Walter Frank Raphael Weldon (1860–1906)

W F R Weldon, along with Karl Pearson, was one of the two main protagonists on the biometrician side of the biometrician-Mendelian debate that roiled evolutionary biology during the early years of the twentieth century. He was born at Highgate, London, on 15 March 1860, the second child of Walter Weldon and Anne Cotton. He had an elder sister, and a younger brother, Dante, who unfortunately died at a young age in 1881. Weldon's father was a chemist and journalist and frequently moved around England, as a result of which Weldon did not undergo a regular school education till the age of thirteen, although he was informally taught by clergymen. In 1873, Weldon joined a boarding school at Caversham, where he spent three years. After some months of private study, he joined University College, London (UCL), for his matriculation in 1876. At UCL, he studied a variety of subjects, aiming to eventually train in medicine. In particular, he was very impressed with the mathematics teaching of Olaus Henrici, who had worked with Weierstrass and Kronecker, and later recalled that Henrici was the first naturally gifted teacher who had taught him (incidentally, Weldon himself was later revered as an amazingly inspiring and lucid teacher). He was also taught by the well-known invertebrate zoologist and Darwinian – Edwin Ray Lankester. Weldon then moved to King's College, London, in 1877, and then to St. John's College, Cambridge, from where he matriculated in 1878. At St. John's, Weldon was much influenced by the comparative embryologist and morphologist Francis Maitland Balfour and shifted his focus from medicine to zoology, eventually taking the Natural Sciences Tripos and graduating with a first-class in zoology in 1881.

After graduation, Weldon travelled to Naples to work at the Zoological Station, a centre established using private funds and donations from individuals and governments by Anton Dohrn, a protege of Ernst Haeckel, in 1872. The Zoological Station was envisioned as a scientific community that would provide accommodation, research facilities, materials, and an extensive library for visiting scholars in residence. At the time, embryology was the most 'happening' subdiscipline of zoology, and numerous biologists from Europe and the Americas passed through the Zoological Station over the years – Driesch, Weismann, Uexküll, Bumpus, Wheeler, Just, Warburg, Boveri, Morgan, and Watson of the DNA fame, to name a few. At Naples, Weldon worked on the comparative embryology and morphology of marine invertebrates. In 1882, he returned to Cambridge and became a Demonstrator in Zoology, got married in 1883 to Florence Tebb, who became a life-long research associate, and went on to become a Fellow of St. John's College and University Lecturer in invertebrate morphology in 1884. In the same year, Weldon became a founding member of the research station of the Marine Biology Association at Plymouth, where he continued to spend time over the next several years as and when his teaching commitments permitted. In 1889, Weldon moved back to UCL, occupying the Jodrell Chair of Zoology, previously held by his teacher, Lankester. Around this time, he was also much impressed by Galton's writings on heredity and selection, and formed the view that "the questions raised by the Darwinian hypothesis are purely statistical, and the statistical method is the only one at present obvious by which that hypothesis can be experimentally checked". This led him away from classical embryology and morphology towards the study of the statistical properties of trait distributions in marine invertebrate populations, and he also continued to tutor himself further in probability and statistics, especially studying the work of Quetelet and Galton. It was at this point that Weldon set out to collect data to test Galton's prediction that quantitative traits in natural populations would be distributed normally, even in populations faced with natural selection. He studied natural variation in four organs of the common shrimp (*Crangon vulgaris*) collected from five different populations, and also studied trait-correlations in these populations, resulting in two landmark papers in 1890 and 1892 that many believe to have laid the foundation of biometry. In these studies, Weldon found that, as predicted by Galton, individual traits were indeed normally distributed within populations, but that different populations showed normal trait distributions with varying means and degrees of dispersion, an observation that Weldon interpreted as being the outcome of differing selection faced by the different populations. This interpretation went significantly beyond and against Galton's ideas, although Weldon couched this departure from his hero's views very diplomatically in his paper. He also observed that, although individual trait distributions varied across populations, the pattern of correlations among traits was fairly consistent among populations, indicating a certain stability of 'type'.

