

# Meiotic drive does not cause condition-dependent reduction of the sexual ornament in stalk-eyed flies

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## Abstract

Meiotic drive systems are associated with low-frequency chromosomal inversions. These are expected to accumulate deleterious mutations due to reduced recombination and low effective population size. We test this prediction using the 'sex-ratio' (SR) meiotic drive system of the Malaysian stalk-eyed fly *Teleopsis dalmanni*. SR is associated with a large inversion (or inversions) on the X chromosome. In particular, we study eyespan in males carrying the SR chromosome, as this trait is a highly exaggerated, sexually dimorphic trait, known to have heightened condition-dependent expression. Larvae were raised in low and high larval food stress environments. SR males showed reduced eyespan under the low and high stress treatments, but there was no evidence of a condition-dependent decrease in eyespan under high stress. Similar but more complex patterns were observed for female eyespan, with evidence of additivity under low stress and heterosis under high stress. These results do not support the hypothesis that reduced sexual ornament size in meiotic drive males is due to a condition-dependent response to the putative increase in mutation load. Instead, reduced eyespan likely reflects compensatory resource allocation to different traits in response to drive-mediated destruction of sperm.

## KEYWORDS

condition dependence, meiotic drive, sexual ornament, sexual selection, stalk-eyed fly

## 1 | INTRODUCTION

A key tenet of the handicap principle (Grafen, 1990; Iwasa et al., 1991; Zahavi, 1977) is that sexual ornaments show heightened condition-dependent expression (Cotton et al., 2004a; Pomiankowski & Møller, 1995; Rowe & Houle, 1996). Historically, empirical support was limited as studies omitted comparisons with nonsexual control traits (Cotton et al., 2004a). But there are a growing number of studies showing that heightened condition dependence is a feature of many sexual traits used in mate

preference (Bonduriansky & Rowe, 2005; Izzo & Tibbetts, 2015; Johns et al., 2014). A canonical example is eyespan in the Malaysian stalk-eyed fly, *Teleopsis dalmanni* (Cotton et al., 2004b). Stalk-eyed flies are characterized by lateral elongation of the head capsule into eyestalks (Wilkinson & Dodson, 1997). Many species of stalk-eyed fly, including *T. dalmanni*, are highly sexually dimorphic for this trait, with males possessing much larger eyespan than females (Baker & Wilkinson, 2001). Eyespan is used as a signal in female choice (Hingle et al., 2001; Wilkinson & Reillo, 1994) and male–male interactions (Panhuis & Wilkinson, 1999; Small et al., 2009). In the wild,

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females prefer to roost and mate with males with larger eyespan, both in absolute terms and relative to body size (Cotton et al., 2010; Wilkinson & Reillo, 1994). Male eyespan is highly sensitive to both a range of environmental (Bjorksten et al., 2001; Cotton et al., 2004a; David et al., 1998) and genetic stresses (Bellamy et al., 2013; David et al., 2000; Howie et al., 2019).

The sexual ornament in *T. dalmanni* is also associated with *sex-ratio* meiotic drive (SR), a common type of selfish genetic element located on the X chromosome that causes selective destruction of Y-bearing sperm and the production of female-biased broods (Hurst & Pomiankowski, 1991; Jaenike, 2001; Lindholm et al., 2016). The  $X^{SR}$  chromosome exists at moderate frequencies (~20%) in wild populations (Cotton et al., 2014; Paczolt et al., 2017; Wilkinson et al., 2003). Male carriers of  $X^{SR}$  have reduced eyespan both under laboratory conditions (Johns et al., 2005; Meade et al., 2019; Wilkinson et al., 1998) and in the wild (Cotton et al., 2014). The drive and standard ( $X^{ST}$ ) chromosomes are differentiated by a large paracentric inversion (or inversions; Johns et al., 2005), spanning at least one third of the chromosome (Paczolt et al., 2017). Inversions are a common feature of many meiotic drive systems that restrict recombination (Hoffmann & Rieseberg, 2008; Kirkpatrick, 2010) and are presumed to have been selected to maintain linkage on  $X^{SR}$  between genes contributing to meiotic drive (Charlesworth & Hartl, 1978; Jaenike, 2001). The lack of recombination between  $X^{SR}$  and  $X^{ST}$  has contributed to their divergence, with multiple differences becoming fixed (Reinhardt et al., 2014) over an estimated half million year separation (Paczolt et al., 2017; Swallow et al., 2005).

Long-term recombination suppression within drive-associated inversions is expected to lead to a weaker response to selection and an increase in the accumulation of deleterious mutations (Gordo & Charlesworth, 2001), as observed *in extremis* on Y chromosomes (Orr & Kim, 1998). Several meiotic drive inversions are associated with mutations that severely impact fitness (Jaenike, 2001). For example, in the t-haplotype autosomal drive system in the house mouse, *Mus musculus*, many drive haplotypes carry factors that cause embryonic lethality when homozygous (Silver, 1985). In *Drosophila recens*, the entire SR drive X chromosome is composed of a series of overlapping inversions and is fixed for a recessive mutation causing female sterility (Dyer et al., 2007). In the stalk-eyed fly, there are a large number of fixed sequence differences between  $X^{SR}$  and  $X^{ST}$  (Reinhardt et al., 2014) and carriers of the  $X^{SR}$  chromosome have reduced egg-to-adult viability in both sexes (Finnegan et al., 2019). These findings suggest that the  $X^{SR}$  haplotype carries an increased mutation load, leading to an overall reduction in genetic quality. We hypothesized that this should be reflected in a condition-dependent reduction of eyespan, with the difference between SR and ST male eyespan being small under low environmental stress and large when environmental stress is high, since the reduced genetic quality of SR males should render them less able to cope with stressful conditions.

