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Charles Darwin as a statistical thinker☆

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ABSTRACT

Recently historians and philosophers of science have been interested in the role of statistics and probability in investigating population variation. The focus is typically on investigators applying statistics and probability to explain large scale phenomenon that arise out of the collective behavior of numerous and varied individuals. The case studies that inform this work come mostly from molecular physics and 20th century genetical versions of evolutionary theory. Charles Darwin's work on evolution is rarely mentioned in this context except to point out his shortcomings—he made evolutionary theory "ripe" for statistical investigations, but he was not a statistical thinker. But this is a mistake, Darwin was a statistical thinker. In this essay I describe two instances where Darwin utilized statistical methods to investigate evolution. In the light of these cases, we ought to revise our views about Darwin's scientific methodology, in particular, how he came to develop his ideas about evolution and about the nature of his "population thinking". Furthermore, Darwin's cases provide us with an expanded view about what constitutes "statistical thinking" in the biological sciences. In the examples we will find Darwin using statistical measures of type frequencies to *detect* large scale ensemble effects, *confirm hypotheses* by comparing between expected and observed averages, and applying the astronomer's law of error to *explain* evolutionary trends.

1. Introduction

According to Ernst Mayr (1959), one of Darwin's most significant contributions to science was to introduce "population thinking" to biology, a catchy phrase, but what does it mean? In the literature that Mayr instigated, "population thinking" refers to two distinct kinds of ideas, one is metaphysical and the other methodological. The metaphysical conception of population thinking is usually attributed to the novelty of Darwin's theory of speciation. Darwin overthrew a prominent view that types are real, and variation is an illusion. He replaced it with the view that individuals are real, and types are illusionary.[1] Darwin's contribution to the other, methodological, version of population thinking, however, is a bit more controversial. It has to do with methods for analyzing large-scale phenomenon in terms of the collective behavior of numerous individuals. Darwin is rightfully credited for replacing creationism with natural selection. The harmonies of ecosystems and prevalence of exquisite adaptations are not the products of direct intervention by the creator. Rather, they are aggregate result of the lives, deaths, and reproductive activities of individuals operating in conditions of scarcity. For some philosophers (Ariew, 2008; Walsh, 2015) that qualifies Darwin as a population thinker in this methodological sense. Yet, there is another kind of population thinking that was gaining prominence in Darwin's century in which it is said that Darwin did not engage. It involves, as Theodore Porter puts it, "employing a mode of reasoning based on stable numerical frequencies" (Porter, 1986, p. 135). Perhaps a better phrase for this kind of population thinking is "statistical thinking". Most philosophers and historians deny that Darwin was a statistical thinker.[2] While he employed the concept of chance several times in the *Origin of Species*, he made no references to stable numerical frequencies, nor did he invoke the theory of chances to explain long-run evolutionary trends (Walsh, 2015). As Porter puts it, "Darwin never developed anything like a quantitative model of evolutionary change". So, while Darwin

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[1] For a detailed look on the origins of Mayr's distinction see (Chung, 2003). For a defense of typological thinking, see (Lewens, 2009). For a critique of Mayr's assessment of Darwin, see (Wilkins, 2009).

[2] *Pace* Sober 1980. For criticisms of Sober's reasons for attributing statistical thinking to Darwin see Ariew (2008) and Walsh (2015).

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made the investigation of evolution "ripe" for statistics he himself was no statistical thinker (Porter, 1986, p. 134). Gigerenzer et al. concur:

> Darwin could hardly have been unaware that extraneous circumstances will sometimes lead to the death of an ostensibly fit individual, but there is nothing about this in the Origin. A statistical thinker might have said that these peculiarities will average out over a large population, or in the long run … [Darwin] never took advantage of the statisticians' view that what appears as chance in the individual can be dissolved into the large regularities governing the collective" (Gigerenzer et al., 1990).

Statistical thinking dominated evolutionary and ecological sciences beginning in the early 20th century, as a product of the Modern Evolutionary Synthesis (Ariew, 2008; Sober, 1980; Walsh, 2015). However, earlier instances can be found in the 19th century among Darwin's (near) contemporaries. To name a few: Gregor Mendel invoked a combinatorial mathematics to detect and analyze stable proportions of different frequencies of pea plant characteristics that heredity preserves over the course of generations. His statistical work was a crucial step towards the formulation of the theory of inheritance for which he is best known. In molecular physics, James Clerk Maxwell's work on gas laws made him the paradigmatic statistical thinker of the 19th century. Maxwell recognized that the astronomer's "law of error" was the appropriate model for the velocity distribution for molecules of equal mass. His statistical insight led him to explain how gas laws were due to the aggregate effect of individual gas molecules (Fisher, 1953, Hodge,1986). Finally, many historians of statistics cite Francis Galton's explanation for reversion to the mean over the course of generations as an instance of statistical explanation in biology. Galton (who was Darwin's cousin by marriage and with whom he frequently corresponded) explained reversion as a deductive consequence of the law of error: if a feature is distributed in the population in conformity to the law of error, then as a mathematical consequence of the law, the distribution will remain robust over the course of generations (Ariew et al., 2015; Hacking, 1990; Porter, 1986; Sober, 1980; Walsh, 2015). Galton's statistical thinking led him to construct his method of regression analysis, one of the most important analytical techniques of the 20th century (Stigler, 1986, 2016). What these examples show is that various forms of statistical thinking were responsible for a good number of fundamental scientific advances in the 19th century. But on the standard narrative, it wouldn't be until the 20th century, long after Darwin died, before statistical thinking transformed evolutionary theory.

