

# Meiotic drive adaptive testes enlargement during early development in the stalk-eyed fly, *Teleopsis dalmanni*.

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## Background

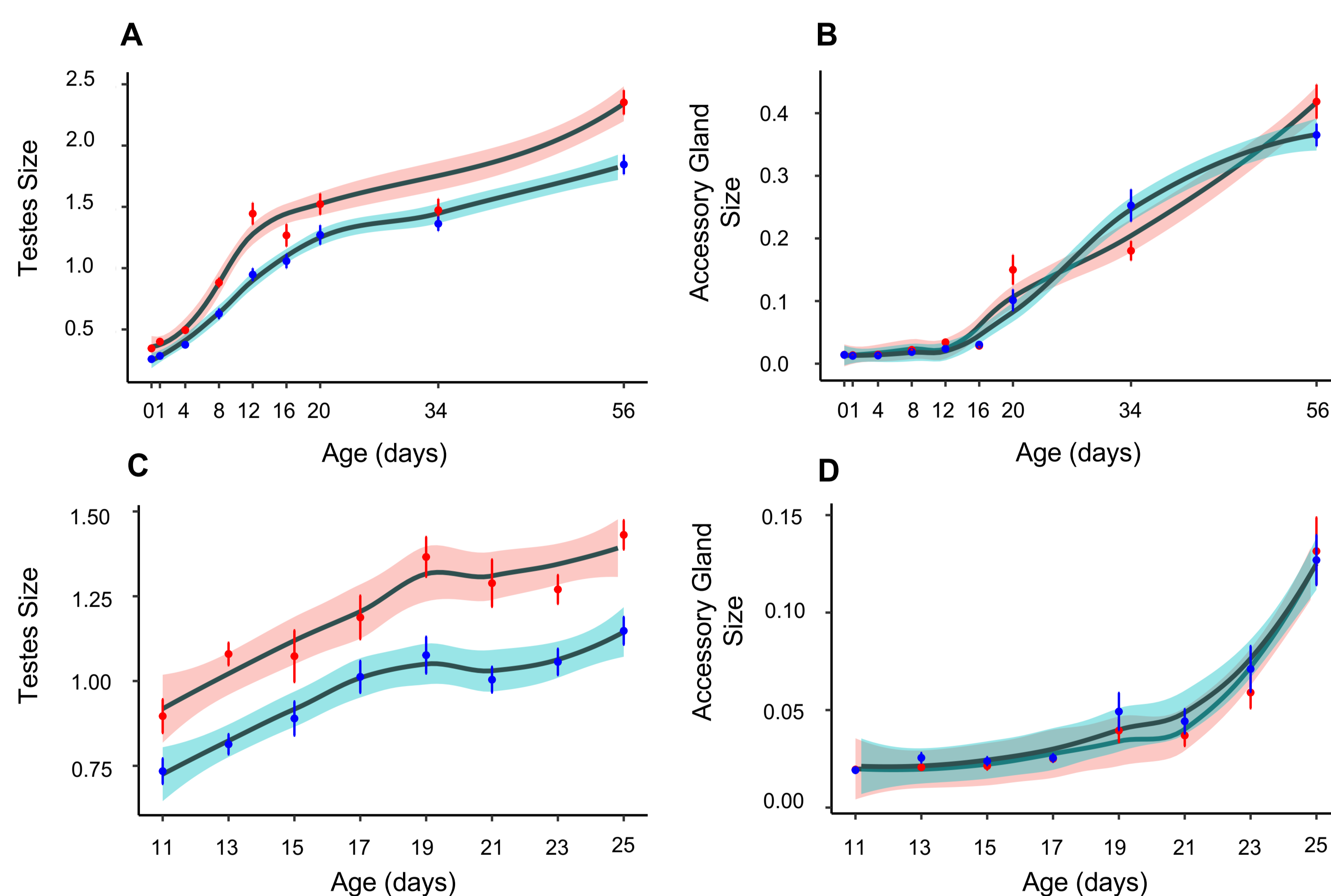
The sex-ratio 'SR' meiotic drive system in the Malaysian stalk-eyed fly, *Teleopsis dalmanni*, involves an X-linked meiotic drive gene that attacks and destroys all Y-bearing sperm, resulting in female-only broods. Despite this sperm destruction, drive males are able to maintain normal fertility due to their greatly enlarged testes. This research aimed to determine whether this is a **novel adaptation** in response to the costly effects of meiotic drive.