There is some evidence that the X chromosome in *T. dalmanni* is associated with additive genetic variance for eyespan. In a quantitative trait locus (QTL) study, Johns et al., (2005) found a major X-linked QTL associated with small male eyespan, located just 1.3cM

from the putative drive locus. In addition, Reinhardt et al., (2014) used RNAseq to identify transcripts that are differentially expressed between  $X^{SR}$  and  $X^{ST}$  males. Although many of these transcripts were associated with testis development, as might be expected, a group of transcripts were associated with eye development, including two genes—*chiffon* and *CG4598*—that had previously been shown to be differentially expressed in stalk-eyed flies artificially selected for long and short eyespan (Baker et al., 2009). However, neither of these studies considered whether these putative markers had condition-dependent effects on male eyespan.

Understanding the evolution and maintenance of male sexual ornaments has been the central focus of a wide body of work. Homologous female traits have received less attention (Amundsen, 2000). The evolution of the female trait is thought to reflect selection on males for exaggeration coupled to a shared genetic architecture opposed by counter-veiling selection on female eyespan (Lande, 1980; Tobias et al., 2012). More recently, it has been recognized that female traits may also act as signals of mate quality maintained by male mate preferences (Amundsen, 2000) or female-female competition (LeBas, 2006). In stalk-eyed flies, female eyespan is an indicator of fecundity, and so males prefer to mate with females with large eyespan (Cotton et al., 2010, 2015; Finnegan et al., 2020). Large eyespan females also manifest stronger mate preference for large males as they are better able to distinguish variation in male eyespan (Hingle et al., 2001). In addition, female eyespan shows heightened condition-dependent expression, although to a lesser extent than male eyespan (Cotton et al., 2004b). To date, there is mixed evidence that the  $X^{SR}$  affects female eyespan. The X-linked QTL linked to meiotic drive explains over a third of the variation in male eyespan but just 9% of the variation in female eyespan (Johns et al., 2005). In wild flies, no association was found between female eyespan and *ms395* allele size, a marker that is strongly associated with meiotic drive and male relative eyespan (Cotton et al., 2014). As female eyespan acts as a trait involved in sexual selection with heightened condition dependence, the relationship between the putative lower genetic quality of the  $X^{SR}$  haplotype and female eyespan warrants further study. We predicted that the putative increased mutation load on the  $X^{SR}$  should be reflected in condition-dependent expression of female eyespan, although to a lesser extent than in males.

Here, we used manipulations of larval dietary stress to determine how environmental stress interacts with the  $X^{SR}$  haplotype to affect condition-dependent expression of male and female eyespan. We reared larvae of all possible male and female  $X^{SR}$  and  $X^{ST}$  genotypes under two food treatments—low and high food stress—and examined the resulting variation in eyespan. Our aims were to determine whether SR and ST male eyespan differs when flies are reared under low stress, and whether high environmental stress amplifies this difference, as expected if the  $X^{SR}$  chromosome is associated with reduced genetic quality. We predicted that  $X^{SR}$  would have a similar, but weaker, condition-dependent effect on the expression of female eyespan. We also estimated the dominance relationship for eyespan, by comparing homozygous standard, heterozygous and

homozygous drive females. Since mildly deleterious effects are generally recessive (Charlesworth & Willis, 2009; Fry & Nuzhdin, 2003), our expectation was that homozygous drive females would show a disproportionate reduction in eyespan.

## 2 | MATERIALS AND METHODS

### 2.1 | Stocks

A standard (ST) stock was obtained from Ulu Gombak in Malaysia (3°19'0N 101°45'0E) in 2005 by Andrew Pomiankowski and Sam Cotton. Meiotic drive (SR) is absent from the standard stock. Flies are maintained in high-density cage culture (cage size approx. 30 × 20 × 20 cm) at 25°C with a 12-hr light:dark cycle that includes 15-min artificial dawn-and-dusk periods. Stock flies are fed 100% corn ad libitum.

A meiotic drive stock was obtained in 2012 by Sam Cotton from the same Ulu Gombak location. Meiotic drive is maintained following a standard protocol (Meade et al., 2020; Presgraves et al., 1997). Briefly, females heterozygous for SR ( $X^{SR}X^{ST}$ ) are crossed to ST ( $X^{ST}Y$ ) males and the female offspring are discarded. The male offspring from this cross, half of which are expected to have inherited SR, are crossed individually to ST ( $X^{ST}X^{ST}$ ) females, and their offspring sex ratio is recorded. Males that produce all-female broods of 15 or more are considered SR ( $X^{SR}Y$ ). Drive strength is 100% in the SR stock so SR males do not sire any male offspring. All offspring of SR males are heterozygous females that are then mated to ST males, and the process is repeated. We note that our breeding protocol has resulted in fixation in the stock of a single  $X^{SR}$  haplotype, causing strong drive. The distribution of brood sex ratios among wild-caught flies is considerably more variable (Cotton et al., 2014; Wilkinson et al., 2003), which is also the case under other laboratory breeding regimes (Meade et al., 2019; Wilkinson et al., 1998). This variation remains to be investigated.

### 2.2 | Experimental flies

Experimental females used in crosses were heterozygous for SR, taken from the SR stock. To obtain experimental males with known genotypes, males were collected from the SR stock and crossed individually to ST females. Their larvae were genotyped for SR to determine the paternal genotype (for genotyping details, see below). Larvae from SR males were heterozygous for SR, whereas larvae from ST males were either females homozygous for ST or males hemizygous for ST.