Darwin's ignorance and dyscalculia are common explanations for the lack of statistical thinking in his work on evolution. The pioneering biometrician Karl Pearson once asked Francis and Leonard Darwin whether their father was aware that the theory of natural selection is applicable to statistical analysis. They responded that their father had a 'non-statistical' mind.[3] In his *Autobiography*, Darwin admitted that as a child in school he thought math work to be "repugnant" and now laments that he did not succeed in math beyond "a very low grade".[4] According to the pioneer Modern Synthesist, R.A. Fisher, Darwin's belief in blending inheritance along with his failure to understand that the best argument for natural selection "lay in statistical considerations" led to "incredible confusion of thought" among the next few generations of theoretical biologists on the issues Darwin raised (Fisher, 1953).

This standard narrative about Darwin and the development of his theory of natural selection is misleading. True, you won't find a quantitative model of evolutionary change in the *Origin of Species* as you do in modern post-Synthesis evolutionary textbooks. Yet, in Darwin's notebooks and letters (both public and private) you can find several occasions where Darwin employed a "mode of reasoning based on stable numerical frequencies" for the sake of solving a problem or satisfying an inquiry related to evolution. I will describe two cases, each involving different kinds of strategies for analyzing statistical information. Darwin conducted the first in 1857. It involved applications of the "botanical arithmetic" and the "rule of three" to analyze numerical correlations between varieties, species, and genera of a variety of plant fauna. In the passages I describe Darwin was trying to determine if a small genus is small because it is undergoing extinction or because it is speciating. By Darwin's own admission the statistical work provided empirical evidence for his claim in the *Origin of Species* that varieties are incipient species which in turn helped him lay out his theory of taxa formation and his principle of divergence.

The second instance of Darwin's statistical thinking came decades later, in a letter he wrote to *Nature* in 1873 entitled "On the Males and Complementary Males of certain *Cirripedes*, and on Rudimentary Structures".[5] Darwin offered a speculative explanation of the evolutionary origins of rudimentary characters based upon the assumption (attributed to Aldolphe Quetelet) that the distribution of characters conforms to the statistical "law of error". The case shows that Darwin was able to do what Gigerenzer et al. say Darwin was incapable of doing, take "advantage of the statisticians' view that what appears as chance in the individual can be dissolved into the large regularities governing the collective". In fact, Darwin's explanation appears to be an early attempt to describe what 20th century evolutionary theorists referred to as "directional selection", whereby the effects of various forces of evolution are shown to affect the distribution of frequency of characters.

The intent of the essay is not merely to prove Darwin's critics wrong. This essay contributes to the philosophy of science project of what Michael Weisberg calls the "practice of theorizing" (2007). Darwin's application of statistical data and analytic techniques reinforce the idea that statistics provide powerful tools for scientific research, especially when coupled with probability theory. Among other possible applications, they allow investigators to *analyze large-scale patterns* that would otherwise be undetected at the level of individuals, *provide empirical tests for hypotheses*, and even *explain* large-scale trends. Between the two cases I discuss in this essay, Darwin does all three, each in different ways. Darwin's work on the botanical arithmetic allowed him to detect large scale correlations between varieties, species, and genera in a variety of plant fauna. Darwin's intent was to look for evidence of speciation and extinction in the various ratios of genus to species presenting varieties. Yet, the data only provided static snapshots, so Darwin employed the "rule of three" to formulate tests to compare what ratios a genus would have had had it been speciating/going extinct. This is an instance of Darwin employing quantitative techniques for analyzing statistical information for the sake of empirical testing (of his hypothesis about speciation and extinction). In 1873, Darwin applied a statistical law as a hypothetical explanation for how rudimentary characters could evolve. More specifically, Darwin applied the statistical law of error to explain how the effects of development, crossbreeding, and selection in scarce conditions will, over the course of generation shift the distribution of traits towards an ever-decreasing mean until the trait in question becomes diminutive or disappears altogether. That is one way that Darwin attempted to use statistics in the service of explanation. In the 1873 letter, Darwin features a second application of statistical explanation: he applied conditional probabilities to estimate the frequency of trait types in one generation based upon their relative frequencies in the prior generation. This is a level of abstraction that is usually attributed to Francis Galton's work on regression, over a decade later.

[3] You can find the relevant correspondence here: https://galton.org/cgi-bin/searchImages/galton/search//vol3a/pages/vol3a_0294.htmPearson.

[4] (Darwin, 1958): http://darwin-online.org.uk/content/frameset?viewtype=text&itemID=F1497&pageseq=1.

[5] Very few historians and philosophers have discussed the Nature article. Two exceptions are Ariew (2007) and Magnello (1996).

