

# **Total reproductive value of juvenile females is twice that of juvenile males under X-linkage and haplodiploidy<sup>†</sup>**

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**Grafen (2014) has shown that, although the total reproductive value of females is not generally equal to that of males in an age-structured population under diploidy and autosomal inheritance, the total reproductive value of juvenile females is equal to that of juvenile males, provided there is a stable class distribution. It is the latter equality that is key to R.A. Fisher's famous explanation for equal investment into daughters and sons. Here, I simplify the derivation of Grafen's key result and extend the analysis to consider X-linkage and haplodiploid inheritance, i.e. scenarios in which a female receives one set of genes from her mother and one set from her father but where males receive genes only from their mother. I find that, although the total reproductive value of females need not be twice that of males, as is commonly supposed, the total reproductive value of juvenile females is twice that of juvenile males. This recovers the principle of equal maternal investment into daughters and sons in panmictic populations.**

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Fisher's (1930) famous explanation for the equal investment of reproductive effort into daughters and sons in panmictic populations hinges upon the idea that the total reproductive value of juvenile females is equal to that of juvenile males (and not, as is commonly supposed, that the total reproductive value of all females is equal to that of all males; e.g. MacArthur, 1961). A consequence of this equality is that if, on average, there is more investment of reproductive resources into offspring of one sex, each unit of parental resource yields greater reproductive value if it is invested into the rarer sex. Hence, natural selection favours parents who act to neutralize any perturbation from equal investment into each sex.

Fisher did not provide explicit derivation for the idea that total reproductive value is the same for juveniles of both sexes. Recently, Grafen (2014) has filled in the missing details. Specifically, Grafen has shown that, although the total reproductive value of females of all ages need not be equal to that of males of all ages – in the context of an age-structured population with diploid, autosomal inheritance – the total reproductive value of juvenile females is equal to that of juvenile males, provided that there is a stable class distribution.

However, Fisherian sex ratios are supposed to extend more widely than diploid, autosomal inheritance. For example, wasps – the workhorses of sex allocation research – are characterized by haplodiploid inheritance, whereby a female receives a set of genes from her mother and a set of genes from her father whereas a male receives all his genes from

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his mother. This mode of inheritance is equivalent to X-linkage under diploidy. Happily, Grafen's analysis can be readily extended to cover these scenarios.

To accomplish this, I first simplify the derivation of Grafen's key result for the diploid, autosomal case. I consider a population with discrete and potentially-overlapping generations, with a census of the population being made in every breeding season. Drawing a gene at random from the population, and tracing it back to a focal census in the distant past, I denote the probability that the gene descended from a female in the focal census by  $x$ , and this is the total reproductive value of all females in that census. I denote the probability the focal female is a juvenile (i.e. belonging to the most recent cohort of newborns) by  $y$ , and hence  $xy$  is the total reproductive value of all newborn females in the focal census. Conversely, with probability  $1-x$  the gene descended from a male, and with probability  $z$  he is a juvenile, so that the total reproductive value of all newborn males in the focal census is  $(1-x)z$ .

Thus, the ratio of the total reproductive values of juvenile females and juvenile males is

$$\phi = \frac{xy}{(1-x)z}. \quad (1)$$

If the focal individual is female, then if she is a juvenile her gene derived from a female in the previous census (i.e. her mother) with probability  $\frac{1}{2}$  and it derived from a male in the previous census (i.e. her father) with probability  $\frac{1}{2}$ , and if she is not a juvenile then her gene derived from a female in the previous census (i.e. herself) with probability 1. If the focal individual is male, then if he is a juvenile his gene derived from a female in the previous census (i.e. his mother) with probability  $\frac{1}{2}$  and a male in the previous census (i.e. his father) with probability  $\frac{1}{2}$ , and if he is not a juvenile then his gene derived from a male in the previous census (i.e. himself) with probability 1.

Accordingly, the probability that the gene was present in a female in the previous census is  $x' = x(y \times \frac{1}{2} + (1-y) \times 1) + (1-x)z \times \frac{1}{2}$ . Provided there is a stable class distribution, then  $x' = x$ , and rearranging yields

$$\frac{x}{1-x} = \frac{z}{y}. \quad (2)$$

Substituting Eq. (2) into Eq. (1) yields  $\phi = 1$ , i.e. the total reproductive value of juvenile females is equal to that of juvenile males.

For X-linkage or haplodiploidy, the argument is exactly the same, except that with probability 1 a gene in a juvenile male derived from a female in the previous census (i.e. his mother), such that the total probability that a gene was present in a female in the previous census is  $x' = x(y \times \frac{1}{2} + (1-y) \times 1) + (1-x)z$  which, setting equal to  $x$ , yields

$$\frac{x}{1-x} = \frac{2z}{y}. \quad (3)$$

Substituting Eq. (3) into Eq. (1) yields  $\phi = 2$ , i.e. the total reproductive value of juvenile females is twice that of juvenile males.

In analogy with Fisher's (1930) argument, Hamilton (1964) initially suggested that the inflated reproductive value of daughters under haplodiploidy would favour a female-biased sex ratio in panmictic populations. MacArthur (1961) made a similar argument for X-linked genes. However, this is not so, owing to the inflated genetic similarity of a mother to her sons, which exactly counters the reproductive value effect (Hamilton, 1972). Specifically, in the absence of inbreeding, the consanguinity of a mother to her daughter is  $\frac{1}{4}$  whereas the consanguinity to her son is  $\frac{1}{2}$  (Bulmer, 1994) so that, although juvenile females transmit twice as many genes to future generations as do juvenile males, a son transmits his mother's genes with twice the fidelity of daughter. Accordingly, an even sex allocation is expected under haplodiploidy and X-linkage, provided it is under maternal control (Hamilton, 1967).

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