### 2.3 | Experimental crosses and egg collection

In order to produce all five genotypes ( $X^{ST}X^{ST}$ ,  $X^{SR}X^{ST}$ ,  $X^{SR}X^{SR}$  females and  $X^{ST}Y$ ,  $X^{SR}Y$  males), two crosses were employed following a standard design (Finnegan et al., 2019). In Cross A,  $X^{SR}X^{ST}$  females were

crossed to  $X^{SR}Y$  drive males (5 of each per cage), generating  $X^{SR}X^{ST}$  and  $X^{SR}X^{SR}$  females. In Cross B,  $X^{SR}X^{ST}$  females were crossed to  $X^{ST}Y$  males (5 of each per cage), generating  $X^{ST}X^{ST}$  and  $X^{SR}X^{ST}$  females, and  $X^{ST}Y$  and  $X^{SR}Y$  males. Four replicates were set up for Cross A and eight for Cross B. Eggs were collected daily (i.e. when  $\leq 24$  hr old), and groups of 12 were allocated per Petri dish; each dish contained a damp cotton wool pad and food. Two larval food treatments were used, based on earlier work (Cotton et al., 2004b). High stress was allocated 0.03 g of pureed sweetcorn per egg, and low stress was allocated 0.12 g per egg. Adults were collected as they eclosed and frozen for later measurement of eyespan (the distance between the distal tips of the eye bulbs) and thorax length (the distance between the anterior-most point of the prothorax and the posterior-most edge of the thorax; Cotton et al., 2004b), using ImageJ (v.1.46). Measured flies were then stored in 100% ethanol for genotyping.

A second experiment was carried out using identical food treatments and rearing conditions. However, eggs from Cross A and Cross B were no longer reared separately but instead mixed together in each Petri dish. Four eggs from Cross A were mixed with eight eggs from Cross B, generating all genotypes ( $X^{ST}X^{ST}$ ,  $X^{SR}X^{ST}$ ,  $X^{SR}X^{SR}$  females and  $X^{ST}Y$ ,  $X^{SR}Y$  males) in a 1:2:1:1:1 ratio on average. This design was used previously for measuring egg-to-adult survival (Finnegan et al., 2019). Morphology measures of eclosed adults were obtained in the same way as in the first experiment.

### 2.4 | Genotyping

To extract DNA, the abdomen of each fly was removed and placed in a 96-well plate containing 50  $\mu$ l of squish buffer (5  $\mu$ l 10 $\times$  Taq Buffer with KCL and 15 mM MgCl<sub>2</sub> (Thermo Scientific), 3  $\mu$ l proteinase K and 42  $\mu$ l UltraPure H<sub>2</sub>O). Abdomens were mechanically lysed, and wells were topped up with a further 100  $\mu$ l squish buffer. The 96-well plates were then transferred to a 2,720 Thermal Cycler (Applied Biosystems) and incubated at 37°C for 30 min, before being heated to 95°C for 3 min to denature the proteinase K. Extracted DNA was stored at 4°C.

DNA was PCR-amplified on a 2720 Thermal Cycler (Applied Biosystems) in 96-well plates containing 1  $\mu$ l of DNA, 0.1  $\mu$ l of 5 $\times$  Phusion Taq polymerase (New England BioLabs), 0.2  $\mu$ l of dNTPs, 6.2  $\mu$ l UltraPure water and 0.5  $\mu$ l each of the 10  $\mu$ M forward and reverse primers for comp162710. Comp162710 is an indel marker developed in the laboratory of Jerry Wilkinson (personal communication) to identify  $X^{SR}$  chromosomes that carry a small allele (201 bp) and  $X^{ST}$  chromosomes that carry a large allele (286 bp). This marker has been successfully used previously (Meade et al., 2020). Comp162710 fragment lengths were assayed by gel electrophoresis on a 3% agarose gel with a 0.5 $\times$  TBE buffer.

### 2.5 | Statistical analysis

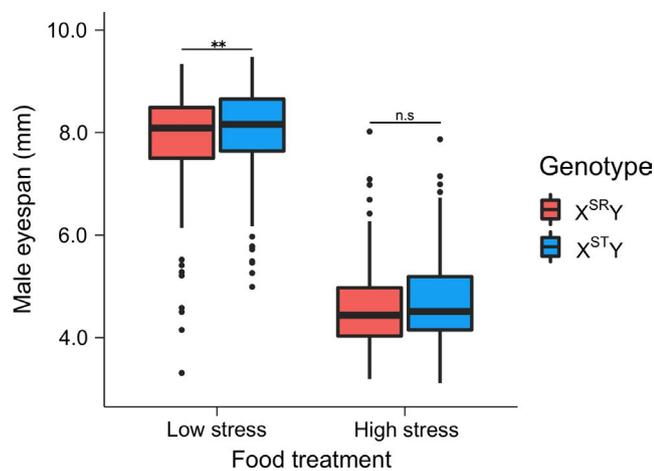
The effects on absolute male eyespan of food treatment, genotype, and the food treatment by genotype interaction were analysed in a

linear model. Then, the effect on residual eyespan was analysed by including thorax in the model. Female eyespan was analysed using similar models and including a factor for parental cross. As parental cross had a strong effect on female eyespan, the data were split by cross and reanalysed. In a further analysis, we controlled for the effect of cross by adjusting Cross B female eyespan values by the percentage difference between heterozygous  $X^{SR}X^{ST}$  eyespan in Cross A and Cross B. Pairwise comparisons of female genotypes were made using Tukey's post hoc comparison tests. We report all model effects in the Supplementary information. The effect of food treatment, genotype and their interaction on thorax length is also included in the Supplementary information.