## Methodology

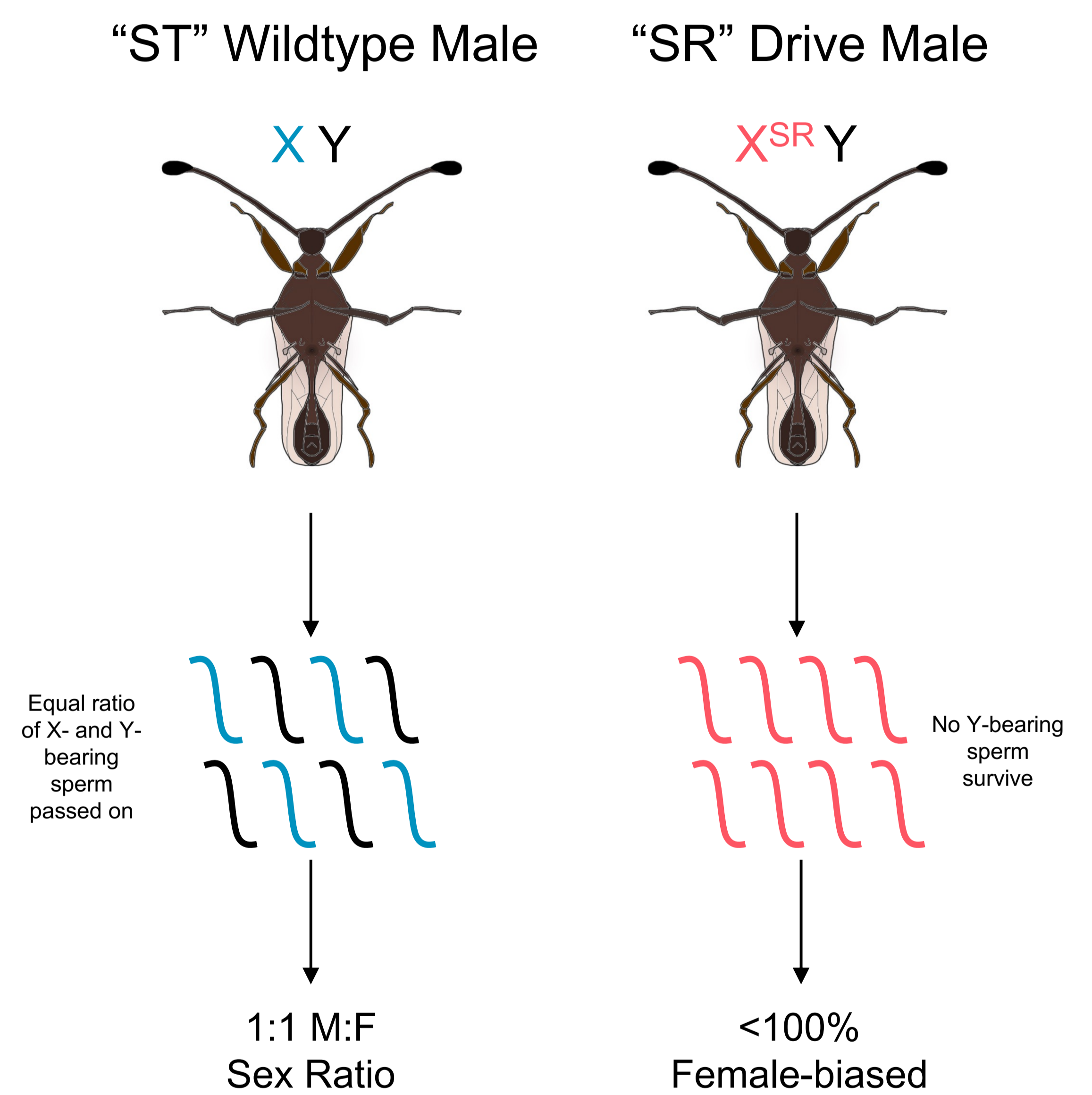
Dissection and measurement of the testes and accessory glands of SR and wildtype (ST) *T. dalmanni* was performed at several time points post-eclosion. One experiment was carried out over a longer period of time (eclosion to 56 days), and a second honed in on a time period of rapid development (11-25 days).