In highlighting how Darwin employed statistical thinking throughout his career we not only transform our understanding about how Darwin came to develop his ideas about evolution we also gain a new understanding about what constitutes the practice of statistical thinking in the 19th century. Philosophical analyses in the population thinking *qua* statistical thinking tend to equate statistical thinking with explanation (Ariew, 2008; Hacking, 1990; Sober, 1980; Walsh, 2015). Through Darwin's examples—where he applies different strategies for analyzing different kinds of statistical information—we will provide a richer account of how "statistical thinking" in the 19th century aided in scientific inquiry. Statistical thinking is not just a matter of explanation, it is also a method associated with pattern detection and hypothesis testing.

I will not argue that Darwin was a brilliant mathematician or statistician. The statistical methodologies he used on these occasions were rather primitive and by the high standards of men like Maxwell, Pearson, and Fisher, rather erroneous and "murky"—as historian Stephen Stigler described it (pers. com.). Nevertheless, each case demonstrates a methodological novelty. Darwin's (1857a, 1857b) analysis of species and number of varieties was based upon applications of "botanical arithmetic" and the arithmetic "rule of three" that he learned as youth.[6] Yet, it had impact. As Janet Browne (1980) argues Darwin's work on the botanical arithmetic served as the "trigger" to modify of his views about the workings of evolution, including the formation of his principle of divergence to explain the branching of taxa. Darwin's (1873a, 1873b) statistical explanation for the evolutionary basis of rudimentary characters was, as Darwin twice reminds the reader, merely "hypothetical". The presentation is opaque, enough so to prompt his son, George, to publish an addendum to *Nature* to clarify his father's model. Nevertheless, Darwin, however clumsily, employed a statistical model to advance a hypothetical explanation for the evolution of rudimentary characters. To be sure, Darwin's letter likely had no direct historical impact on the formation of the mathematical foundations of the late 19th and early 20th century versions of evolution. I doubt any of the pioneers read Darwin's diaries of 1857 or his 1873 letter to *Nature*. Nevertheless, Darwin's statistical thinking (*sans* Mendelian inheritance) anticipates the methodological direction that the Modern Synthesists championed by regarding the effects of natural selection, crossbreeding, and development in the context of an idealized model of changing trait distribution over generational time.

2. The botanical arithmetic and the rule of three: Darwin's argument for varieties as incipient species

In the second chapter of the *Origin of Species*, under the section entitled "Dominant species vary most", Darwin announced that he had previously done some statistical work comparing varieties of several floras, and that the work had important consequences for his theory of natural selection and Principle of Divergence:

> "Guided by theoretical considerations, I thought that some interesting results might be obtained in regard to the nature and relations of the species which vary most, by tabulating all the varieties in several well-worked floras … The whole subject, however, treated as it necessarily here is with much brevity, is rather perplexing, and allusions cannot be avoided to the 'struggle for existence,' 'divergence of character,' and other questions, hereafter to be discussed" (Darwin 1859, p. 53).[7]

Despite his promise, Darwin did not publish his statistical work. Fortunately, today we can find it in his private correspondences and notebooks—especially in his "Big Species" diary (1854–1859).

First some background on what motivated Darwin's statistical work. In his *Sketch of 1842* and *Essay of 1844*—where he laid out an early version of his theories of evolution and speciation—Darwin asserted that very little variation existed in the "wild state". New variants are induced by geological or geographical changes. But, Darwin's eight-year investigation of barnacles (1846–1854) convinced him that his previous views were incorrect, and in fact, variation was superabundant in nature.[8] So, in 1854, Darwin needed to determine whether the presence of all this extant wild-state variation required a revision of his theory of natural selection.

The best way to investigate these issues, Darwin thought, was to turn to a technique, the "botanical arithmetic", that he learned from his botany teacher, John Henslow (Browne, 1980). Botanical arithmetic was useful for investigating the geographical patterns of species distribution for flora and fauna listed in published zoological surveys. Darwin gathered his data from a variety of flora catalogs which he either owned or borrowed from colleagues. The procedure involved calculating the average (mean) number of species in a genus for the sake of determining the relative spread of different species across geological ranges. It was standard practice among contemporary theorists (like Henslow) interested in the distribution of the "creative power" in a region. But, Darwin wished to apply the botanical arithmetic to see if he could discern the nature and biogeographical arrangement of taxa formation, all the while looking for confirming evidence that natural selection had a role to play in the origins of all taxa. The botanical work occupied Darwin for four years.

According to Janet Browne, Darwin's initial application of the botanical arithmetic metamorphosed in two different ways, one concerning the way he analyzed his data, and second, how he applied it to modify his views about the workings of evolution (1980, p. 58). My exposition of Darwin's botanical work supports both of Browne's assertions. What began in Darwin as a simple application of botanical arithmetic to correlate size of genera to species and varieties developed into the application of the rule of three to try to discern from statistical data a dynamic pattern, i.e. the difference between genera undergoing speciation or extinction. As the correspondences with Hooker and Lubbock will reiterate (from Darwin's statement in the Origin of Species, cited above), the statistical work was "so very important for" Darwin: it provided evidence that varieties are incipient species, an important component towards Darwin's "principle of divergence" to explain how taxa are formed.