### 3 | RESULTS

#### 3.1 | Male eyespan

A total of 468 males were collected, of which 423 were successfully genotyped. Food treatment had a strong effect on absolute male eyespan, which was smaller under the high stress food treatment (mean  $\pm$  SE, low stress =  $7.8693 \pm 0.0660$  mm, high stress =  $4.6893 \pm 0.0609$ ,  $F_{1,416} = 1,188.1578$ ,  $p < .0001$ ; Figure 1). SR males had smaller eyespan than ST males overall ( $F_{1,416} = 5.1820$ ,  $p = .0233$ ), although this was only evident under low stress (mean  $\pm$  SE, SR =  $7.7853 \pm 0.0958$ , ST =  $7.9638 \pm 0.0981$ ,  $F_{1,216} = 9.3255$ ,  $p = .0025$ ) and not under high stress (mean  $\pm$  SE, SR =  $4.5749 \pm 0.0907$ , ST =  $4.7824 \pm 0.0934$ ,  $F_{1,199} = 2.5466$ ,  $p = .1109$ ; Figure 1). The magnitude of the difference between SR and ST males did not differ between low and high stress (food treatment by genotype interaction,  $F_{1,416} = 0.1229$ ,  $p = .7261$ ). After controlling for body size, residual male eyespan was still strongly affected by food treatment ( $F_{1,413} = 90.0744$ ,  $p < .0001$ ). SR males had

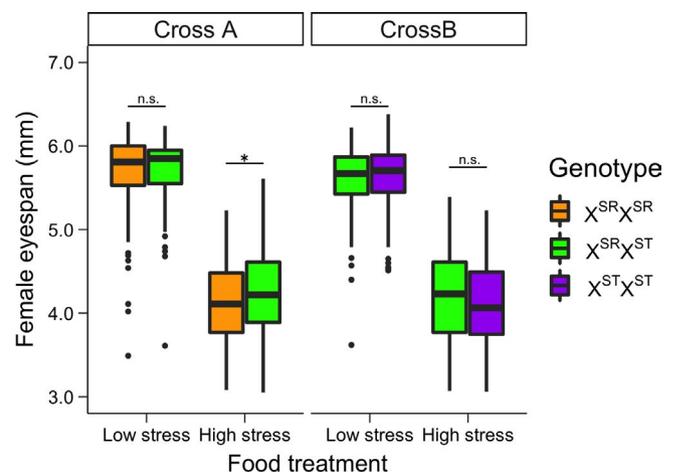


**FIGURE 1** Absolute male  $X^{SR}Y$  (red) and  $X^{ST}Y$  (blue) eyespan in low and high stress larval food treatments. Boxes enclose 1st and 3rd quartiles, with whiskers extending to  $1.5 \times IQR$ . Thick black lines within boxplots show the medians. Significance values reflect  $p$ -values obtained from models where males were split into low and high stress, as opposed to those given by the full model presented in Results section. \*\*  $p < .01$

reduced residual eyespan compared with ST males ( $F_{1,413} = 8.5065$ ,  $p = .0037$ ), and again, the magnitude of this difference did not change across food treatment ( $F_{1,413} = 0.2786$ ,  $p = .5979$ ).

#### 3.2 | Female eyespan

A total of 1,159 females were collected, of which 1,086 were successfully genotyped. As in males, the high stress food treatment had a strong negative effect on absolute female eyespan (mean  $\pm$  SE, low stress =  $5.6557 \pm 0.0188$ , high stress =  $4.1473 \pm 0.0209$ ,  $F_{1,1,063} = 2,824.0524$ ,  $p < .0001$ ). There was a significant effect of cross on female eyespan ( $F_{1,1,063} = 5.7000$ ,  $p = .0171$ ), so genotypes were compared separately for Cross A and Cross B (Figure 2).  $X^{SR}$  homozygotes had smaller absolute eyespan than heterozygous females ( $F_{1,586} = 6.1437$ ,  $p = .0135$ ). There was a significant food treatment by genotype interaction ( $F_{1,586} = 4.0962$ ,  $p = .0434$ ) as  $X^{SR}$  homozygotes were smaller than heterozygotes under high stress (mean  $\pm$  SE,  $X^{SR}X^{ST} = 4.2421 \pm 0.0409$ ,  $X^{SR}X^{SR} = 4.0958 \pm 0.0399$ ,  $F_{1,331} = 7.9483$ ,  $p = .0051$ ) but not under low stress (mean  $\pm$  SE,  $X^{SR}X^{ST} = 5.7118 \pm 0.0401$ ,  $X^{SR}X^{SR} = 5.7096 \pm 0.0347$ ,  $F_{1,254} = 0.0274$ ,  $p = .8687$ ). In Cross B, absolute female eyespan did not differ between heterozygotes and  $X^{ST}$  homozygotes under high (mean  $\pm$  SE,  $X^{ST}X^{ST} = 4.0866 \pm 0.0415$ ,  $X^{SR}X^{ST} = 4.1947 \pm 0.0489$ ,  $F_{1,266} = 2.9528$ ,  $p = .0883$ ) or low stress (mean  $\pm$  SE,  $X^{ST}X^{ST} = 5.6153 \pm 0.0415$ ,  $X^{SR}X^{ST} = 5.5876 \pm 0.0398$ ,  $F_{1,208} = 1.1933$ ,  $p = .2759$ ), nor was there a food treatment by genotype interaction ( $F_{1,475} = 2.8579$ ,  $p = .0916$ ). After controlling for body size, genotype no longer explained variation in residual female eyespan in Cross A ( $F_{1,585} = 0.0703$ ,  $p = .7910$ ) or Cross B ( $F_{1,474} = 0.1824$ ,  $p = .6695$ ), and there was no food treatment by genotype interaction in either cross (Cross A,  $F_{1,585} = 0.2084$ ,  $p = .6482$ ; Cross B,  $F_{1,474} = 0.2221$ ,  $p = .6377$ ).