As a result of his first biometrical study, Weldon was elected as a Fellow of the Royal Society in 1890. Weldon's growing interest in using statistical approaches to empirically examine phenomena in heredity and evolution led him into a close collaboration with his UCL and Gresham College mathematical colleague, Karl Pearson. The collaboration continued even after Weldon's move to Oxford in 1899 to occupy the prestigious Linacre Chair in Zoology. Weldon and Pearson made sure to spend Christmas, Easter and summer vacations together, and they continued their joint studies in biometry till Weldon's untimely death in a London nursing home in 1906, due to acute pneumonia developed from influenza contracted during an Easter vacation in the country at Woolstone. It was Weldon, around 1890–91, who first introduced Pearson to problems in biometry and to Francis Galton, and their collaboration over the next fifteen years or so contributed hugely to the statistical understanding of heredity and natural selection. It also led to the development of many statistical techniques and measures by Pearson to specifically deal with the problems Weldon and Galton were interested in. To the extent that Pearson is deservedly regarded as the father of modern statistics, to Weldon must surely go the honor of having supplied the biological problems that necessitated the invention of much of statistics. Here, I briefly summarize Weldon's work and its impact on the trajectory of evolutionary thinking. Some of his most consequential work is discussed in greater detail in another article in the same issue.

In 1892, Weldon and his wife collected extensive data on Mediterranean populations of the crab, *Carcinus moenas*, and observed that one trait (frontal breadth of the carapace) in the crabs around Naples actually showed a highly skewed, rather than a normal, distribution. In a paper on this data set in 1893, Weldon wondered whether this distribution could be the result of the population being a mix of two different normal distributions, with the possible implication that the population consisted of two different races or 'types' in the same locality. This study sparked off the major collaboration with Pearson, who set about devising the mathematical techniques for dissecting non-normal distributions into normally distributed component distributions. In an 1884 article entitled 'Contributions to the mathematical theory of evolution', the first of 18 such articles over the next 18 years with this common title, Pearson developed the concept of 'moments' of a distribution. He used this concept to develop techniques for analyzing whether or not a non-normal distribution was the result of a mix of multiple normal distributions in the sample under consideration. The application of this technique to Weldon's crab data was included as an appendix to Weldon's 1893 paper. This work of Pearson's is considered a landmark both in the study of evolution and in statistics. Sparked off by this work, Alfred Russel Wallace (independent co-discoverer of the principle of natural selection) persuaded the Royal Society to set up a 'Committee for conducting statistical studies on the measurable characteristics of plants and animals'. The committee consisted of Galton, Weldon, Francis Darwin (son of Charles Darwin), and the mathematician Donald MacAlister along with Ralph Meldola and Edward Poulton, both Darwinians who had worked extensively on mimicry. Very soon, Pearson was also included in the committee.

For four years, the committee was largely discussing the continuing work of Weldon and Pearson, albeit in the face of severe and increasing criticism by those who favored discontinuous variations as being more evolutionarily consequential than continuous variations. Thus, in 1887, Galton proposed enlarging the committee to include William Bateson, a major proponent of the importance of discontinuous variations in evolution, and an opponent of biometry with its focus on continuous variation. Galton hoped that this might help foster dialogue and collaboration between the two rival schools of evolutionary thought, both of which traced their inspiration to his work. The committee was accordingly renamed in February 1887 to the 'Evolution (plants and animals) committee of the Royal Society'. However, rather than promoting reconciliation between the two schools, the enlarged committee became the focus of increasingly bitter and personal debates between Bateson and Weldon, as a result of which Weldon and Pearson resigned from the committee in early 1900, and Bateson became its secretary. Thereafter, the committee increasingly focused on the evolutionary and genetic implications of the rediscovery of Mendel's work and became the focal point of the biometrician-Mendelian debates. After Weldon's death in 1906, Bateson and Pearson became the chief antagonists and acrimony generated by these ongoing debates rendered the committee relatively fruitless. The biometrician-Mendelian debates on the nature of evolutionarily relevant variations (discontinuous versus continuous), the laws of heredity (Mendel's laws versus Galton's statistical formulation of ancestral heredity as correlations between trait values in ancestors and descendants), and whether evolution was discontinuous or gradual, eventually got resolved with the publication of R A Fisher's landmark paper of 1918, which showed that Mendelian inheritance, correlations between relatives, and continuous variations were perfectly compatible.

During the period between his 1893 paper and his death in 1906, Weldon continued his work on crabs, trying to find empirical evidence for natural selection in action. He was able to show that the distribution of frontal breadth of the carapace in adults had less spread than the corresponding distribution in younger crabs, even though the distributions remained normal across life-stages. Following extensive and careful analysis as to how differential mortality could account for the observed life-stage-specific changes in the trait distributions, he interpreted the results in terms of what we today term 'stabilizing selection', or an increased risk of mortality for individuals with trait values relatively more deviant from the population mean. He also found that, over the course of five years (1893–1898), mean frontal breadth of the crabs from the Plymouth Sound population had reduced regularly for all age-classes. He then hypothesized that larger frontal breadth might have become a mortality risk because of the increased amount of suspended kaolin and other muddy matter in the waters as a result of increased waste discharge in the sewers and the effects of the construction of a dyke. Indeed, as the waters of Plymouth Sound had become muddier over these five years, several species of coastal invertebrates had disappeared altogether. He then tested this hypothesis experimentally by subjecting crabs in laboratory tanks to a high concentration of ground white clay, or actual coastal mud, in seawater. In both cases, some proportion of crabs died, and Weldon found that the mean frontal breadth of the survivors was less than that of the crabs that died. He also tried to functionally link the mortality to the effects of suspended clay on the filtration of water in the gill chambers of the crabs. This set of studies remains one of the best early demonstrations of what we call directional selection and is an excellent example of how to empirically study natural selection in action.

