

NEWS AND COMMENTARY

Population genetics

XYZW as nature's language of love?

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Fisher, Haldane and Wright obtained most of the classic results of population genetics in the first half of the last century, threatening to leave modern population geneticists with only slim pickings. Fortunately, for the career prospects of present-day geneticists, this triumvirate lacked detailed molecular data and knowledge of several asymmetries and imbalances in the heredity process. A recent study (Albert and Otto, 2005) studied such asymmetries in different mechanisms of sex determination to explain why animals end up using different mating systems.

Most patterns of inheritance are straightforward; each sexual organism has two parents, leaves an average of two surviving offspring, and each of its genes has a 1/2 chance of being transmitted to any offspring. However, asymmetries and imbalances exist, which can create disturbances and conflicts in evolutionary forces. Analyses of these systems provide deeper insights into evolutionary dynamics, and can generate elegant explanations for many natural phenomena; the analysis of such imbalances is now one of the most exciting fields in modern evolutionary genetics. Most armchair viewers of TV nature programmes recognise that the paradigms of sexual selection are the colourful male displays, most often associated with birds, and intermale conflict for access to females, most often portrayed in mammals. Albert and Otto (2005) use the differing mechanisms of sex determination in birds, butterflies and mammals to explain why birds and butterflies tend towards female-choice based on ornate male display, and mammals tend more to intermale competition for females.

Mammals use the familiar XY sex determination system where Y is the sex-determining (SD) chromosome and encodes maleness. Birds and butterflies use the analogous ZW system but in this case the SD chromosome, the W, encodes femaleness; thus males are ZZ and females ZW in this system. Consequently, in mammals the Y is passed down the male lineage and never occurs in females, whereas in birds the W is passed down the female lineage and

never occurs in males (Figure 1). The Y and the W chromosomes have lost most of their genes during their evolution in mammals and birds, so analysis has concentrated on the X and Z chromosomes that have retained a wide range of genes.

Previous work shows X chromosomes are more likely than autosomes to encode sexually antagonistic genes (advantageous in one sex, deleterious in the other) and/or genes that encode traits subject to sexual selection. Albert and Otto's insight is that they combine these observations and consider the evolution of female preference for males exhibiting antagonistic traits encoded on the X or Z chromosome; furthermore, they considered how the XY and ZW systems might differentially affect the sexual selection process.

The antagonistic trait is generally assumed to be beneficial to males but disadvantageous in females. A plausible example is the large colourful peacock's tail, which may be advantageous in attracting potential mates, while its expression as the smaller, drabber tail of the peahen may incur an aerodynamic penalty. Albert and Otto reasoned that if such a trait is encoded on the X chromosome of an XY male, then it incurs an immediate disadvantage because it would, by definition, only be passed onto his daughters, where it would be disadvantageous. By contrast, if the trait is encoded on the Z chromosome of a ZZ male, the trait would be passed onto sons 50% of the time (Figure 1). Thus, the barrier to female preference evolving for antagonistic traits may be much lower in ZW than in XY systems.

There are several other nuances in the argument. For example, the trait gene is heterozygous in XX females but hemizygous in ZW females, so its degree of dominance is important because a sexually antagonistic trait on the Z of birds will always be fully expressed in females (because the W is largely devoid of genes), while its equivalent on the X in female mammals may be ameliorated, or even obscured, by expression of the 'normal' gene on the other X chromosome. These nuances required a

formal population genetics model that tracks the two genes (encoding the trait and female preference), their linkage disequilibrium, dominance and so on, but the assertions appear robust that female preference for male display traits may evolve more easily in species such as birds and butterflies with ZW sex determination than in species with the more familiar XY system.

So, how convincing is the above explanation for the phylogenetic differences in how sexual selection is manifested? We cannot truthfully know – the evolutionary process has been lost in time – so we really have to consider how plausible the varying models are. The models use two main explanations for the evolution of female choice based on exaggerated male traits. The first is the 'runaway' process, first identified by Fisher (1930), where the male trait becomes favourable solely because it increases attractiveness to females. The second is the 'good genes' hypothesis that proposes that males with exaggerated traits must have good genes (Hamilton and Zuk, 1982) to have accumulated the energy reserves necessary to produce the trait and/or to have survived despite 'the handicap' of carrying the trait; females choosing such males benefit through their offspring inheriting these good genes.

The first model to explicitly investigate how the mechanism of sex determination can affect sexual selection (Hastings, 1994) proposes a good genes model where the female preference was encoded on the W chromosome. This chromosome is restricted to the female lineage so is never associated with the male trait 'handicap', hence female choice should evolve more easily in species such as birds with a ZW system of sex determination. Drawbacks of this model were that the trait was assumed to be sex-limited, and the inconvenient empirical observation that the W chromosomes of many species, including birds, are largely devoid of genes. It is possible to rescue the model by postulating that choice genes on the W could have arisen before or during the process of genetic denaturation of the W from its autosomal ancestor (Fridolfsson *et al.*, 1998), or by translocation, but such post hoc explanations are not particularly robust.