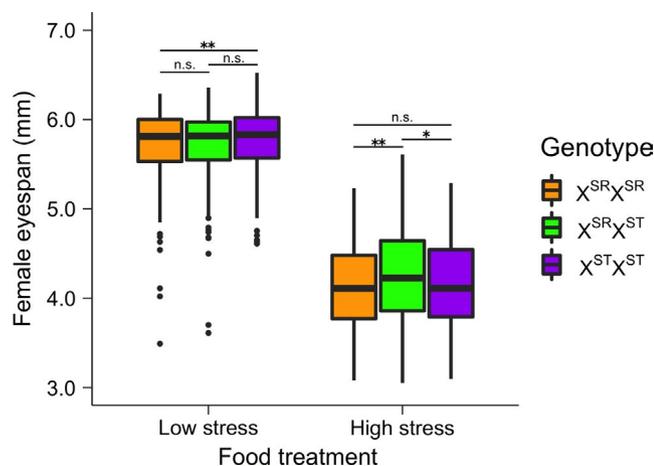


**FIGURE 2** Absolute female eyespan in low stress and high stress larval food treatments, where females from each cross category were reared separately. Cross A produces  $X^{SR}X^{SR}$  (orange) and  $X^{SR}X^{ST}$  (green) genotypes. Cross B produces  $X^{ST}X^{SR}$  (green) and  $X^{ST}X^{ST}$  (purple) genotypes. For details of the presentation, see Figure 1. \*  $p < .05$

To compare the three female genotypes (Figure 3), we controlled for cross by equalizing measurements of female heterozygotes, which were common to Cross A and Cross B (see Methods). Absolute eyespan depended on genotype ( $F_{2,1,064} = 4.6997$ ,  $p = .0093$ ), and the effect of genotype varied across food treatment (food treatment by genotype interaction,  $F_{2,1,064} = 3.4041$ ,  $p = .0336$ ). Under low stress,  $X^{ST}$  homozygous females had the largest absolute eyespan (mean  $\pm$  SE =  $5.74013 \pm 0.0425$ ), which was larger than  $X^{SR}$  homozygous females (mean  $\pm$  SE =  $5.7096 \pm 0.0347$ ; Tukey's test,  $p = .0026$ ). Heterozygous females had intermediate absolute eyespan (mean  $\pm$  SE =  $5.7118 \pm 0.0285$ ), not different from either homozygote (Tukey's  $X^{ST}X^{ST} - X^{ST}X^{SR}$  comparison,  $p = .0508$ ;  $X^{SR}X^{ST} - X^{SR}X^{SR}$  comparison,  $p = .3581$ ). Under high stress, heterozygous females had the largest absolute eyespan (mean  $\pm$  SE =  $4.2422 \pm 0.0315$ ), larger than  $X^{SR}$  homozygotes (mean  $\pm$  SE =  $4.0958 \pm 0.0399$ , Tukey's test,  $p = .0040$ ) but not larger than  $X^{ST}$  homozygotes (mean  $\pm$  SE =  $4.1328 \pm 0.0420$ , Tukey's test,  $p = .1303$ ). As before, when controlling for body size genotype did not affect residual female eyespan ( $F_{2,1,063} = 0.5412$ ,  $p = .5822$ ), and there was no food treatment by genotype interaction ( $F_{2,1,063} = 0.5656$ ,  $p = .5682$ ).

### 3.3 | Female eyespan (second experiment)

In a second experiment, eggs from Cross A and Cross B were mixed together, so that all genotypes potentially emerged from the same Petri dish. In particular, this eliminated specific differences associated with Cross A and Cross B among the three female genotypes, and avoids the need to equalize them statistically. Female absolute eyespan again depended on food treatment ( $F_{1,446} = 1,678.7142$ ,  $p < .0001$ ) and genotype ( $F_{2,446} = 5.6035$ ,  $p = .0039$ ). There was no food treatment by genotype interaction ( $F_{2,446} = 2.0007$ ,  $p = .1364$ ). However, the largest genotype was different across the treatments.



