

Forgotten fathers: paternal influences on mammalian sex allocation

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Sex allocation research in mammals has focussed almost exclusively on mothers under the assumption that the male contribution is genetically determined during meiosis and therefore not under adaptive control. Although early studies on sperm traits suggested that sex ratios were at parity, technological advances have made analysis more reliable and cheaper. Subsequently, more studies have shown variation in the production of X-/Y-chromosome-bearing spermatozoa. We review the evidence that the X/Y ratio varies between and within individuals in mammals, and test whether there are consistent predictors of these sex ratio biases and finally discuss their implications for future studies on sex allocation.

Evidence for paternal adjustment

Variation in the production of sons and daughters is a key life history variable in evolutionary theory. It is predicted that parents would be advantaged if they could adjust the sex ratio (see [Glossary](#)) of offspring when fitness returns vary between the sexes in a condition, environment, or gene specific manner [1,2]. For example, if one sex has more variable reproductive success, then parents would be advantaged by producing more of the reproductively variable sex when they have extra resources to invest, or more of the less variable sex when they have fewer resources to invest. Such a strategy would result in more grand-offspring for these parents, enhancing their own lifetime reproductive success [1]. The hypothesis has since been extended to include other ways that parents might be advantaged by adjusting the sex ratio in relation to, for example, local density (local resource competition [3,4]), need for helpers (local resource enhancement [5,6]), or even mate attractiveness [7,8]. Sex ratios at birth do vary, although the results can be inconsistent, largely explained by methodological differences (reviewed in [9,10]). However, sex ratio skews can be less than expected, suggesting constraints on the ability of parents to adjust the sex ratio [11].

Hypotheses of sex ratio adjustment rely on the benefits to parents of adaptive manipulation. However, research in

most species has focussed on mothers under the implied assumption that the male contribution is genetically determined during meiosis and therefore not variable or under adaptive control. This seems generally reasonable, but specific patterns may depend on male and female heterogamety [12]. In birds, for example, females are the heterogametic sex and thus it is assumed generally that sex ratio manipulations are under female control [13–15], whereas in haplodiploid insects, the sex of the offspring is determined by whether the ovum is fertilised, and controlled by the female as she determines when to release stored sperm [16]. However, in mammals, males are heterogametic with the sex of the offspring determined by the inheritance of either an X or Y chromosome from their father. Although the production of X- and Y-chromosome-bearing sperm (CBS) may usually be fixed by meiosis, it is possible that X- and Y-CBS incur different costs in packaging, for example, because X-CBS are larger as they contain more DNA [17]. Additionally, X- and Y-CBS may have different survival rates even before ejaculation, as seen in the female reproductive tract [18]. Consequently, male mammals may have more control over sex allocation than males of other taxa.

In many taxa sperm traits are highly variable, and spermatozoa are among the most variable of cells [19,20]. For example, ejaculates can vary in factors such as sperm or flagellum length, sperm velocity, sperm concentration, sperm motility, and even amount of energy (ATP) can vary between populations and within populations [21–25]. Mammals show similar variation in sperm traits [22,26]. For example, sperm velocity, rate of sperm production and concentration, motility, velocity, morphology, and viability all vary between individuals (e.g., [27–30]), and with factors such as sperm competition [31,32], social environment [20,33], heterozygosity, captive breeding or inbreeding [34,35], mtDNA [36], and age [37].

Glossary

Ejaculate: a composition of sperm and non-sperm (including parasperm, seminal proteins, water, and macromolecules) materials that are ejected from the male sex organ during copulation.

Heterogametic sex: the sex that is determined by the presence of two different sex chromosomes.

Sex allocation: the determination of offspring sex by presence of the sex chromosomes.

Sex ratio: the ratio of male to female offspring at birth, unless otherwise stated.

Sperm competition: the competition between sperm within the female tract, for fertilisation of the ova.

X-CBS: the female sex chromosome; X-chromosome-bearing spermatozoa.

Y-CBS: the male sex chromosome; Y-chromosome-bearing spermatozoa.