## Results

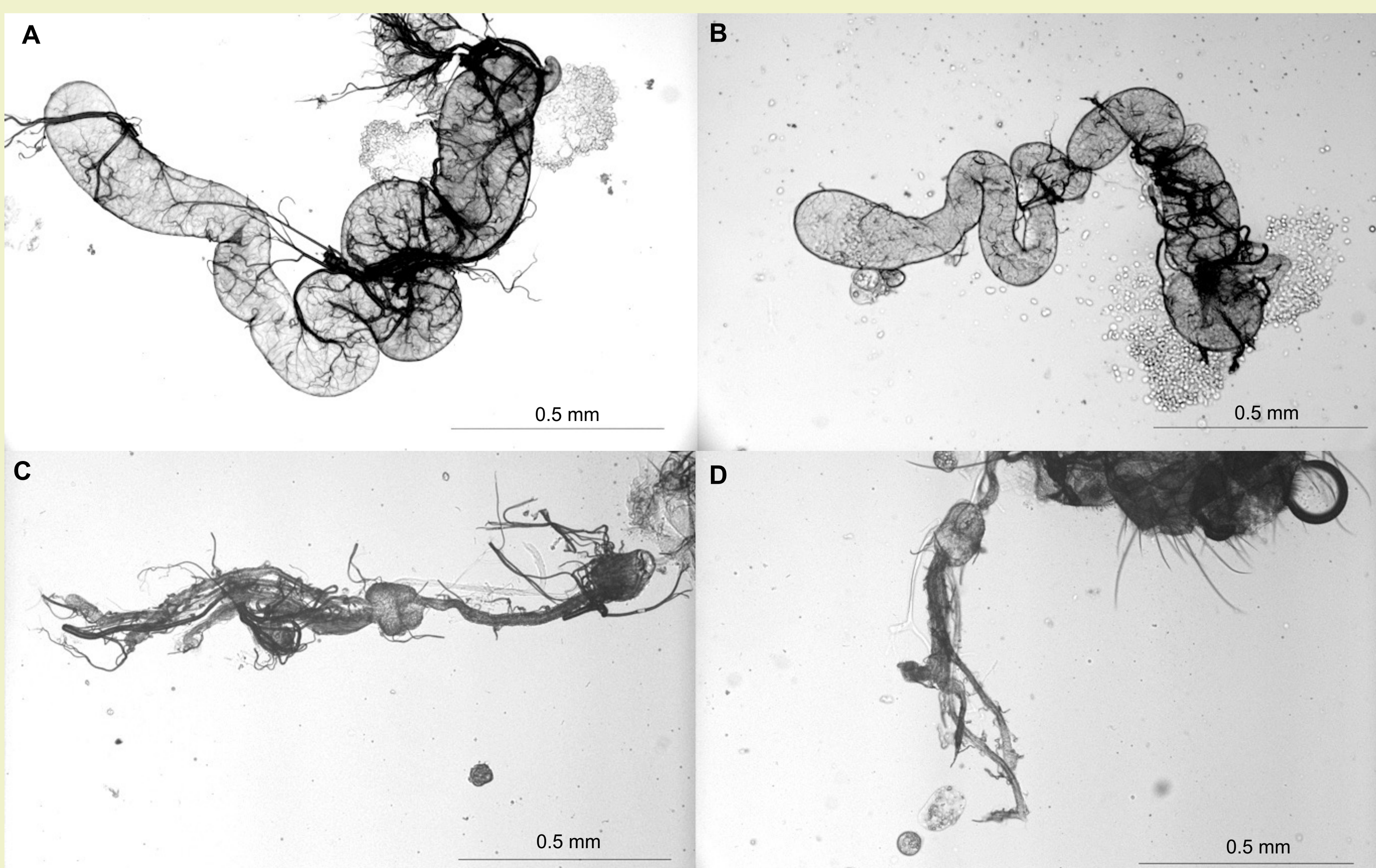
- SR males had larger testes (**mean  $\pm$  s.e. =  $1.006 \pm 0.050$** ) than ST males ( **$0.793 \pm 0.040$** ;  $F_{1,356} = 11.155$ ,  $p < 0.001$ ; **Fig 1A**) in the long dataset, and this held after controlling for body size and relative eyespan ( $F_{1,353} = 57.275$ ,  $p < 0.001$ ). The same was found for the short dataset (**SR:  $1.202 \pm 0.023$ , ST:  $0.97 \pm 0.018$** ;  $F_{1,344} = 84.038$ ,  $p < 0.0001$ ; **Fig 1C**), and again this held after controlling for body size and relative eyespan ( $F_{1,342} = 107.194$ ,  $p < 0.001$ ).
- SR testes were larger on days 0, 1, 4, 8, 12, 20, and 56 ( $p < 0.05$ ) but not on days 16 and 34 ( $p > 0.05$ ) in the long dataset. When repeated in the short dataset at a higher sample size, SR testes were larger on days 11, 13, 17, 19, 21, 23, and 25 ( $p < 0.05$ ), but marginally not on day 15 ( $p = 0.052$ ).
- There was no overall size difference between SR and ST accessory glands in either the long (**SR:  $0.085 \pm 0.012$ , ST:  $0.077 \pm 0.009$** ,  $F_{1,315} = 0.339$ ,  $p = 0.561$ ; **Fig 1B**) or short dataset (**SR:  $0.047 \pm 0.004$ , ST  $0.051 \pm 0.004$** ,  $F_{1,345} = 0.358$ ,  $p = 0.550$ ; **Fig 1D**) even after controlling for body size and relative eyespan (**Long:  $F_{1,313} = 0.425$ ,  $p = 0.515$ , Short:  $F_{1,343} = 0.027$ ,  $p = 0.870$** ).
- Males with larger accessory glands had larger testes after controlling for body size ( $F_{1,339} = 13.457$ ,  $p = 0.001$ ). The growth of the accessory glands was predicted by relative eyespan, where males with larger relative eyespan had larger accessory glands ( $F_{1,338} = 10.965$ ,  $p = 0.001$ ). Testis size showed a more complex relationship as males with larger relative eyespan had larger accessory glands but smaller testes ( $F_{1,337} = 6.021$ ,  $p = 0.015$ ). These relationships between relative eyespan and reproductive organ size did not differ with genotype.