Early on, Darwin constructed a hypothesis (born out of his theory of descent with modification) that the difference between large and small genera is the difference between a genus increasing its number of associated species by the process of speciation and a genus decreasing its numbers by the process of extinction. The key to confirming his hypothesis, thought Darwin, was to detect asymmetries in the relative frequency of "well-marked varieties" between species of large and small genera. Well-marked varieties were variants (featuring common individual differences) that are distinct enough to be listed in the catalogs, but not distinct enough to warrant the designation of a new species. Darwin's hypothesis was that the presence of varieties was an indication of, as it were, speciation in action.

However, Darwin's initial foray in botanical arithmetic did not give him a satisfactory way to distinguish between small genera that are small because they are aberrant and those that are small because they are early in the process of growing in numbers of associated species. So, in 1857, in consultation with his polymath neighbor John Lubbock,

[6] As Darwin wrote in a letter to his second cousin, William Darwin Fox in 1855, "I have no faith in anything short of actual measurement and the Rule of Three": https://www.darwinproject.ac.uk/letter/DCP-LETT-1686.xml. See Stigler (2016) for why it is a poor form of statistical extrapolation.

[7] http://darwin-online.org.uk/content/frameset?itemID=F373&viewtype=text&pageseq=1.

[8] There is some disagreement among historians about the purpose of Darwin's barnacle work. See Ospovat (1980, p. 270, nt 39). For a longer discussion see Love (2002).

Darwin devised a new test which involved first, distinguishing genera listed in the botanical catalogs which were known, *a priori*, to be truly large from the genera known to be truly small. The next step was to look at the differences between the two groups with respect to the quantitative feature in question. By arranging the data in this way Darwin could analyze certain counter-factual situations that better support his hypothesis that species of large genera more often present varieties than species of small genera. Notice the statistical thinking involved in Darwin's proposed procedure: he proposed that he could predict the evolutionary dynamics of a genus by analyzing the statistical data through an arithmetic procedure that provided him with a counter-factual tests ranging over frequency ratios.[9] In a letter to Lubbock on 14 July 1857 Darwin described how he conducted his analysis with real data:

> "I have divided N. Zealand Flora as you suggested. There are 339 species in genera of 4 & upwards & 323 in genera of 3 & less. The 339 species have 51 species presenting one or more varieties-- The 323 species have only 37: proportionally (as 339:323 :: 51.:48.5) …" (Darwin, Letter no. 2123).

I represent Darwin's data in the following chart to better understand how he conducted his analyses. He first divided the flora of New Zealand into two categories of genera, "large" and "small", where "large" contains more than four species, and "small" contains three or fewer species. Among the 339 species that belonged to large genera, 51 presented at least one "well-marked" variety. In comparison, only 37 species of the small genera featured at least one variety. The inequality between large and small genera provided Darwin some evidence for his hypothesis that species of large genera more often present varieties than species of small genera.

Genera size	Large (containing 4+ species)	Small (containing 3– species)
Number of species	339	323
Number of species presenting at least one variety	51	37

However, Darwin was aware that if the data was to serve as confirmation for his hypothesis, he would have to provide independent evidence that the inequality, 51 > 37, reflects a greater reproductive tendency of large over small genera. The stakes were high: as he later explained it in the *Origin of Species*, his grand theory was that genera become large because they, in the past, possessed varieties that were favored by natural selection. On the other hand, small genera are small because they failed to produce winning varieties, and hence are on their way to becoming extinct. To test the assumption about the appropriate interpretation of the inequality, Darwin constructed a test out of the "rule of three",[10] the procedure of which he described in the letter to Lubbock. The following picks up where I left off above:

> "… they ought to have had 48 1⁄2 species presenting vars.-- So that the case goes as I want it, but not strong enough, without it be general, for me to have much confidence in. I am quite convinced yours is the right way". (Darwin, Letter no. 2123)

Darwin applied the "rule of three" to determine how many species presenting varieties a small genus "ought to have had" if it had the productive tendency of a large genus. To answer Darwin solved for x in the following inequality $339/323 = 51/x$. On the left side of the equation Darwin compares the ratio of number of species belonging to the large genera with that of the number of species belonging to small genera 339/323 (in the chart these are the values for the quadrants along the first row). On the right side of the equation the numerator is the number of species that present one or more varieties, and the denominator is the unknown, x, which, by cross-multiplying = 48.5. Darwin took this number to represent what the number of species producing varieties would be *if* the species were contained in the large genera. The difference between the actual number of species with varieties (51) and the number it *ought to have had if it were acting like a large genus* (48.5) suggested to Darwin that the productive tendency for large genera is greater than it is for small genera. Notice what Darwin was doing. The botanical arithmetic provided static information about ratios of genera, species, and varieties. Darwin was applying the rule of three as a means of extrapolating from the static data a prediction of the future direction of evolutionary change for a small genus.