Alongside his crab work, Weldon was also led into a bitter polemic battle with Bateson that resulted in the souring of a very cordial personal relationship. Bateson, a bit younger than

Weldon, had been a student at St. John's with him, and it was Weldon who inspired him to work with Balfour, thus nudging Bateson along the same evolutionary trajectory as himself. Weldon was also briefly Bateson's teacher at St. John's and the two were close friends, with Bateson particularly looking up to Weldon with great regard as a mentor. They remained close friends through the 1880s, but then, from the early 1890s on, began to find themselves increasingly on opposite sides of the debate on discontinuous versus continuous variations and their respective roles in evolutionary change. Though initially both Weldon and Bateson had been inspired by Galton, by the late 1880s their views had begun to diverge. Weldon was attracted to Galton's statistical approach to heredity and selection. He believed that a theory of evolution *via* continuous variations could be built up by examining correlations between those variations in parents and offspring, among different life-stages, and, finally, the correlations between variations and mortality. This was a purely statistical approach that did not depend on the knowledge of underlying mechanisms of either heredity or selective mortality. Bateson, thorough the writings of W K Brooks, with whom he worked in the USA after his studies at Cambridge, and also through his own extensive fieldwork across Eurasia, was increasingly convinced that continuous variations were often not heritable and thus would be irrelevant to evolution. He believed that understanding the genesis of discontinuous variations, and inherent biases in their generation, would be key to understanding the mechanisms of evolution. Moreover, Bateson had the typical classically trained biologist's dislike for purely mathematical arguments and thus, was in a sense primed to be suspicious of the biometricians' statistical arguments and theories. In his widely-read book *Materials for the study of variation* (1894), Bateson argued the case for the importance of discontinuous variations in evolutionary change at length. Weldon, by now equally committed to the importance of continuous variations to the Darwinian scheme, wrote a critique of Bateson's views in a book-review for *Nature*. Bateson was incensed, and took it rather personally, even though Weldon had praised much of the book and criticized only Bateson's arguments for the evolutionary importance of discontinuous variations. Bateson responded, in part, by criticizing Weldon's crab work that was being discussed at the Royal Society in a series of letters to Galton, who was then steering the committee. Around this time, too, Bateson entered into a very spirited debate with W T Thiselton-Dyer over the importance of discontinuous versus continuous variations to speciation in the plant *Senecio cruentus* (cineraria). After a series of pointed back-and-forth letters to *Nature* by the two, Weldon intruded upon the debate, and sided with Thiselton-Dyer in favour of the role of continuous variations. Once again, Bateson was personally offended by what he saw as a betrayal by his erstwhile friend. The two made some attempts to patch up, but the rift had become too deep and was worsened after the rediscovery of Mendel's work on heredity in 1900.

Bateson became the leading champion of Mendel's work and saw that Mendel's 'factors' (Discrete particles of heredity – today's genes) fit in beautifully with his views on discontinuous variations. Weldon, like Fisher many years later, was struck by the suspiciously good fit of Mendel's data to predictions. He also noted that peas typically varied much more continuously rather than in the neatly dichotomous manner observed in Mendel's experiments. For example, Weldon showed that peas naturally produced seeds coloured yellow and green, and most shades of yellowish-green in between. Mendel had done extensive inbreeding to obtain the pure green and yellow lines that he used for his crosses. To Weldon, this implied that Mendel's results were an artefact of having removed all continuous variations between green and yellow seed colour from his lines before starting his hybridization experiments. By this time, fed up with the debates at the Royal Society committee from which they had resigned, Weldon and Pearson founded the journal *Biometrika* after a paper of theirs for the *Proceedings of the Royal Society* was heavily criticized by Bateson and consequently had its publication delayed. Weldon published critiques of Mendel's work, especially its implications and presumed universality, in *Biometrika*, and Bateson responded with a spirited defence of Mendelism, including vitriolic attacks on Weldon. Over the next couple of years, Udney Yule and Pearson both suggested that Mendelism and biometry were not incompatible, but their suggestions were ignored in the fury of battle. Bateson and Weldon continued to marshal empirical data from breeding studies in support of their respective, somewhat extreme, positions, and the debates grew ever more bitter. At one point, in 1904, the editor of *Nature* refused to publish any further correspondence between Weldon and Bateson on the issue of Mendelism versus biometry.