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Furthermore, sperm traits can vary within individuals in relation to perceived sperm competition (e.g., [22]). For example, sperm traits in humans can be artificially selected, demonstrating selectable variation within an ejaculate [38]. Therefore, a variety of factors can influence the quality of sperm across a range of situations (reviewed in [39]).

Several of these variable sperm traits are also consistent with differences between X- and Y-CBS. For example, the variation in size between X- and Y-CBS is consistent enough to make sex-sorting a reliable technique for agricultural purposes in a variety of species (e.g., [40,41]). It therefore seems odd that there is such a vast amount of literature discussing the maternal influence on sex ratio manipulation in mammals with such a minimal consideration of the potential male influence, or even research confirming an even sex ratio in ejaculates. Gomendio

et al. [42] suggested that sperm traits were associated with the sex of the chromosome carried, because increased fertility of red deer was associated both with a faster swimming speed and a higher ratio of Y-CBS. Early studies on sperm did suggest that sex ratios were at parity within sperm samples, but technological advances have made analysis of the sex ratio of sperm more reliable, cheaper, and less invasive [43]. Consequently, there is mounting evidence that males do produce unequal numbers of X- and Y-CBS (Table 1), and that offspring sex ratio can be predicted from the Y-CBS ratio in ejaculates [44]. If paternal traits influence the ratio of X- and Y-CBS, it may constrain maternal control over sex allocation, or may enhance skews, depending on whether paternal and maternal fitness advantages are complementary or antagonistic.

In this review, we bring together data from a variety of empirical fields to determine whether the ratio of X- and

Table 1. The % Y-chromosome-bearing spermatozoa (CBS) and variation in ejaculates of different species noting the possible causes of variation^a

	Species	Categories	Sperm sex ratio (% Y-CBS) average (variance)	Refs
Exposure to environmental contaminants				
2,3,7,8 Tetrachlorodibenzo-p-dioxin	Mice	Control Exposed	50.39 (50.09–50.92) 50.03 (48.38–50.19)	[67]
Perfluorooctanesulfonate	Humans	High exposure (51.65 ng/ml) Low exposure (12.12 ng/ml) Lowest exposure (8.20 ng/ml)	51.3 50.3 50.8	[70]
Boron	Humans	Control (1.4 mg/day) Nearby community (4.25 mg/day) Boron worker (31.3 mg/day)	49.75 48.98 48.19	[71]
2,2',4,4',5,5'-Hexachlorobiphenyl	Humans	High exposure (260 ng/g and 350 ng/g) Low exposure (54 ng/g) Lowest exposure (22 ng/g) Sweden and Greenland	51.2 50.7 50.3	[69]
2,2',4,4',5,5'-Hexachlorobiphenyl	Humans	Control (200 ng/g) Exposed (328 ng/g)	51.3 51.5	[45]
Dichlorodiphenyl dichloroethene	Humans	Control (242 ng/g) Exposed (472 ng/g)	51.2 51.7	[45]
Scrotal heat stress	Mice	Treatment group	50	[68]
Fertility				
	Bovine		(46.9–52.7)	[94]
	Bovine		46.5 (41.0–50.7)	[49]
Sexual rest				
	Bovine		45 (17–71)	[82]
	Bovine		48.40	[44]
	Humans	With abstinence Without abstinence	<52.4 ^b <50.4 ^b	[81]
Age				
	Humans		49.02 (48.22–49.74)	[47]
	Humans	Control Older men	55.5 (48.5–60.5) 52.6 (48.7–56.9)	[84]
Diet				
	Mice	Control Low fat Very high fat	51 51 50	[55]
Unknown cause of variation				
	White-tailed deer		49.9 (48–52)	[54]
	Humans		44.17 (24.97–51.63)	[53]
	Humans		(27–68)	[95]
	Humans		(42–57)	[96]
	Pygmy hippopotamus	Captive populations	43.37 (41.70–44.50)	[43]

^aAverage Y-CBS are listed with the variance in parentheses where reported.

^bOnly reported % X-CBS.

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