As you can see from the rest of the letter to Lubbock (immediately above), Darwin seemed at least "convinced" that this procedure was sufficient to provide a wide range of tests for his general hypothesis.[11] Darwin hired a village schoolmaster from Downe to sort out the data for him (Browne, P. 81). On August 1, 1857, Darwin writes to his friend J.D. Hooker indicating that he found what he was looking for, that his tabulations support his hypothesis "that varieties are only small species--or species only strongly marked varieties." Here's the passage in full where Darwin proclaims how important the finding are to him:

> "I am got *extremely* interested in tabulating according to mere size of genera, the species having any varieties marked by greek letters or otherwise: the result (as far as I have yet gone seems to me one of the most important arguments I have yet met with, that varieties are only small species—or species only strongly marked varieties. The subject is in many ways so very important for me[12,13];

But, the real payoff of the botanical work for Darwin was a new theory of taxa formation. According to Browne, Darwin's four-year statistical investigation of the botanical arithmetic was "the 'trigger' which sparked off Darwin's sudden formulation of the principle of divergence" (1980, p. 77).[14] Indeed, Darwin's next letter to Hooker, dated 22 August 1857, reveals, Darwin's botanical work instigated a theory that explains taxa formation, involving a "principle of divergence":

> I am very glad to hear that you have been tabulating some Floras about varieties … If it will all hold good it is very important for me; for it explains, as I think, all classification, ie the quasi-branching & sub-branching of forms, as if from one root, *big* genera increasing &

[9] Darwin alludes to this novel technique (without bringing attention to its novelty) in the *Origin of Species*: "I have arranged the plants of twelve countries, and the coleopterous insects of two districts, into two nearly equal masses, the species of the larger genera on one side, and those of the smaller genera on the other side".

[10] The "rule of three" has been used since at least the 1600s. According to Stigler (2012, p. 3) John Graunt and William Petty applied it to estimate population and economic activity based upon extrapolation from death rates in parishes.

[11] Of course, we should not be easily convinced: "the Rule works well for the trivial mathematical problems of Euclid and commercial arithmetic; it fails to work in all other cases. Darwin's faith in the Rule was misplaced (Stigler, 2012, p. 3).

[12] https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-2130.xml;query=;brand=default.

[13] Darwin expanded on his argument in Chapter Two of the *Origin of Species* in the section entitled "Dominant species vary most": "my tables … show that, in any limited country, the species which are most common, that is abound most in individuals, and the species which are most widely diffused within their own country … often give rise to varieties sufficiently well-marked to have been recorded in botanical works. Hence it is the most flourishing, or, as they may be called, the dominant species … those which range widely over the world, are the most diffused in their own country, and are the most numerous in individuals,—which oftenest produce well-marked varieties, or, as I consider them, incipient species" (pp. 53–54).

[14] For an account of Darwin's rather complex theory of divergence in the Origin of Species see Kohn (2009).

splitting up &c &c, as you will perceive.— But then comes, also, in what I call a principle of divergence, which I think I can explain, but which is too long & perhaps you would not care to hear.— (Darwin, Letter no. 2130).[15]

The upshot is that Darwin's botanical arithmetic provides us an instance Darwin's development of his ideas of evolution were conducted in no small part to his "employing a mode of reasoning based on stable numerical frequencies". This is an important result for someone who possessed a "non-statistical mind".

We have already acknowledged that Darwin's techniques lacked the mathematical rigor and sophistication of, say, Maxwell and Mendel.[16] Yet, both were trained physicists, the former was a pioneer. So, a fairer comparison would be to look at what other evolutionists were doing. Marco Tamborini (2015) describes the work of German statistical paleontologists in the late 19th and early 20th century who challenged Darwin's theory of evolution with applications of the "botanical arithmetic" to the fossil record for the sake of detecting large-scale evolutionary trends. (They were looking for, and not finding, evidence of gradual evolution in the statistical data.) Darwin's statistical work clearly went further. Darwin's analyses involved *both* the detection of large-scale regularities, and empirical hypothesis testing (through the hypothetical values generated by the rule of three). This is beyond what the "statistical paleontologists" did with their data. Darwin's employed the rule of three to discern the direction of evolutionary change, in this case whether a genus is speciating or going extinct.

3. Darwin's 1873 statistical explanation for the evolution of rudimentary characters

My argument has been that statistical thinkers use statistics and probability theory for a variety of scientific inquiry, including pattern detection, hypothesis testing, and explanation. Darwin was no exception. As we saw, in 1857 Darwin applied the botanical arithmetic and the rule of three for the sake of pattern detection and hypothesis testing. In Darwin's 1873 letter to *Nature*, we find Darwin applying statistics and probability in the service of explanation.

Earlier I mentioned Gigerenzer et al.'s charge that Darwin never took advantage of the statisticians' view that what appears as chance in the individual averages out in the long run. Yet, in the 1873 letter Darwin does just that. Moreover, he applied the statistical law of error to explain how it is theoretically possible for a rudimentary character to be the product of evolution. The probability distribution curve serves Darwin's account in two ways, both of which provide us a sketch of the multiple ways that Darwin was (in this instance) a "statistical thinker". First, Darwin's overall intent is to employ an idealized statistical law about the distribution of characters to model the effects of development, random mating, and natural selection on the dynamics of evolution. The second is contained within his exposition. As we shall see, to explain how diversity of characters is maintained despite selection eliminating the diminutive characters, Darwin invoked the statistical fact that there is a high frequency of individuals available for mating that possess characters whose size tends towards the mean (or greater).

