



## Letter to Editor

## W. D. Hamilton and the golden sex ratio

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## ARTICLE INFO

## Keywords

Golden ratio  
Haplodiploidy  
Male haploidy  
Rarer-sex effect  
Sex allocation

## ABSTRACT

In his famous two-part paper, published in *Journal of Theoretical Biology* in 1964, W. D. Hamilton predicted that natural selection acting in male-haploid populations favours a ratio of males to females that is in accordance with the golden ratio. This prediction has found its way into the pages of one of the best-selling books of all time, Dan Brown's 2003 novel *The da Vinci Code*, and is therefore in the running for the most widely known quantitative result in the history of evolutionary biology. Unfortunately, this golden-ratio result is wrong, and was later corrected by Hamilton, who showed that natural selection actually favours an unbiased sex ratio in this setting. But it has been unclear exactly how Hamilton arrived at the golden-ratio result in the first place. Here I show that the solution to this puzzle is found in unpublished work held in the British Library's W. D. Hamilton Archive. Specifically, in addition to employing a faulty method for calculating relatedness, Hamilton had also employed a faulty method for calculating reproductive value, considering only genetic contributions to the next generation rather than to the distant future. Repeating both mistakes recovers his erroneous golden-ratio result.

Thus if individuals all incur the same expenditure irrespective of sex, which must be the case for instance with a bee which provisions a series of cells with equal amounts of food, the ratio is the well-known ratio 1:1.618 (Hamilton 1964, p. 32)

In his famous two-part paper, published in *Journal of Theoretical Biology* in 1964, W. D. Hamilton presented an intriguing result concerning the sex ratio under male-haploidy. In its standard form, this mode of genetic inheritance involves females being produced sexually via fertilised eggs, with a mother and father each contributing a single genome to their daughter, and males being produced asexually via unfertilised eggs, with a mother contributing a single genome to her son and without the involvement of a father. For the simplest scenario—of a fully panmictic population with sex ratio under maternal control and sons and daughters being equally costly to produce—Hamilton suggested that natural selection favours a ratio of males to females that is in accordance with the golden ratio, i.e.  $1:\phi$ , where  $\phi = (1+\sqrt{5})/2 \approx 1.618$  (Hamilton, 1964, p. 32). This prediction has found its way into the pages of one of the best-selling books of all time, Dan Brown's 2003 novel *The da Vinci Code* (Brown, 2003, Ch. 20), and is therefore in the running for the most widely known quantitative result in the history of evolutionary biology (Gardner, 2023).

Unfortunately, Hamilton's golden-ratio result is wrong. In 1967, Hamilton remarked that he had made an error and that, in fact, an unbeatable sex ratio of 1:1 obtains in this scenario (Hamilton, 1967, p.

477). In 1971, he explained that although male-haploidy leads to a doubling of the relative reproductive value of daughters—in comparison with the usual diploidy scenario—it also leads to an exactly compensating doubling of the relatedness of mother and son, such that there is no net impact of male-haploidy upon the sex ratio (Hamilton, 1971, pp. 87–88). In 1972, he provided further mathematical details of the 1:1 result (Hamilton, 1972, pp. 202–204). These can be expressed as follows.

The value that a mother places on her newborn son is given by the product of their relatedness  $r_{\text{male}}$ —i.e. the extent to which they share genes in common—and her son's reproductive value  $v_{\text{male}}$ —i.e. his expected asymptotic genetic contribution to future generations. Her son's reproductive value is given by the total reproductive value of all newborn males  $c_{\text{male}}$  divided by the total number of newborn males  $n_{\text{male}}$ . Similarly, the value that a mother places on her newborn daughter is given by the product of their relatedness  $r_{\text{female}}$  and her daughter's reproductive value  $v_{\text{female}}$ . And her daughter's reproductive value is given by the total reproductive value of all newborn females  $c_{\text{female}}$  divided by the total number of newborn females  $n_{\text{female}}$ . Accordingly, the return on investment into each sex is equal when  $r_{\text{male}} v_{\text{male}} = r_{\text{female}} v_{\text{female}}$  and hence the unbeatable ratio of males to females  $n^*_{\text{male}}:n^*_{\text{female}}$  is given by  $r_{\text{male}} c_{\text{male}}:r_{\text{female}} c_{\text{female}}$ . Under male-haploidy we have  $r_{\text{male}} = 2 r_{\text{female}}$  and  $c_{\text{male}} = \frac{1}{2} c_{\text{female}}$  such that the unbeatable sex ratio is 1:1 (see Box 1 of Gardner, 2023 for more details).