Kirkpatrick and Hall (2004) recently presented a comprehensive, and more biologically rigorous, investigation and discussion of the impact of XY and ZW on the manifestation of sexual selection, which is highly recommended. The model of Albert and Otto adds to this

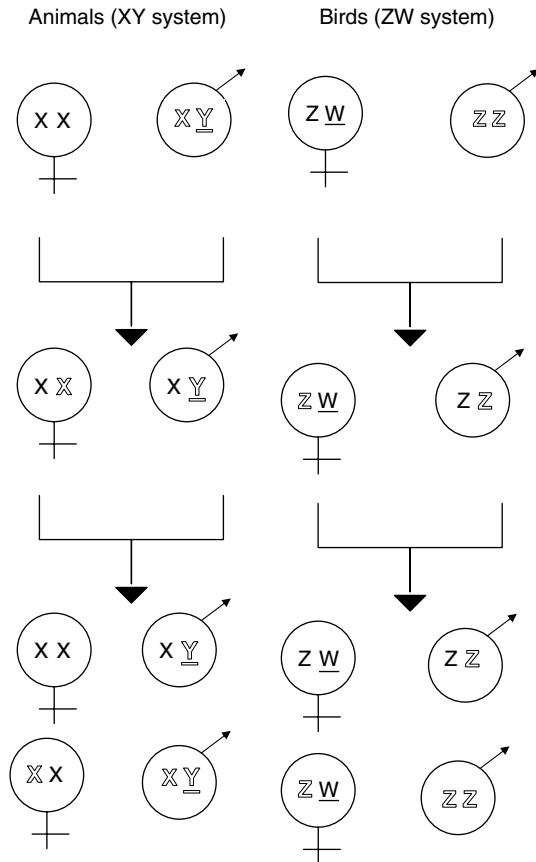


Figure 1 The XY and ZW mechanisms of sex determination. Inheritance is illustrated over three generations. The sex-determining (SD) chromosome is underlined: in mammals the Y chromosome encodes 'maleness' so is restricted to the male lineage, while in birds the W chromosome encodes 'femaleness' so is restricted to the female lineage. The non-SD chromosomes are coloured black or white, depending on whether they are present in females or males, respectively, in the first generation; as can be seen, they interchange between male and female lineages. The XY system of sex determinations is generally more familiar (mammals, *Drosophila*) but there are important exceptions such as birds, butterflies, and many fish that utilise a ZW system.

work by considering sexual antagonism, i.e. the trait is expressed in both sexes rather than being male-limited. So we are now in the happy situation of having several plausible explanations as

to why sexual selection can take different forms in different taxa.

The next step is to undertake phylogenetic analyses of sexual selection and its relationship to sex determination

in taxa where sexual display and conflict are less spectacular than that in birds and mammals (Reeve and Pfennig, 2003; Mank *et al.*, 2006). However, the main legacy of this work will be the intellectual satisfaction of understanding how imbalances in inheritance caused by sex determination may ultimately lead to the evolution of some spectacular natural phenomena, such as male ornamentation in birds of paradise and the sexual dimorphism and intense inter-male conflict of elephant seal colonies in the southern oceans.

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- Albert AYK, Otto SP (2005). Sexual selection can resolve sex-linked sexual antagonism. *Science* **310**: 119–121.
- Fisher RA (1930). *The Genetical Theory of Natural Selection*. Clarendon: Oxford.
- Fridolfsson AK *et al.* (1998). *Proc Natl Acad Sci USA* **95**: 8147–8152.
- Hamilton WD, Zuk M (1982). *Science* **218**: 384–387.
- Hastings IM (1994). *Proc Natl Acad Sci USA* **258**: 83–87.
- Kirkpatrick M, Hall DW (2004). *Evolution* **58**: 683–691.
- Mank JE, Hall DW, Kirkpatrick M, Avise JC (2006). *Proc Roy Soc London* **273**: 233–236.
- Reeve HK, Pfennig D (2003). *Proc Natl Acad Sci USA* **100**: 1089–1094.

Further Reading

- Charlesworth D, Charlesworth B, Marais G (2005). Steps in the evolution of heteromorphic sex chromosomes. *Heredity* **95**: 118–128 (01 August 2005).
- Filatov D (2005). Evolutionary genetics: Stickleback's view of sex chromosome evolution. *Heredity* **94**: 275–276 (01 March 2005) – News And Commentary.
- Tobler A, Kapan D, Flanagan NS, Gonzalez C, Peterson E, Jiggins CD *et al.* (2005). First-generation linkage map of the warningly colored butterfly *Heliconius erato* – Short Review. *Heredity* **94**: 408–417 (01 April 2005) – Original Article.