Darwin's letter to *Nature* in 1873 was prompted by Prof. Wyville Thomson's account of rudimentary males in certain barnacles (*cirripedes*). In species of several distinct genera the males are, compared to the females, "extremely minute … cannot feed, short-lived". In *Scalpellum regium*, the males are "half as large as a head of a pin … they consist of little more than a mere sack, containing the male reproductive organs". The issue was how did these rudimentary males evolve?[17] Darwin writes: "He who admits the principle of evolution will naturally inquire why and how these minute rudimentary males … have been developed". After revealing flaws in his previous evolutionary conjectures, Darwin offers "the following conjectural remarks … made solely in the hope of calling the attention of naturalists to this subject". He proceeds to invoke the statistical "law of error" to model the effects of evolution in conditions of scarcity over the course of generations.

Here's some background. The statistical law of error describes a continuous probability distribution for random variables. The graphical representation of the law of error is a bell-shaped curve peaked around the mean. In the 1708, Abraham De Moivre described a means to generate the bell-shaped curve as a limit of a binomial distribution in coin tosses.[18] In the 19th century observational astronomers applied the bell-shaped distribution curve to solve difficult problems involving how to discern accurate measurements from an aggregate of data, much of which was known to be erroneous. Assuming that the observational data is numerous and gathered from numerous independent sources, the law says that the aggregate will distribute itself in conformity to the bell-shaped curve with a peak around the mean, just like De Moivre described for coin tosses.[19] Reliable data clusters tightly around the mean (peak) of the curve, "error" is dispersed around it. (See Stigler, 1986 for a detailed discussion). That's why 19th century investigators called it the "law of error".

In the letter to *Nature* Darwin invokes the law of error in the context of the work of Aldolphe Quetelet, an astronomer turned social scientist who a wrote popular treatise in 1835 espousing a new social science which he called "social physics".[20] The appearance of the error curve in statistical data indicated to Quetelet the existence of constant causes—represented by the height of the curve or the mean—perturbed by accidental causes, represented by the curve's tail ends. Quetelet coined the term "l'homme moyen" or ‘‘average man’’ to represent the culmination of these bell-shaped curves that defined a human population. Quetelet compared the value of the average man to social science with the value of the center of gravity to physics: both allow us to identify the central facts for the discipline by abstracting away from the vagaries of individual differences (Ariew, 2007; Sober, 1980). Then, in 1844 Quetelet transformed his average man concept into a law of nature. He conjectured that the distribution of many biological and social characteristics conforms to the law of error. He offered only a few examples of support, including the distribution of height and chest sizes of 5000 Scottish soldiers whose distribution is bell-shaped, in near conformity to the astronomer's law of error (Ariew, 2007; Hacking, 1990; Stigler, 1986).

[15] https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-2130.xml;query=;brand=default.

[16] See Stigler (2016, pp. 107–111), for a description of the shortcomings of Darwin's application of the "rule of three". But, it should be noted that Stigler portrays the "rule of three" as a precursor to Francis Galton's technique of "regression".

[17] There are a host of interesting questions concerning sexual dimorphism in barnacles. For instance, why didn't Darwin notice that barnacles are a problem for his theory of sexual selection—a subject that he was writing about at this time? I thank an anonymous reviewer to bringing up my attention to this. In what follows I consider the more general question about the evolution of rudimentary characters, rather than barnacle males in particular.

[18] See Hacking (1990) and Stigler (1986) for more details. De Moivre used coins. Toss a coin n-times and indicate the proportion of heads to the total number of tosses on the x-axis of a graph from 0 to n. The y-axis represents the number of times in the sequence of trials where the coin lands heads. As the number of tosses increases, n gets larger (without bound), the resulting graph increasingly resembles a bell-shaped curve with its peak at the mean value and sloping sides representing the amount of dispersion around the mean.

[19] The pioneering astronomers, Gauss and LaPlace demonstrated that the bell-shaped curve of distribution describes both binomial and continuously variable distributions.

[20] Many of Darwin's contemporaries were aware of Quetelet's work, including Maxwell and Galton, and many claimed to have been influenced by it (Ariew, 2007). Darwin first mentioned Quetelet in notebook entries dated mid-to-late 1838, around the time he wrote his famous passage on Malthus, for a discussion of Darwin's use of Quetelet's analysis of sex ratios in the *Descent of Man*.

In the 1873 essay Darwin demonstrated his keen understanding of Quetelet's conjecture. As the following passage demonstrates, Darwin understood that multiple trials of a random sampling process, if outcomes are independent, will produce a graphical representation of the curve of error. Darwin even accurately described Quetelet's only real world-examples, heights and chest sizes of soldiers[21]

> "It is known from the researches of Quetelet on the average height of man, that the number of individuals who exceed the average height by a given quantity is the same as the number of those who are shorter than the average by the same quantity; so that men may be grouped symmetrically about the average with reference to their height. I may add, to make this clearer, that there exists the same number of men between three and four inches above the average height, as there are below it. So it is with the circumference of their chests, and we may presume that this is the usual law of variation in all the parts of every species under ordinary conditions of life. That almost every part of the body is capable of independent variation we have good reason to believe, for it is this which gives rise to the individual differences characteristic of all species."

