

Darwin, Fisher, and a theory of the evolution of the sex ratio

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I wrote the first version of this note before I was aware of a passage in Bulmer's (1994) book that points out the main fact that I discuss. The remaining content of the note is a report of the results of my search for the reason Darwin changed his mind.

February 2019: Anthony Edwards has recently made me aware of his fascinating (and independent) paper "Natural selection and the sex ratio: Fisher's sources" (*American Naturalist* **151** (1998), 564–569). Edwards studies the probable sources of Fisher's idea. His arguments show that my application of current scientific citation practices to Fisher is misplaced; the fact that Fisher does not give a source for the idea does not indicate that he thought it was his own, as I implicitly assume.

Summary: A theory of the evolution of the sex ratio, universally attributed to Fisher (*The genetical theory of natural selection*, 1930) is contained in the first edition of Darwin's *Descent of man* (1871). I raise the question of why Darwin eliminated the theory from the second edition.

In his book *The genetical theory of natural selection*, R. A. Fisher proposes a simple, and now well known, theory of the evolution of the sex ratio (1930, 141–143), a theory that is the foundation of much subsequent work. Before

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presenting the theory, he quotes a paragraph from Darwin's *Descent of man* in which Darwin writes that he cannot see how a 1:1 sex ratio could be the result of natural selection. Darwin's paragraph concludes "I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future." As Bulmer (1994, 207–208) has pointed out, the paragraph occurs in the *second* edition of Darwin's book (1874, 252–256). Neither Fisher, nor any scholar prior to Bulmer, appears to have noticed that the section in which it occurs replaces a section in the *first* edition that contains the essence of Fisher's theory!² I quote from Darwin (1871, 316):

Let us now take the case of a species producing from the unknown causes just alluded to, an excess of one sex—we will say of males—these being superfluous and useless, or nearly useless. Could the sexes be equalised through natural selection? We may feel sure, from all characters being variable, that certain pairs would produce a somewhat less excess of males over females than other pairs. The former, supposing the actual number of the offspring to remain constant, would necessarily produce more females, and would therefore be more productive. On the doctrine of chances a greater number of the offspring of the more productive pairs would survive; and these would inherit a tendency to procreate fewer males and more females. Thus a tendency towards the equalisation of the sexes would be brought about.

This passage expounds the theory that Fisher (1930) describes, a modern statement of which is given by Hamilton (1967, 477) (I have interchanged "male" and "female" throughout this quotation to make it directly comparable to Darwin's statement):

- 1) Suppose female births are less common than male.
- 2) A newborn female then has better mating prospects than a newborn male, and therefore can expect to have more offspring.
- 3) Therefore parents genetically disposed to produce females tend to have more than average numbers of grandchildren born to them.
- 4) Therefore the genes for female-producing tendencies spread, and female births become commoner.

²Fisher, in fact, erroneously locates the quotation in the *first* edition. Maynard Smith (1983) appears to be alone in having noticed the difference between the first and second editions of Darwin's book. See also footnote 3 below.

- 5) As the 1:1 sex ratio is approached, the advantage associated with producing females dies away.
- 6) The same reasoning holds if males are substituted for females throughout. Therefore 1:1 is the equilibrium ratio.

(Fisher's theory is more general in arguing that the only stable state is one in which parents' expenditures on male and female offspring are equal. If mortality rates during the period of parental care differ by sex, or the sexes requires different amounts of parental care, then a sex ratio different from 1:1 may result. Hamilton's description gives the central idea of the theory.)

After stating his argument, Darwin points out that the adjustment in the sex ratio would result in the species being more productive, which might, in the presence of limited resources, be disadvantageous to the species. He then considers the implications of a mutation that yields the same number of females and fewer males, rather than the same *total* number of offspring, fewer of which are male. He argues that the offspring of such a mutant may be stronger than those of the remaining organisms, since each benefits from more parental resources, leading to an excess of males (or females) being "eliminated through natural selection in [an] indirect manner". He states that a slight excess of either sex could not be eliminated in this manner, and notes that there are cases in which the sex ratio is indeed not 1:1. "Nevertheless we may conclude that natural selection will always tend, though sometimes inefficiently, to equalise the relative numbers of the two sexes" (Darwin 1871, 318).³ Darwin devotes the remainder of the section to a discussion of the regulation of fertility through natural selection.

