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The ability to gain matings, not sperm competition, reduces the success of males carrying a selfish genetic element in a fly

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Females are expected to avoid low-quality males fathering their offspring. X chromosome meiotic drive (XCMD) makes males very low-quality mates. XCMDs are X chromosomes that, in males, cause the failure of all Y chromosome sperm, so all functional sperm carry the driving X and produce daughters. This transmission advantage can allow the XCMD to spread through populations. However, XCMD males typically have low fertility, are very poor at sperm competition, only produce daughters, and bear low fitness alleles associated with XCMD. This imposes significant costs on females that mate with these males. Recently, several studies have shown that females can reduce the risk of their offspring inheriting XCMDs by mating with multiple males (polyandry), as XCMD males typically lose out to normal males in sperm competition. Hence it has been suggested that increased polyandry may be likely to evolve whenever a costly XCMD is common in a population, and that polyandry may be a key factor in preventing XCMDs spreading through populations. We tested this by examining the fruit fly *Drosophila subobscura*, in which females are known to mate only once in European populations where XCMDs are absent. However, in North African populations an XCMD, referred to as 'SRs', occurs. If the association between XCMDs and polyandry is true, then these North African populations should have evolved polyandry. However, we found no evidence of polyandry in North African *D. subobscura* populations. Instead, we found some evidence that males that carry SRs are slightly less successful at gaining matings in noncompetitive situations. These results show that polyandry does not necessarily evolve in response to the presence of harmful X chromosome drive. With both sperm competition and female choice both being unlikely to substantially reduce the success of XCMD in *D. subobscura*, the factors that prevent SRs spreading through these populations remain mysterious.

For females, the fitness benefits of choosing a high-quality mate can directly increase the number of offspring she produces or can enhance them via genetic benefits (Andersson & Simmons, 2006; Trivers, 1972). In many species, however, males carry traits or genes that make them very poor mates, for example they may carry sexually transmitted diseases (Hurst et al., 1995) or low-fitness genes (Lesna & Sabelis, 1999). Mating with these males may be costly, and there can be selection for females to avoid mating with them. In many species, females can choose to avoid mating with low-quality males (Jennions & Petrie, 1997). Alternatively, females may avoid these costs after mating by selecting to use sperm only from high-quality males or dumping ejaculates from low-quality males (Birkhead & Pizzari, 2002; Parker, 1970; Simmons, 2001). If high-quality males produce ejaculates that outcompete other ejaculates inside the female, then females can increase the average quality of their offspring's sire by simply mating with multiple males (Parker, 1970).

Mating with the wrong male can be costly to females when some males carry harmful selfish genetic elements. Selfish genetic elements (SGEs) are genes that increase their own frequency in subsequent generations beyond fair Mendelian inheritance, without increasing the fitness of the organism that carries them (Burt & Trivers, 2006). These systems are near ubiquitous across the living world, ranging from transposable elements that replicate within an organism's genome to extreme systems such as the supernumerary chromosome PSR that in male wasps eliminates all other chromosomes carried by the male. As SGEs are often costly to the individual that carries them, it has been proposed that females, across a broad range of taxa, will benefit by reducing the risk that SGE-bearing males will father their offspring (Lande & Wilkinson, 1999; Lindholm et al., 2016; Tregenza & Wedell, 2000).

One particular SGE, X chromosome meiotic drive ('XCMD'), has been found to be intimately related to female mating decisions

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(Price, Bretman, et al., 2008; Price et al., 2014; Price, Hodgson, Lewis, Hurst, & Wedell, 2008; Pinzone & Dyer, 2013; Wilkinson, Presgraves, & Crymes, 1998). XCMD occurs when a particular X chromosome carries the ability to kill Y chromosome-bearing sperm produced by the host male (Jaenike, 2001). This benefits the XCMD chromosome, which is passed on to most or all offspring, resulting in strongly female-biased broods. The transmission advantage gained by the driving X can allow XCMD to spread rapidly through populations (Bastide et al., 2011; Carvalho & Vas, 1999; Price, Hurst, & Wedell, 2010), and reach substantial frequencies in nature (Jaenike, 2001; Pinzone & Dyer, 2013; Price et al., 2014). However, for a female, mating with an XCMD male typically imposes significant costs. First, XCMD males typically transfer small ejaculates, owing to the loss of half their sperm, which may reduce a female's ability to produce offspring (Price & Wedell, 2008). Second, drive loci are often associated with large areas of low recombination, such as inversions, which can result in an accumulation of linked deleterious mutations that reduce the carrier's fitness (Jaenike, 2001). Third, XCMDs typically cause female-biased population sex ratios. As offspring fathered by an XCMD male are all female, their value is lower in female-biased populations in almost all circumstances (Bryant, Beckenbach, & Cobbs, 1982; Fisher, 1930; Jaenike, 2001). These costs suggest that females could evolve measures to reduce the likelihood that an XCMD male will father their offspring (Haig & Bergstrom, 1995; Jaenike, 2001).

