

Notes and Comments

How Common Are Meiotically Driving Sex Chromosomes in Insects?

Francis M. Jiggins,^{1,*} Gregory D. D. Hurst,^{2,†} and Michael E. N. Majerus^{1,‡}

1. Department of Genetics, Cambridge CB2 3EH, United Kingdom;

2. Department of Biology, University College London, London NW1 2HE, United Kingdom

Submitted November 6, 1998; Accepted April 21, 1999

Keywords: sex chromosome, meiotic drive, sex ratio, Diptera.

Sex chromosome meiotic drive, the transmission of one of the sex chromosomes to greater than half of the progeny, is a phenomenon frequently observed within the Diptera. First recorded within the *obscura* group of *Drosophila*, it has now also been observed in the *melanica*, *tripunctata*, *testacea*, *melanogaster*, and *quinaria* groups of this genus. Outside of *Drosophila*, there are records from two mosquitoes (*Aedes* and *Culex*) and from sciarid flies and diopsids (stalk-eyed flies; Jaenike 1996) (Presgraves et al. 1997). Jaenike (1996) found that out of a random sample of nine species of *Drosophila*, five bore meiotically driving sex chromosomes. This growing number of records within the Diptera has led to the suggestion that sex chromosome meiotic drive may in fact be common within insects (Hurst and Hurst 1996). If this is true, meiotic drive may be an important force in insect evolution, including the evolution of sex determination mechanisms, sexual selection, and speciation (Hurst et al. 1996; Wilkinson et al. 1998).

We argue here that the conclusion that sex chromosome meiotic drive is common in insects outside of the Diptera is premature. Possible cases of sex chromosome meiotic drive in other insect orders, particularly the Lepidoptera, have been included in previous reviews (Hurst and Pomiankowski 1991). However, none of these cases is proven. Indeed, recent studies suggest caution over the conclusion

that sex chromosome meiotic drive is a cause of sex-ratio biases. The first of these are studies of two butterflies, *Danaus chrysippus* (Smith et al. 1998) and *Acraea encedon* (Jiggins et al. 1998). These two species were recorded in the literature as showing certain matrilines producing all-female broods, and it was suggested that the most likely explanation was sex chromosome drive. However, in both these cases, the female bias is associated with high egg mortality, indicating that the bias is secondary and not present at fertilization. The data suggest the involvement of a maternally inherited male-killing agent. In the case of *A. encedon*, the trait was also shown to be susceptible to antibiotics. Meiotic drive must thus be rejected as an explanation of biased sex ratios in these butterflies.

The second study that casts doubt on the implication of meiotic drive in the production of female-biased sex ratios within certain Lepidoptera is a study on the Asian corn borer *Ostrinia furnacalis* (Kageyama et al. 1998). Certain matrilines of this species also produced female-biased sex ratios. In this case, there is no increase in embryonic mortality, and the bias is thus a primary one. It would thus appear to be an excellent candidate to be a meiotic driver. However, the trait is again antibiotic sensitive and has been attributed to a bacterium that feminizes genetically male hosts. The ability of a microorganism to create a primary sex-ratio bias is important in that it casts doubt on the interpretation of meiotic drive even in cases of female-biased primary sex ratios in the Lepidoptera.

Hurst and Pomiankowski (1991) also cite the possible occurrence of sex chromosome meiotic drive in cyclically parthenogenetic aphids. However, the role of the X chromosome in the sex-ratio effect is uncertain, and this may represent adaptive control of sex ratio rather than meiotic drive.

There is thus little empirical evidence for meiotic drive outside the Diptera and much within. Could this merely be a study bias? The argument could be raised that it is within the Diptera, and the genus *Drosophila* in particular, that defined genetic crosses are carried out. Thus, the number of records of meiotic drive in the Diptera merely represents study bias, not an observation of a hot spot. We

* To whom correspondence should be addressed; e-mail: fmj1001@mole.bio.cam.ac.uk.

† E-mail: g.hurst@galton.ucl.ac.uk.

‡ E-mail: menm@mole.bio.cam.ac.uk.

would argue that this is unlikely. Sex chromosome meiotic drive and male killing are two distortions of sex ratio that are initially detected in the same way, through the observation of distorted sex ratios in defined crosses. Whereas sex chromosome meiotic drive has been recorded in 21 species of Diptera (Hurst and Pomiankowski 1991; Jaenike 1996; Presgraves et al. 1997) with no definitive records from other insects, male killing has been observed in a taxonomically diverse host range. Among insects with sex chromosomes, male killing has been observed in five species of Diptera, eight species of Lepidoptera, two species of Hemiptera, and 13 species of Coleoptera (Carson 1956; Cavalcanti et al. 1957; Poulson 1966; Groeters 1996; Hurst et al. 1997, 1999; Jiggins et al. 1998; F. Jiggins, unpublished data; T. Majerus, unpublished data). The frequent observation of male killing outside of the Diptera suggests that, were meiotic drive common throughout the insects, it would have been commonly recorded in other insect orders.

This argument could be criticized if initial detection of sex chromosome meiotic drive required more genetic crosses to be done and larger numbers of progeny to be reared than are required for detection of male killing. This could create a bias in records of meiotic drive toward insects that are easily reared in the laboratory, such as *Drosophila*, and also to intensively studied insect species.

The number of crosses required for initial detection of meiotic drive would be larger if the prevalence of the trait were lower than for male killing. However, the majority of cases of sex chromosome meiotic drive in *Drosophila* were initially detected from populations where between 4% and 30% of wild individuals produced a biased sex ratio, figures broadly similar to the prevalence of male-killing bacteria.

The size of families required for initial detection of drive would be larger if the crosses exhibiting drive showed less pronounced sex-ratio distortion. Clearly, suppression of drive may produce such an effect and has retarded the detection of drive in certain cases, such as *Drosophila simulans* (Cazemajor et al. 1997). Although it may be argued that cases of suppressed drive are more likely to be found in *Drosophila* because of the large families created, it is also true that drive is not always suppressed. In the majority of cases in *Drosophila*, the wild individuals in which drive was initially detected produced <5% sons, a sex-ratio bias similar to that produced by male killers.

A further bias may arise from the increased complexity of formally proving drive as the cause of a detected sex-ratio bias compared to proving male killing. Although male killing may be proven in two generations, X chromosome drive requires three generations of crossing to characterize its inheritance. The completion of such extended crossing schemes may be biased toward the easy-to-rear Diptera

and again produce some systematic bias. This seems unlikely to fully explain the absence of confirmed cases of meiotic drive outside the Diptera, as there are few records of primary sex-ratio distortion where the inheritance is unknown in other taxa.

We thus conclude that a small bias for initially detecting meiotic drive in the Diptera will exist owing to the nature of the organisms. However, these biases do not appear to be so great as to adequately explain the dichotomy in the data. The absence of meiotic drive outside the Diptera remains suspicious.

In summary, we argue that the hypothesis that sex chromosome meiotic drive is common within the insects is in fact not proved. We feel that, although it is unlikely that it will be found exclusively in the Diptera, there is a case to be made that the Diptera are a hot spot for the occurrence of sex chromosome meiotic drive. Further research is clearly necessary to clarify this point. If the Diptera are found to be different, then we must ask why this is so. Meiotic drive often involves the destruction of gametes that do not bear the drive allele causing a reduction in the number of functional gametes. This may mean that meiotically driving sex chromosomes are unlikely to spread in female heterogametic taxa such as the Lepidoptera because a reduction in the number of eggs is more costly than a reduction in the number of sperm. Among male heterogametic taxa, it is unclear what could make Dipteran meiosis special.

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Associate Editor: David E. McCauley