In the second edition, Darwin abandons these arguments entirely. He writes that though he has very little evidence, "analogy would lead to the belief" (1874, 252) that the sex ratio of offspring is heritable. He gives some evidence to support this belief, though he cautions that he "cannot decide whether [the evidence] I have found is trustworthy" (1874, 253). (The evidence concerns the sex ratio among the native people of New Zealand and the Sandwich Islands [Hawaii], which remained unequal long after the practice of female infanticide may have biased it.) He proceeds to briefly give group selection arguments

³In the preceding sentence Darwin writes of "the survival of those varieties which were subjected to the least waste of organised matter and force by the production of superfluous individuals of either sex". This statement, combined with Darwin's discussion in the second edition of his book, leads Maynard Smith (1983) to conclude that, in the first edition of his book, Darwin "saw the sex ratio as being an advantage for the variety or species, and not for the individual parent producing offspring of a given sex." In private correspondence, Maynard Smith writes that he "was misled by the statement in the second edition '... was advantageous to the species ...' into thinking that Darwin really had used a group selection argument in the first edition, without checking".

for the preponderance of female bees and the possible excess of males among herding animals. The section closes with the paragraph that Fisher quotes.

In summary, the first edition of Darwin's book contains a nicely argued exposition of the theory rediscovered by Fisher, together with thoughts about the influence of natural selection on general fertility. The second edition, by contrast, presents some weak evidence for the heritability of the sex ratio and suggests, tentatively, that group selection may explain some unequal sex ratios.

Why did Darwin change his mind so completely? I have found no clues in his voluminous correspondence. The full texts of his letters are currently being published by Cambridge University Press; so far the first nine of 33 planned volumes, covering the period up to 1861, have appeared. The most comprehensive source of information about his later correspondence, which is relevant to the current discussion, is Burkhardt and Smith (1985), which provides carefully-indexed summaries of all the letters. Judging by these summaries, none of Darwin's correspondence concerning the sex ratio sheds light on his change of mind.

During the writing of his 1930 book, Fisher had extensive correspondence with Leonard Darwin (1850–1943), the second youngest of Charles' five sons. As he wrote chapters, he sent them to Leonard, who made many comments. Leonard received a draft of Chapter VI (originally numbered V) of Fisher's book (Bennett 1983, 94), which ends with an exposition of the theory. However, though he was very familiar with his father's work, he appears not to have discussed the theory with Fisher.

The two-volume edition of *Descent* published in 1888 contains at the front a "Table of the principal additions and corrections to the edition of 1874". (The list contains differences between the 1871 and 1874 editions, with references to the page numbers of the relevant passages in the 1888 edition too.) Regarding the section under consideration, the list contains only the statement "Excess of males perhaps sometimes determined by selection" (Darwin 1888, xi), a reference to the group selection arguments at the end of the section in the second edition.

In summary, I have found no direct evidence for the reasons for Darwin's change of mind. He was preoccupied by other projects when he prepared the second edition of *Descent*; he wrote to Alfred Russel Wallace on November 19, 1873, "I never in my lifetime regretted an interruption so much as this new edition of the 'Descent.'" (Darwin 1896, 354). So it seems possible that he (or his son George, who helped him prepare the second edition?), in his haste to make revisions, misunderstood his earlier argument, deleting it because of a wrongly-perceived flaw. Certainly there is some confusion in his statements in the last sentence of the section in the second edition: he writes that "In no case, as far as we can see, would an inherited tendency to

produce both sexes in equal numbers or to produce one sex in excess, be a direct advantage or disadvantage to certain *individuals* more than to others” (emphasis added), though his arguments in the section concern *group* selection, and that “I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to *the species*, it would follow from natural selection” (emphasis added), though his arguments in the first edition concern *individual* selection.

I conclude that the credit for the theory, universally given to Fisher, should instead go to Darwin. The theory appears to be the first (implicitly) game-theoretic argument in evolutionary biology; finding it in *Descent* provides further evidence (if any is needed!) of Darwin’s extraordinary vision.

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