occupying IUPs between two males (2M males) have greater blood concentrations of testosterone than do their brothers in IUPs between two females (2F males). Similarly, female foetuses located between male foetuses (2M females) have higher testosterone titres than do their sisters (2F females) located between two female foetuses. The 50% or more of foetal rodents situated in IUPs adjacent to a single male foetus have levels of testosterone that lie between those of foetuses from 2M and 2F IUPs^{4–6}. Thus, IUP during gestation has powerful effects on the hormone levels to which a foetus is exposed during development.

Although there has been considerable controversy as to how steroids travel from one foetus to another^{7–9}, recent studies involving the transport of dye within the uterus of pregnant rats and of radioactively labelled testosterone between foetuses indicate that androgens secreted by male foetuses late in gestation diffuse through the amniotic fluid and across foetal membranes to adjacent foetuses^{10,11}. Such diffusion of testosterone causes a foetus located between male foetuses to receive greatest exposure to exogenous testosterone.

Over the past two decades, evolutionary and behavioural ecologists have become increasingly interested in the adaptive consequences of intraspecific variability in life history and behavioural strategies. Recently, behavioural endocrinologists have begun to uncover surprising relationships between levels of prenatal exposure to gonadal hormones and variation in reproductive behaviour in adulthood. Such relationships may provide a causal explanation for many variations in adult phenotype that are of interest to behavioural and evolutionary ecologists.

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The reproductive behaviours of adult rodents from different IUPs are greatly affected by the different levels of exposure to androgen that they experienced prenatally (Table 1). For example, female mice from 2M IUPs have higher plasma testosterone levels during foetal life, are more aggressive as adults, have longer oestrus cycles, are less sexually attractive to males, and have a shorter reproductive life than do 2F females. In virtually all characters measured, the phenotypes of 2M females are more masculine than are those of 2F females^{4,5}. Foetal IUP affects a similar suite of traits in Mongolian gerbils (*Meriones unguiculatus*)^{12–14}, though the direction of

effects of IUP on adult phenotype sometimes appears to differ between gerbils and mice. For instance, 2M male Mongolian gerbils are more successful than are 2F male gerbils in impregnating females they encounter¹⁵, while 2F male mice are more sexually active than are their 2M brothers⁵.

Effects of IUP on primary sex ratio in rodents

Intra-uterine position affects not only the phenotypes of rodent offspring but also the sex ratios of the litters in which they are born. 2M female house mice and Mongolian gerbils give birth to male-biased litters (>57% males), while 2F females of both species deliver female-biased litters (<43% males)^{16,17}. Although the process producing such variance is presently unknown, it is unlikely to be the result of differential mortality either during or shortly following vaginal delivery¹⁸. The percentage of males (61.9%) in litters delivered by caesarian section from 2M gerbils on the last day of their gestation is significantly greater than the percentage of males found in caesarian-delivered litters of 2F females (43.4% males)¹⁹ on the last day of their gestation.

The difference in sex ratios of litters of 2M and 2F females may result from differences in their timing of copulation with respect to ovulation. Because the sex ratios of rodent litters change with the temporal relationship between insemination and ovulation^{20,21}, females from different IUPs

Table 1. Effects of intra-uterine position on the reproductive and aggressive behaviours of house mice^a

	2M	2F
Females		
Onset of oestrus	late	early
Oestrous cycle	long	short
Reproductive life	short	long
No. litters	low	high
Sex ratio of litters ^b	high	low
Aggression	high	low
Sexual attraction	low	high
Males		
Sexual activity	low	high
Paternal behaviour	high	low
Aggression	high	low
Infanticide	low	high

^aData from Refs 4 and 5. ^bData from Ref. 17.

may alter the sex ratios of their litters simply by varying the point in oestrus when they mate¹⁷.

Transmission of acquired characteristics

Regardless of its source, variance in the sex ratios of litters of dams from different IUPs has potentially important consequences. The probability that a foetus will develop in 2F or 2M IUPs is determined, in part, by the sex ratio of the litter of which it is a member; the greater the proportion of males in a litter, the greater the likelihood that a foetus in that litter will occupy an IUP between two males. Litters delivered by 2M females tend to be male-biased, while litters of 2F females tend to be female-biased; thus, the IUP that a dam occupied as a foetus affects the expected frequency with which her sons and daughters will occupy 2M and 2F IUPs¹⁶. Daughters born to 2M mothers are more likely to themselves be 2M females than are daughters born to 2F mothers. Conversely, daughters born to 2F mothers are more likely than are daughters born to 2M mothers to be gestated in 2F IUPs (see Table 2).

This influence of IUP on the sex ratios of litters of gerbils¹⁶ and house mice¹⁷ will result in a form of hormonally mediated transmission of acquired characteristics that produces concordance between mothers and daughters in those characteristics affected by prenatal level of exposure to testosterone. Daughters tend to resemble their mothers not only because they and their mothers share a relatively large proportion of their genes, but also because mothers and daughters tend to have similar histories of foetal exposure to steroids, as a consequence of a statistical tendency towards congruence in their IUPs.