**FIGURE 3** Absolute eyespan of  $X^{SR}X^{SR}$  (orange),  $X^{SR}X^{ST}$  (green) and  $X^{ST}X^{ST}$  (purple) females (after controlling for thorax length), in low and high stress food treatments, after adjusting for cross. Points show mean relative eyespan  $\pm$  one standard error. For details of the presentation, see Figure 1. Significance values reflect  $p$ -values from Tukey's post hoc comparison tests, \*\*  $p < .01$

In low stress,  $X^{ST}X^{ST}$  eyespan (mean  $\pm$  SE =  $6.0766 \pm 0.0252$ ) is larger than  $X^{SR}X^{SR}$  (mean  $\pm$  SE =  $5.9246 \pm 0.0352$ ; Tukey's test,  $p = .002$ ) and  $X^{SR}X^{ST}$  is intermediate (mean  $\pm$  SE =  $5.9888 \pm 0.02659$ ; Tukey's  $X^{SR}X^{ST} - X^{ST}X^{ST}$  comparison,  $p = .0872$ ,  $X^{SR}X^{ST} - X^{SR}X^{SR}$  comparison,  $p = .2529$ ). In high stress, heterozygous  $X^{SR}X^{ST}$  eyespan (mean  $\pm$  SE =  $4.4860 \pm 0.0577$ ) is larger than  $X^{SR}X^{SR}$  (mean  $\pm$  SE =  $4.2596 \pm 0.0691$ ; Tukey's test,  $p = .0424$ ) and  $X^{ST}X^{ST}$  is intermediate (mean  $\pm$  SE =  $4.4257 \pm 0.0676$ , Tukey's  $X^{SR}X^{ST} - X^{ST}X^{ST}$  comparison,  $p = .7784$ ,  $X^{SR}X^{ST} - X^{SR}X^{SR}$  comparison,  $p = .2498$ ). After controlling for body size, genotype affected residual eyespan in low stress ( $F_{2,246} = 4.7519$ ,  $p = .0094$ ), but not in high stress ( $F_{2,198} = 1.5412$ ,  $p = .2167$ ). The results from the second experiment are therefore in broad agreement with those from the first experiment.

## 4 | DISCUSSION

Male eyespan in stalk-eyed flies is a canonical example of an exaggerated sexual character that is highly condition-dependent, in response to both environmental (Cotton et al., 2004b; David et al., 1998) and genetic stress (Bellamy et al., 2013; David et al., 2000; Howie et al., 2019). *T. dalmanni* stalk-eyed flies show reduced eyespan in males carrying SR meiotic drive. Here, we tested the hypothesis that this reduction is a condition-dependent response arising from the low genetic quality of the  $X^{SR}$  chromosome. As reported previously (Cotton et al., 2010; Wilkinson et al., 1998), eyespan was reduced in SR males and this effect persisted after controlling for body size (Figure 1). But the difference in eyespan between males carrying the  $X^{SR}$  and  $X^{ST}$  chromosomes was not condition-dependent; there was no evidence for amplified reduction in the sexual ornament of SR males under high environmental stress.

The environmental stress used in this study follows previous work on stalk-eyed flies using larval food reductions (Cotton et al., 2004b), which has a similar effect to other stresses, such as thermal shock and desiccation (Bjorksten et al., 2001). The 'low' stress treatment constituted a plentiful amount of the standard laboratory food. The 'high' stress treatment was chosen using previous work, at a level at which eyespan substantially declined but before any large increase in mortality (Cotton et al., 2004b). Previous work has also shown that genetic differences in the male sexual ornament are constrained under low stress but amplified as environmental stress increases (Bellamy et al., 2013; David et al., 2000; Howie et al., 2019). This is not the pattern observed here as the smaller eyespan of SR males was consistent across environmental stress treatments (Figure 1). This pattern is further supported by prior experimental work using dietary stress based on varying protein: carbohydrate ratios (rather than varying the amount of food per larva), where SR male eyespan was reduced relative to ST, but no amplification was reported as the protein content of the diet declined (Cotton, 2016).

The lack of an amplified reduction in SR male eyespan under environmental stress is not consistent with the expected low genetic

quality of the  $X^{SR}$  haplotype. Reduced genetic quality is thought to be typical for low-frequency meiotic drive genes located in or close to chromosomal inversions or other areas of low recombination, indicative of weak selection leading to the accumulation of mutation load (Dyer et al., 2007; Johns et al., 2005; Larracuente & Presgraves, 2012; Silver, 1993). There are many examples of viability and fertility deficits in males and females carrying X-linked meiotic drive (Curtsinger & Feldman, 1980; Dyer et al., 2007; Dyer & Hall, 2019; Jaenike, 1996; Lerner et al., 2019; Unckless & Clark, 2014), although it is not known whether these are side effects of drive itself or due to the accumulation of deleterious mutations at linked loci. In *T. dalmanni*, a large inversion covers at least a third and possibly substantially more of the  $X^{SR}$  chromosome (Johns et al., 2005; Reinhardt et al., 2014). The  $X^{SR}$  chromosome is estimated to be half a million years old (Paczolt et al., 2017), so there has been considerable time for mutants to spread and accumulate, which is reflected in considerable sequence divergence from the  $X^{ST}$  chromosome (Reinhardt et al., 2014). Why then is there a lack of evidence for a condition-dependent deficit in eyespan in males carrying the  $X^{SR}$  haplotype? One possibility arises from the relatively high frequency of  $X^{SR}$ , around 20% in natural populations (Cotton et al., 2014; Paczolt et al., 2017; Wilkinson et al., 2003). At this frequency, the rate of recombination of  $X^{SR}$  is only a quarter of the standard  $X^{ST}$  chromosome, and this may be sufficient to allow the removal of a substantial fraction of deleterious mutations on the  $X^{SR}$  chromosome. Even if this is the case, the  $X^{SR}$  chromosome has been shown to cause a fitness deficit as carriers have reduced egg-to-adult viability, both in males and in females (Finnegan et al., 2019). This supports the idea that the  $X^{SR}$  haplotype has low genetic quality and results in reduction of the sexual ornament under low and high environmental stress. It means that female preference will discriminate against males that carry the meiotic drive haplotype. But the low genetic quality of drive males is not reflected in a condition-dependent expression of the male sexual ornament.