It is important to understand the historical significance of Darwin's reference to Quetelet's conjecture. In Quetelet's previous work (from which he constructed his social physics) the bell-shaped distribution curve was a quantity used to measure features of populations (the "average man"). But, with Quetelet's later conjecture on the distribution of chest sizes—which Darwin is referring—Quetelet transformed a theory of measuring features of populations into a phenomenon of nature itself, a real-world large-scale population law of nature and society (Ariew, 2007; Hacking, 1990; Sober, 1980).[22] To Ian Hacking this was a 'game changer' in the history of statistics, "which was to determine the entire future of statistics". Quetelet transformed what he previously described as an arithmetical abstract of heights to an objective feature of real-world populations (Hacking, 1990, p. 109).[23] In Darwin's letter to *Nature*, Quetelet's "usual law of variation" served as an idealized representation of the diversity of characters in a population. What he did in the rest of the passage was to show how in unfavorable conditions, development, random mating, and selection would "in the course of time" result in "the steady diminution and ultimate disappearance of all such useless parts." In this way Darwin's application of the law of error was importantly different than Quetelet's. Quetelet applied the law of error to describe static features of adult populations, chest sizes of Scottish soldiers. But, Darwin applied it to model a *dynamic process*, the effects of evolution over the course of generations.[24] On Darwin's application the diversity of characters is maintained over the course of generations (in accordance with the law of error) but the effects of development, random mating, and natural selection—in conditions of scarcity—is to shift the diversity around an ever-decreasing mean.

The problem is Darwin's description is difficult to follow, so much so that it prompted his mathematically inclined son George to write a correction that was published in a later edition of *Nature* (4 October 1874). George sent an earlier draft to his father for approval, stating: "I think it is worth-while, since everything you write attracts so much attention, that it is a pity to let people break their heads over your meaning" (Darwin Letter no. 9084).[25] Father replied approvingly, and suggested a few alterations (Darwin Letter no. 9085).[26] George's letter in part clarifies what father was trying to say, and in part it shows us what father was *striving* to say. Recall, I am not claiming that Darwin was a brilliant statistician. What I am claiming that Darwin was engaged in statistical thinking. In the botanical arithmetic case, Darwin's engagement was in the form of correspondence with his mathematically inclined neighbor, John Lubbock. In the 1873 case, Darwin is engaging in statistical thinking with the aid of his son George. It is important to remember that the Darwins were trying something new, they were explaining an evolutionary process, indirectly, through a statistical model of trait distribution. So, it matters not that Charles "botched it".[27] The important point is that he is engaged in thinking about evolution from the point of view of statistical distributions.

In the 1873 letter, (Charles) Darwin described the evolutionary dynamical process in three steps, to be repeated each generation: stunted development, elimination of the most diminutive characters, and intercrossing and production of offspring. In the first, the developmental conditions are poor resulting in numerous stunted individuals. This is reflected in the statistical model as a distribution curve that is asymmetrical around a lowered mean with a longer tail towards diminution than towards the bigger than average sizes. As Charles put it:

> "Now it does not seem improbable that with a species under unfavourable conditions, when, during many generations, or in certain areas, it is pressed for food and exists in scanty numbers, that all or most of its parts should tend to vary in a greater number of individuals towards diminution than towards increment of size; so that the grouping would be no longer symmetrical with reference to the average size of any organ under cross."

In the second step, selection eliminates the most diminutive characters: "the individuals which were born with parts diminished in size and efficiency, on which the welfare of the species depended, would be eliminated". What remains are, "those individuals alone surviving … which possessed such parts of the proper size". "Proper size" here refers to the spectrum of characters that remain after selection eliminated the extreme.

It is at this point where Charles's explanation becomes both interesting and difficult to interpret at the same time. Reference to the statistical distribution of characters entered his explanation in two ways, but the passage seems to run them together. Here's the passage in full.

> "But the survival of none would be affected by the greater or less diminution of parts already reduced in size and functionally useless. We have assumed that under the above stated unfavourable conditions a larger number of individuals are born with any particular part or organ diminished in size, than are born with it increased to the same relative degree; and as these individuals, having their already reduced and useless parts still more diminished by variation under poor conditions, *would not be eliminated, they would intercross with the many individuals having the part of nearly average size, and with the few having it of increased size.* The result of such intercrossing

[21] Some historians doubt that Darwin would have understood Quetelet's statistical methods (Hodge, pers com.). To them I offer this passage where Darwin concisely describes Quetelet's empirical finding.

[22] An Anonymous reviewer asks: How much of this is Darwin aware? According to Sheynin (1980), Darwin learned of Quetelet's research on chest sizes from correspondences with Galton (though clearly, as we shall see below, Darwin had conversations about it with his son Charles).

[23] See also Sober (1980) and Porter (1986) for a discussion of the philosophical ramifications of Quetelet's work population averages.

[24] In 1877, Francis Galton noted Quetelet's chest sizes did not demonstrate the "law of deviation" in action. To remedy Galton reported on a heredity experiment with pea plants to show that the law of deviation is preserved over the course of generations. Although Galton does not mention it Darwin was one of the "many friends and acquaintances [who] undertook the planting and culture of a complete set".

[25] https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-9084.xml.

[26] https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-9085.xml.