Field evidence

The laboratory data suggest that male and female rodents from different IUPs should exhibit different behavioural and reproductive profiles in the field. Present data are encouraging, but not conclusive. Zielinski *et al.*²² monitored the movement patterns and reproductive success of female house mice from known IUPs for several weeks after the females had been released onto highway islands. As predicted, 2M females had significantly larger territories than did 2F females. No effects of IUP on either survival or number of uterine scars were found, but post-mortem examination was conducted only eight weeks after release. In a similar study, Ims²³ released large numbers of laboratory-reared male and female voles (*Clethrionomys rufocanus*) onto a small

island where they had to compete for resources. Successful colonists came from larger, more female-biased litters. Female voles from large, female-biased litters are more likely to be 2F females than are female voles from smaller, male-biased litters, again suggesting that, as in the laboratory, the reproductive strategies of 2F and 2M females differ.

Non-mammalian systems

While most of the work on effects of prenatal exposure to gonadal hormones has been carried out in rodents, striking effects of prenatal hormonal environment on important adult reproductive characteristics are beginning to be found in other vertebrate species as well. Schwabl²⁴ has discovered that the testosterone content of samples of yolk taken from eggs in a canary (*Serinus canaria*) clutch on the day that they were laid increases with order of laying and that measures of social rank of canaries are positively correlated with the concentration of testosterone in the yolk of the egg from which they hatched.

Crews and Bull²⁵ have suggested a prenatal hormonal basis for the production of female mimics in male red-sided garter snakes (*Thamnophis sirtalis parietalis*). In this species, mating aggregations are sometimes centred not on females but on genetic males (she-males) that release a pheromone that attracts males as does the mating pheromone normally released by females. Because administration of oestrogen to neonatal (but not to adult) males caused them to elicit courtship from other adult males²⁶, Crews and Bull²⁵ hypothesized that differential prenatal exposure to oestrogens produces she-males. As yet, there has been no direct test of this hypothesis.

In another recent paper (reported in *TREE* last year²⁷), Hews *et al.*²⁸ explored the role of perinatal exposure to testosterone on the development of irreversible, alternative male morphs in the tree lizard (*Urosaurus ornatus*). In this species, orange males have a mostly orange dewlap, are non-territorial and are larger than orange-blue males. Orange-blue males have an orange dewlap with a central blue patch and are territorial. When adult, males castrated on the day that they hatched were smaller and more likely to have an orange dewlap than were males castrated and implanted with a capsule containing testosterone on the day of hatching. The behaviour of castrated males and those implanted with testosterone has yet to be examined.

Conclusion

The growing evidence that prenatal exposure to hormones can profoundly affect variation in subsequent reproductive life histories of male and female vertebrates has implications for our understanding of sex ratio theory^{29,30}, alternative reproductive strategies² and behavioural variation³. Recent progress in developmental endocrinology

Table 2. Expected proportion of daughters of 2M and 2F Mongolian gerbil dams in 2M and 2F intra-uterine positions^a

		Mothers	
		2M	2F
Daughters	2M	0.090	0.070
	2F	0.052	0.116

^aData from Ref. 16.

offers the prospect of integrated studies of the development of alternative reproductive profiles from their induction in the womb to their consequences in populations.

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The potential for computer-aided identification in biodiversity research

Marion Edwards and David R. Morse

Routine species identification has always posed problems for ecologists, often because of a lack of appropriate tools or keys to assist with identification¹. The greatest problems will be encountered in specimens collected during biodiversity surveys, particularly those conducted in areas where there is a high proportion of new species². The quality of these surveys will largely be determined by the accuracy of their species identifications³. Consequently, it is recognized that new taxonomic tools and techniques will be required to support biodiversity studies^{2,4,5}, and Alberch proposed the need for 'appropriate information technology, which would allow routine identification of material by nonexperts'².

The use of computers in taxonomy has a long history, beginning in the 1960s with work in numerical taxonomy⁶, followed by investigation of computer-aided identification⁷ and databases⁸. Pankhurst⁹ provides a comprehensive review of progress to the late 1980s, and with Fortuner¹⁰, discusses the most recent developments in the field. These include

Species identification lies at the heart of most ecological studies, but it is recognized as a difficult and often frustrating task. Taxonomists have sought to overcome the difficulties of species identification by developing a range of tools and techniques that have increasingly involved the use of computers.

We describe recent developments in computer-aided species identification, which have been in four main areas: multi-access keys; hypertext keys; expert systems; and neural networks. We also suggest which technique might be appropriate for a particular taxonomic group.

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expert systems, neural networks, and more speculatively, computer vision in species identification, and the potential for geographic information systems (GIS) to hold species distribution data. Here, we review computer-aided species identification, concentrating on progress made in the 1990s (hence, we do not include matching techniques or probabilistic methods – see Pankhurst⁹).

At present, the most frequently used tool in species identification is the dichotomous key. The disadvantages of such keys are well known^{11–13} and have led to the investigation of numerous alternatives, including computer-based techniques. Tools for the latter fall into two classes: (1) those aimed at generating optimal dichotomous keys and the typesetting of such keys, and (2) interactive identification tools. Although developments in the two areas began at about the same time⁷, there has been little progress in key generation, compared to interactive tools, which have continued to develop and diversify (largely because of the rise of the microcomputer).