**Fig 1:** **A)** Testes size (mm<sup>2</sup>) days 0–56 for SR (red) and ST (blue) males. **B)** Accessory gland size (mm<sup>2</sup>) days 0–56. **C)** Testes size days 11–25. **D)** Accessory gland size days 11–25. Error bars represent  $\pm$  s.e. Shading represents 95% confidence intervals.



**Fig.3:** Mode of action of the X-linked meiotic driver in *Teleopsis dalmanni* causing female-biased broods.



**Fig 2:** **A)** SR testis day 0; **B)** ST testis day 0; **C)** SR accessory glands day 0; **D)** ST accessory glands day 0; Scale = 0.5 mm.

## Discussion and Conclusions

- Hypothesis:** Enlarged testes arise from extended development with resources re-allocated away from the accessory glands, which tend to be reduced in size in SR drive males.
- Result 1:** Instead, SR testes were enlarged on the day of eclosion (day 0) and increased resources to the testes during development did not retard accessory gland growth, whose size did not differ between genotypes, contrary to previous reports.
- Result 2:** There was evidence of a general trade-off with eyespan, as males with larger relative eyespan had larger accessory glands but smaller testes. More attractive males (larger eyespan) require the capability to re-mate more highly, made possible through relatively larger accessory glands.
- Conclusion:** These results point to adaptive changes in the allocation of resources to traits that affect male reproductive success in drive and wildtype males.