Where exactly did Hamilton go wrong in his 1964 treatment? This is

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<https://doi.org/10.1016/j.jtbi.2023.111599>

Received 12 June 2023; Received in revised form 4 August 2023; Accepted 7 August 2023

Available online 16 August 2023

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not clear from his published work. In 1971, Hamilton pointed out that his relatedness calculations for male-haploidy had contained an error (Hamilton, 1971, pp. 87–88)—specifically, he had assigned haploid males an additional “cipher” gene at every locus to render them diploid for the purpose of calculating relatedness (Hamilton, 1964, p. 31), and this resulted in the relatedness of mother and son being erroneously calculated at half of its true value and equal to that of mother and daughter i.e.  $r_{\text{male}} = r_{\text{female}}$  rather than  $r_{\text{male}} = 2 r_{\text{female}}$  (cf. Crozier, 1970). However, this error alone cannot explain his derivation of the golden-ratio result, as making this substitution along with  $c_{\text{male}} = \frac{1}{2} c_{\text{female}}$  into the above expression for the unbeatable sex ratio yields 1: 2 rather than 1:  $\phi$  (Gardner, 2023).

The solution to this puzzle is found in a colloquium typescript—titled *Natural selection and the sex ratio* and dated 24 Feb 1965—held in the British Library’s W. D. Hamilton Archive (Hamilton, 1965). In this document, Hamilton explains that the erroneous sex-ratio result owes not only to the above relatedness error but also to his having incorrectly calculated an individual’s reproductive value as their genetic contribution to the very next generation, which the simpler diploidy scenario had led him to believe was equivalent to their asymptotic genetic contribution. Specifically, if there are  $n'_{\text{male}}$  males and  $n'_{\text{female}}$  females in the next generation, then each of the  $n_{\text{male}}$  males in the present generation expects to contribute  $v_{\text{male}} = n'_{\text{female}}/n_{\text{male}}$  genomes to the next generation and each of the  $n_{\text{female}}$  females expects to contribute  $v_{\text{female}} = (n'_{\text{male}} + n'_{\text{female}})/n_{\text{female}}$  genomes. Accordingly, the unbeatable sex ratio satisfies  $r_{\text{male}} (n^*_{\text{female}}/n^*_{\text{male}}) = r_{\text{female}} (n^*_{\text{male}} + n^*_{\text{female}})/n^*_{\text{female}}$ , and hence is given by 1:  $(r_{\text{female}} + \sqrt{(r_{\text{female}} (r_{\text{female}} + 4 r_{\text{male}}))})/(2 r_{\text{male}})$ . Incorporating the erroneous relatedness calculation  $r_{\text{male}} = r_{\text{female}}$  recovers the golden-ratio result, 1:  $\phi$ .

Interestingly, Hamilton points out that, had he not made the relatedness error, his faulty handling of reproductive value would have given the right answer, but for the wrong reason. That is, combining the erroneous reproductive value calculation with the correct relatedness calculation  $r_{\text{male}} = 2 r_{\text{female}}$  does in fact yield the correct 1: 1 unbeatable sex ratio. This is because Hamilton’s ‘next generation’ method coincidentally gives the correct reproductive values when the sex ratio is unbiased. For other sex ratios, the faulty method yields incorrect results—for example, in a fully inbred population with  $r_{\text{male}} = r_{\text{female}} = 1$  it once again gives an unbeatable sex ratio of 1:  $\phi$  rather than the correct result of 1: 2 (cf. Hamilton, 1972).

The importance of Hamilton’s (corrected) result for the unbeatable sex ratio under male-haploidy went well beyond its application to animals with this particular mode of genetic inheritance. It revealed more generally that reproductive value and relatedness of sons versus daughters combine multiplicatively to govern the action of natural selection in relation to the sex ratio (Gardner, 2023). The rarer-sex effect—incorrectly framed by Darwin (1871) and Düsing (1883) in terms of neutralising imbalance in the adult sex ratio—was first formulated in terms of the reproductive values of newborn males and females by Cobb (1914). Hamilton’s result clarified that although male-haploidy is associated with an increase in the relative reproductive value of daughters, it is also associated with an exactly compensating increase in the relative relatedness value of sons, so as to yield the usual 1: 1

unbeatable sex ratio in the simplest, outbreeding scenario (Hamilton, 1971). And he showed that inbreeding per se favours female bias, through its effect of increasing the relative relatedness value of daughters (Hamilton, 1972).

Although Hamilton’s golden sex ratio result for male-haploidy is incorrect, the golden ratio arises in relation to male-haploidy in other ways. One instance is that, as every female has one mother and one father, and every male has one mother and no father, the asymptotic ratio of males to females among any individual’s ancestors is 1:  $\phi$  (cf. Land, 1960, p. 216). This mathematical result appears of little evolutionary significance; in particular, it does not follow that the expected proportion of an individual’s genes tracing their ancestry to male versus female ancestors is in the ratio 1:  $\phi$ , because these ancestors do not make equal genetic contributions to the focal individual. For example, a gene picked at random from a female has probability  $\frac{1}{4}$  of tracing its ancestry to her maternal grandmother and probability  $\frac{1}{2}$  of tracing its ancestry to her paternal grandmother. Factoring in these asymmetries results in the class reproductive values of males and females being in the ratio 1: 2—assuming non-overlapping generations (cf. Hitchcock and Gardner, 2020).

### Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgements

I am grateful to Eleanor Casson and Jonathan Pledge for assisting with access to the British Library’s W. D. Hamilton Archive, and to Thomas Hitchcock and two anonymous reviewers for helpful feedback. This work was supported by a European Research Council Consolidator Grant (no. 771387).

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