In August 1904, Weldon and Bateson clashed for perhaps the last time at the meeting of the British Association for the Advancement of Science. This debate became famous enough to be mentioned twenty months later in the *Times*' obituary of Weldon: *Mr William Bateson, as President of Section D for that year, had devoted his address to a vindication of Mendelian principles in regard to heredity and variation, and subsequent discussion on the same subject provoked from Professor Weldon and Professor Karl Pearson some rather severe criticism, to which Mr Bateson replied. The debate, which was conducted before a large and somewhat agitated audience, resolved itself into a dialectical duel between the President of the section and Professor Weldon, and developed quite a considerable amount of heat.*

The debates cooled down a bit for a while after Weldon's sudden death in 1906, as both Bateson and Pearson were greatly saddened by the loss. Bateson, in particular, regretted to his wife that scientific disagreements had marred his warm personal friendship with Weldon. Before too long, however, the debates continued, with the biometricians slowly losing ground as Mendelian principles of heredity were increasingly accepted by biologists around the world. Perhaps because of a frustrating realization that Mendelian principles were gathering ever wider acceptance, Pearson in 1910 did away with the entire editorial board of *Biometrika*, after two members of the board, Raymond Pearl and Charles Davenport published work favourable to Mendelism.

An unfortunate aspect of the Bateson–Weldon, and later, Bateson–Pearson debates was that the two sides were led to take ever more extreme positions, in part because the debate was so personally acrimonious. Had the relationship between Weldon and Bateson not already deteriorated before 1900, it is possible that the reconciliation of the statistical approach of biometricians with Mendelian principles of heredity might have occurred well before 1918. Perhaps even more unfortunate is the fact that Weldon has gone down in history as the principal protagonist of the 'losing' side in the debate (although, really, there were no losers) – a label that has detracted from a more widespread appreciation of his amazingly important contributions to evolutionary thought. His active work on selection spanned only about 11 years, but in that relatively short time, he and Pearson laid the foundations for a rigorous statistical understanding of evolution by natural selection, ironed out various misunderstandings of Galton and other heirs of Darwin, and also provided an exemplar of how to empirically study natural selection in action through a combination of field observations and laboratory experiments. More importantly, the discussions in Weldon's crab papers are striking for the lucidity and clarity with which he delineates the fundamental problems in understanding evolution by natural selection, and the rigour with which he prescribes the experimental means to address them. Philosophically, too, Weldon's thinking is very 'modern' and foreshadows in many ways the approach of the Neo-Darwinian Synthesis in his emphasis that the actual mechanisms of heredity or of mortality are not as important to understanding adaptive evolution as are establishing the timing and magnitude of mortality in the life-cycle, the correlations between trait variants in parents and offspring, and the correlations between trait variants and mortality. Thus, he diverged from the views of the staunch adaptationist Darwinians like Wallace, who held that working out the functional and ecological details of why trait variants differ in mortality was critical to understanding evolution. He equally differed from those, like Bateson, who held that the nature of variations and the mechanisms of their inheritance were crucial to understanding evolution. Weldon believed that the statistical approach had very wide applicability, regardless of the nature of the variations, the mechanisms of inheritance or the ecological details through which variants suffered differing levels of mortality.

There is a certain beauty in this abstract approach to a real-life biological problem, and the development, many decades later, by George Price of a simple general equation capturing the dynamics of traits under selection largely through correlations perhaps vindicates Weldon's stance. In 1970, George Price, an eccentric amateur evolutionary biologist, developed a simple equation that captures the essence of how the composition of an ensemble, whether a biological population or anything else, changes under the process of selection. His equation requires only the covariance of the characteristics of individual entities with the rate at which they make copies of themselves, and the covariance of characteristics between 'parent' and 'offspring' individual entities, to predict how the composition of the collection of entities is altered in one time-step. It is the most general and biology-free description of the process of selection possible, and it is seen that the earlier quantitative genetic formulation of Fisher's Fundamental Theorem of Natural Selection is actually a special case of the Price equation under the assumption of Mendelian inheritance. Weldon was perhaps the first person to see that a statistical description of selection would suffice and, moreover, be relatively unaltered by the details of the biology that gave rise to the consequential correlations. It is most likely in appreciation of Weldon's ability to rise above messy biological details and appreciate the conceptual structure needed to understand the process of evolution that Karl Pearson wrote in an obituary memoir of his friend in *Biometrika: He was by nature a poet, and these give the best to science, for they give ideas*.

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