An additional interpretation is that the allocation of limited resources to one trait during development produces compensatory changes in the relative size of other traits (Nijhout & Emlen, 1998; Stevens et al., 1999). This hypothesis suggests that the observed pattern of trait size is a reflection of adaptive changes in resource investment to cope with drive. In SR males, fertility is comparable to that of ST males despite sperm destruction (Meade et al., 2019, 2020). This is accomplished by SR males having greatly enlarged testes, which allows them to deliver the same number of sperm per ejaculate as ST males (Meade et al., 2019) and to maintain their fertility even under conditions of multiple mating (Meade et al., 2020), although there is evidence of fertility loss under an extreme regime of multiple mating and sperm competition (Wilkinson et al., 2006). The allocation of increased resources to testes presumably means that SR males have less to invest in other traits. This may explain the reduced accessory gland size of SR males, as testes and accessory glands develop over a period of several weeks post-eclosion (Baker et al., 2003; Meade et al., 2020; Rogers et al., 2008). It is less obvious why increased investment in testes constrains eyespan

development, as the latter reflects pre-eclosion resource allocation. However, a mechanistic connection may exist as topical application of a juvenile hormone analogue to final instar larvae results in the development of males with larger testes and smaller eyespan (Fry, 2006). These observations suggest that larger testes, smaller eyespan and reduced accessory gland size are outcomes of resource investment decisions in SR males. One way to test this hypothesis would be to examine the size of these traits at eclosion. Increased allocation of resource to testes is predicted to cause a reduction in allocation to eyespan (which is fixed at eclosion) and the accessory glands. The resource allocation hypothesis would not be supported if there was no evidence of increased testes size and decreased accessory gland size at eclosion, with the difference of these reproductive organs in SR males reflecting post-eclosion development, which is extensive in stalk-eyed flies, as they only reach sexual maturity after several weeks of adult life (Baker et al., 2003).

These changes could be adaptive as modelling work shows that males with fewer resources are expected to produce similar size ejaculates to those of resource-rich males, but at the expense of investment in traits that contribute to the mating rate (Tazzyman et al., 2009). We have previously shown in stalk-eyed fly SR males that their larger testes enable them to maintain ejaculate sperm allocation and fertility in single and multiple mating, despite drive causing the loss of half of their sperm (Meade et al., 2019, 2020). But the smaller eyespan of SR males, independent of environmental conditions, means they attract fewer females to their lek sites and hence mate less frequently (Burkhardt & de la Motte, 1988; Cotton et al., 2010; Hingle et al., 2001; Wilkinson & Reillo, 1994). This may explain why they have reduced accessory gland size, a trait positively associated with the mating rate (Rogers et al., 2005). This combination of investment in traits fits general ideas about life history trade-offs between secondary sexual traits and ejaculate expenditure (Simmons et al., 2017), and the specific theoretical prediction that resources are diverted into maintaining ejaculate size at the expense of the mating rate (Tazzyman et al., 2009). Strategic resource investment likely occurs in a condition-independent manner because drive is a cellular developmental process disconnected from environmental stress. This predicts that the strength of drive should be invariant across environmental stress regimes, which has not yet been explicitly tested.

Compensatory responses to meiotic drive that restore organismal fitness have been investigated previously for resistance mechanisms, which are highly diverse and widely distributed among species suffering from both X-linked drive and autosomal drive (Price et al., 2020). There is also evidence for changes in female polyandry in systems where sperm competition impedes the success of sperm from meiotic drive males (Manser et al., 2020; Price et al., 2008). In addition, a suite of behavioural and metabolic traits have been hypothesized to be involved in compensatory mechanisms to t drive in the house mouse. The t inversion carries recessive lethals, making carrier fitness negatively frequency-dependent (Runge & Lindholm, 2018). Juvenile mice carrying the driving t haplotype show increased dispersal that could be adaptive if it reduces the likelihood of matings between male

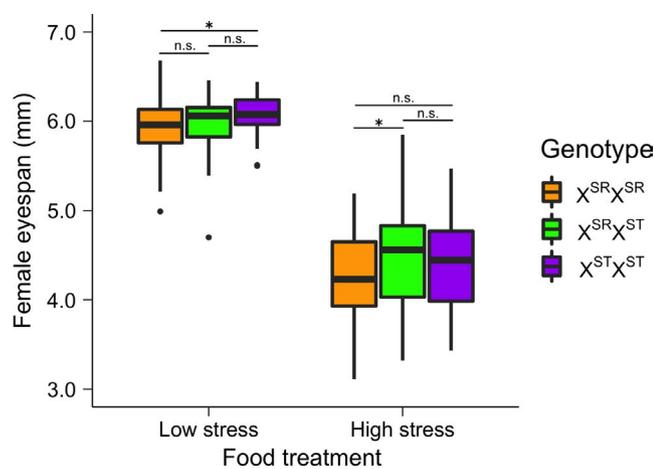
and female carriers and consequently the probability of producing homozygous offspring (Sutter & Lindholm, 2015). Female carriers of the *t* haplotype may additionally compensate for smaller litter size when they mate with male carriers by having evolved reduced resting metabolic rate (Lopes & Lindholm, 2020). This is associated with extended lifespan and the production of additional litters in later life (Ferrari et al., 2019). These life history changes contrast with resistance to drive and female polyandry because they enhance the fitness and spread of the meiotic driver itself (Meade et al., 2020). There are parallels here to alterations in host behaviour associated with other selfish genetic elements such as *Wolbachia*, though it is often unclear whether changes are detrimental or beneficial to host fitness (Awrahaman et al., 2013; Wedell, 2019). It seems likely that coevolutionary compensation in host fitness is more common than currently realized.