Polyandry, females mating with multiple males within a single reproductive episode, is a general method by which females can reduce the chance of XCMD males fathering their offspring. Carrier males are expected to be disproportionately poor sperm competitors compared to standard males because drive kills half of their sperm (Haig & Bergstrom, 1995), and laboratory studies support this (Angelard, Montchamp-Moreau, & Joly, 2008; Price, Bretman, et al., 2008; Price, Hodgson, et al., 2008; Sutter & Lindholm, 2015; Wilkinson & Fry, 2001). Moreover, increased polyandry can evolve in response to the presence of XCMD rapidly in the laboratory (Price, Bretman, et al., 2008; Price, Hodgson, et al., 2008). Recent work in wild populations of two species have shown negative correlations of polyandry and the frequency of XCMD (Pinzone & Dyer, 2013; Price et al., 2014). Hence polyandry has been suggested as a general mechanism that suppresses meiotic drive (Holman, Price, Wedell, & Kokko, 2015; Manser, Lindholm, Konig, & Bagheri, 2011; Pinzone & Dyer, 2013; Price et al., 2014, 2010). This proposition, however, is challenged by an XCMD system at apparently stable frequencies in *Drosophila subobscura*, a species in which females are reported as monandrous in their European range (Fisher, Doff, & Price, 2013; Maynard Smith, 1956).

Alternatively, there could be differences in a male's ability to gain matings, through either female preference or male competitive ability. Female preference requires a detectable trait to be linked to the XCMD locus (Lande & Wilkinson, 1999); however, as XCMD systems often involve large areas of low recombination, traits important for female choice or for males to compete for females may be linked to drive loci. Female choice against males carrying XCMD has been found in stalk-eyed flies in relation to eye stalk length, a trait linked to XCMD (Cotton, Földvári, Cotton, & Pomiankowski, 2014; Johns, Wolfenbarger, & Wilkinson, 2005; Wilkinson et al., 1998). However, in a well-studied XCMD system in *Drosophila pseudoobscura*, there is no evidence that females are able to identify and avoid XCMD males, despite the system being very old (Price, Lewis, Smith, Hurst, & Wedell, 2012; Price, Lizé, Marcello, & Bretman, 2012) and being associated with large inversions (Beckenbach, 1996; Sturtevant & Dobzhansky, 1936). This is true in several other systems (reviewed in Price & Wedell, 2008), although female preference remains to be investigated in the majority of XCMD systems (Jaenike, 2001).

Drosophila subobscura, a Palearctic woodland fly that has recently spread worldwide (Krimbas, 1993), harbours an XCMD system in North African populations, henceforth referred to as 'SRs' (Jungen, 1967). SR*s* only exists in North Africa at up to 30% frequency (Hauschteck-Jungen, 1990; Jungen, 1967). As outlined earlier, mating with an SR*s* male is expected to be costly for multiple reasons. Hence female *D. subobscura* are expected to have evolved mechanisms to reduce the likelihood of SR*s* males fathering their offspring.

However, while most *Drosophila* species are polyandrous (Holman, Freckleton, & Snook, 2008; Simmons, 2001), *D. subobscura* from Europe are monandrous (Fisher et al., 2013; Maynard Smith, 1956; but see Loukas, Vergini, & Krimbas, 1981). Monandry is an unusual mating system (Taylor, Price, & Wedell, 2014), and is expected to have major impacts on pre- and postcopulatory mate choice mechanisms (Hosken, Stockley, Tregenza, & Wedell, 2009). First, monandrous females cannot use sperm ejection or sperm competition to bias paternity away from XCMD males. Second, monandrous females are often expected to be highly choosy in their mates (Hosken et al., 2009) because they cannot trade up by remating, but also because when females mate only once, the operational sex ratio is likely to be male biased, giving females an extensive choice of mates. Selection pressure to avoid mating with XCMD males may therefore be greater in a monandrous species. *Drosophila subobscura* females are also selective of mates in other circumstances (Immonen, Hoikkala, Kazem, & Ritchie, 2009; Lizé, Price, Heys, Lewis, & Hurst, 2014; Verspoor, Cuss, & Price, 2015).

Polyandry cannot, however, be immediately discounted in *D. subobscura* as a mechanism to prevent SR*s* males fathering a female's offspring. While *D. subobscura* is reported to be monandrous in Europe (Maynard Smith, 1956; Fisher et al., 2013; but see Loukas et al., 1981), North African populations may be polyandrous as female mating behaviour remains to be tested here. Significant latitudinal clines in polyandry have been observed across species' ranges in several other species of *Drosophila* (Pinzone & Dyer, 2013; Price et al., 2014). Further, females in many insect species are more likely to remate when provided with a smaller ejaculate (Charlat et al., 2007; Kaitala & Wiklund, 1995; Perry & Rowe, 2008). This may be reflected in females mating with SR*s* males being more likely to remate, as the males transfer fewer sperm (Hauschteck-Jungen, Burkard, Jungen, & Burch-Schwaller, 1987).

Three central questions are examined. First, are North African flies monandrous, as they are in European populations? We predicted that North African flies would be polyandrous, because increased polyandry can evolve in response to the presence of meiotic drive (Price, Bretman, et al., 2008; Price, Hodgson, et al., 2008), and because stable levels of meiotic drive in natural populations can indicate polyandry is present (Holman et al., 2015; Price et al., 2010). Second, we predicted that females that mate with SR*s* males would be more likely to remate, because SR*s* males transfer small ejaculates, and because remating will allow the female to 'trade up' (Watson, 1991). Third, we predicted that SR*s* males will be less able to gain matings than standard males, because the SR*s* inversion could have accumulated deleterious alleles (Dyer, Charlesworth, & Jaenike, 2007). These provide the first examination of pre- and postcopulatory mechanisms used by females in relation to a selfish gene in *D. subobscura*.

METHODS

Fly Stocks and Maintenance

We collected populations of *D. subobscura* from Tabarka, Tunisia (36.57°N 8.45°E) in April 2013 using baited traps (see