A further aim of the work here was to examine female eyespan. This trait shows high condition dependence in stalk-eyed flies, but to a lesser extent than in the homologous male trait (Cotton et al., 2004b). We examined eyespan condition dependence in females and found it was more complex than in males. Under low and high environmental stress,  $X^{SR}$  homozygotes had smaller eyespan than  $X^{ST}$  homozygotes (though this difference was not significant under high stress; Figures 2–4). As with males, there was no evidence for a condition-dependent amplification of genetic differences; the eyespan difference between  $X^{SR}$  and  $X^{ST}$  homozygotes was not exaggerated by high environmental stress. The pattern in heterozygous females was different (Figures 2–3). Under low stress, heterozygotes were intermediate between the homozygotes. But under high stress, there was evidence for heterosis as heterozygous females had the largest eyespan, greater than either homozygote. This heterosis likely reflects the masking of deleterious alleles (Wilton & Sved, 1979) when the nonrecombinant and hence highly diverged  $X^{SR}$  and  $X^{ST}$  chromosomes are brought together. Our results suggest that heterosis is

dependent on environmental conditions. Under low stress, additive differences between haplotypes dominate. Under high stress, low fitness recessive mutations are exposed and the eyespan of homozygotes declines, whereas heterozygotes mask this reduction. As we do not see an amplification of the difference between homozygous SR and homozygous ST eyespan, these results do not support the prediction of a condition-dependent reduction due to the SR haplotype. More work will be necessary to determine whether reduced homozygous SR female eyespan is the result of strategic resource allocation, as suggested for males. It would be particularly illuminating to examine the relationship between drive genotype, eyespan, and fecundity under varying environmental conditions.

An unforeseen complication in this study arose from the experimental design. In order to collect the full range of male and female genotypes, two experimental crosses were carried out, Cross A ( $X^{SR}X^{ST}$  mated to  $X^{SR}Y$ ) and Cross B ( $X^{SR}X^{ST}$  mated to  $X^{ST}Y$ ). Larvae from the two crosses were kept separately throughout egg-adult development. Although the rearing conditions of the two crosses were identical (larval density, food type, all other environmental variables), there was a clear effect of cross on female eyespan as heterozygous female eyespan was larger in Cross A than in Cross B samples. These heterozygous offspring have the same nuclear genotype, they share the same maternal genotype (all heterozygotes), and their mothers are drawn from the same stock cages and do not differ in maternally inherited cytotypic. These offspring do differ in paternal genotype ( $X^{SR}Y$  in Cross A and  $X^{ST}Y$  in Cross B), but there is no obvious paternal effect to explain the difference in eyespan of heterozygous female offspring. A possible cause is that in Cross A, only female offspring are produced, whereas in Cross B, the offspring sex ratio is approximately 1:1, suggesting that male larvae have a negative competitive effect on female eyespan. This was despite efforts to limit the amount of competition between larvae by plating a small number of eggs (12) onto each Petri dish. Differences in male and female larval competitive ability have been reported previously in fruitflies and mosquitoes (Nunney, 1983; Steinwascher, 2018). In *D. melanogaster*, Nunney (1983) reported that male larvae of some strains were better at exploiting a limited food supply than females. This was true even for a strain where females eclosed earlier than males, as is the case in stalk-eyed flies (unpublished data). In our analysis, we dealt with this inconsistency by statistically controlling for the effect of cross on female eyespan (Figure 3). In addition, a further experiment was carried out (Figure 4) in which eggs were mixed together from Cross A (4 eggs) and Cross B (8 eggs). The pair of experiments gave qualitatively similar results, implying that the statistical adjustment for the effect of cross was appropriate.

In summary, meiotic drive causes a reduction in male eyespan, the sexual ornament in stalk-eyed flies. This occurs under low and high food stress, in a manner that is not strongly condition-dependent. A similar reduction is observed in female eyespan, again across environmental stress levels. But the pattern in females is complicated by heterosis in heterozygotes that is dependent on environmental stress. It seems likely that the reduced eyespan in SR males reflects contrasting resource allocation to different traits during



**FIGURE 4** Absolute female eyespan in low and high stress larval food treatments in the second experiment when eggs from Cross A and Cross B were reared together to generate all three female genotypes:  $X^{SR}X^{SR}$  (orange),  $X^{SR}X^{ST}$  (green), and  $X^{ST}X^{ST}$  (purple). Points show mean absolute eyespan  $\pm$  one standard error. For details of the presentation, see Figure 1. Significance values reflect *p*-values from Tukey's post hoc comparison tests, \* *p* < .05

development in order to compensate for the destruction of sperm caused by meiotic drive.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## AUTHOR CONTRIBUTIONS

SRF, KF and AP designed the project and methodology; SRF, KF and MM collected the data; SRF and MM carried out the genotyping; and SRF and AP analysed the data and wrote the paper.

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## DATA AVAILABILITY STATEMENT

Data and scripts used in the analyses are available at the Dryad data depository <https://doi.org/10.5061/dryad.x0k6djhvh>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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# Meiotic drive does not cause condition-dependent reduction of the sexual ornament in stalk-eyed flies

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## Graphical Abstract

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Malaysian *Teleopsis dalmanni* stalk-eyed flies carry an X-linked meiotic drive chromosome, which reduces eyespan, the male's sexual ornament. Smaller eyespan reflects compensatory resource allocation and is not a condition-dependent response to the mutation load on the drive chromosome.

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