[27] Jon Hodge and Greg Radick (pers com.) have challenged the significance of Darwin's 1873 letter because, as Radick said, "Darwin botched it" and that is what prompted George to publish the addendum. What Darwin botched was the exposition (admittedly opaque), not the theoretical idea. As I have said, I am not claiming that Darwin was a brilliant statistician. I am claiming that Darwin practiced statistical thinking to attempt an evolutionary explanation.

would be, in the course of time, the steady diminution and ultimate disappearance of all such useless parts (italics mine)."

The first instance of statistical explanation is found if we summarize the remaining steps of the evolutionary process and how they are reflected as changes in the distribution curve. The second instance is marked in italics; I will discuss each in turn.

Recall that in the second step, selection has eliminated the most diminutive. The remaining individuals are available for mating. The curve that represents the distribution of characters at the mating stage will compensate for the loss of the most diminutive characters. Darwin is not clear about what that looks like, but (if George's presentation can serve as evidence—see below) what he seems to be saying is that under the conditions of free intercrossing, or random mating, the distribution of characters in the offspring generation will revert back to conformity with the law of error (in obeyance with Quetelet's conjecture). However, the dispersion will be around a new, lower mean. Since the poor developmental conditions persist, the offspring generation will reiterate the three steps, developmental stunting, selection, and random mating. The cumulative effect over the course of generations will be reflected in the distribution curve as a shift of the distribution of characters towards the diminutive, that is, the entire distribution curve will continuously shift towards a lower mean value: "the result of such intercrossing would be, in the course of time, the steady diminution and ultimate disappearance of all such useless traits".

George's provided a more vivid picture than his father did of the dynamics of evolution as represented by the statistical distribution over the course of generations:

> "two operations going on side by side—the one [under unfavorable conditions] ever destroying the symmetry of distribution, and the other [evolution with or without selection for horn size] ever restoring it through the shifting of the cluster downwards … Thus, supposing the hypothesis to be supported by facts (and my father intends to put this to the test of experiment next summer), there is a tendency for useless organs to diminish and finally disappear, besides those arising from disuse and the economy of nutrition." (Darwin, 1874a, 1874b)

An animated graph plotting the distribution of characters at adulthood over generational time would depict a symmetrical bell-shaped curve constantly shifting towards the diminutive side of the graph until the character is eliminated from the population (which is what Darwin concluded). That is to say, an animated graph would come close to representing the phenomenon of "directional selection". To fathom the prescience of Charles' and George's statistical explanation, consider that according to John Endler, Simpson in the mid-1940s and Mather in the early 1950s were the first to point out that natural selection can affect frequency distributions—in particular, bell-shaped distributions—through directional selection where selection favors individuals toward one end of the distribution. According to Endler the significance of taking the statistical point of view is that it reveals that "Natural selection does not necessarily result only in a change in the mean and should therefore be described as well as defined in terms of the entire trait frequency distribution and particular environmental conditions" (Endler 1986). This is what Charles and George in fact show—they describe the environmental conditions that would result in the evolution of a rudimentary character.

What are the ramifications for understanding Darwin's innovations in statistical thinking? Darwin drew from Quetelet's conjecture that character variability exhibits a large-scale pattern, the distribution of characters is distributed in conformity to the astronomer's law of error. But, Quetelet (not Darwin) was interested in identifying group differences, and for that purpose variability represented "accidental" as opposed to "constant" causes. As Elliott Sober puts it, Quetelet was applying the law of error to "see through" individual differences. But, for Darwin variation is not accidental to explanation, he did not aim to see through individual differences. Rather, his intent was to explain how variability is maintained throughout the evolutionary process. Since Darwin knew nothing of genes, his explanation is instead in terms of reiterated processes of development, selection and intercrossing. To Ian Hacking, identifying the law of variation as a real phenomenon—both itself lawful and causally efficacious—marks another monumental shift in statistical thinking. Hacking attributes the revolutionary idea to Francis Galton in 1887 (more about this below). As we have just seen, Darwin describes it (even if vaguely) sixteen years earlier.

Now we come to the second instance where Charles invokes statistics in his explanation. It comes in the way he expresses what happens in the third step of intercrossing. Charles makes a provocative suggestion. Despite the most diminutive characters being eliminated by selection, it will reappear in the next generation. Why? His overall answer is that random mating preserves a distribution of characters in the offspring generation and the poor conditions stunts them all. The result is that the offspring of the relatively diminutive parents will be stunted, some of which will be as diminutive as the ones that were previously eliminated by selection. Hence, the eliminated character reappears in the baby generation.

Let's look at the part of the passage in Charles's letter, above (p. 16), that I set off in italics. Darwin is explaining why he thinks that random mating will preserve a distribution of characters. His answer is that most diminutive individuals that remain in the mating pool will likely mate with individuals that are larger than them because most potential mates are, *as a matter of statistical fact*, larger than them. According to the law of error (even if skewed) the frequency of the individuals possessing diminutive characters available in the mating pool is low, hence most of the available mates are going to be larger than them, the most populous are going to be some degree towards average height. Darwin must have assumed that offspring will possess offspring whose characters are some size between that of the smallest and largest parent. That would explain why he thinks that the distribution of characteristics for the offspring generation will conform to the law of error with a lower mean.

The significance of Darwin's thinking here is both historical and substantive. According to DM Walsh a distinctive feature of statistical explanation is that the investigator seeks to explain the distribution of inherited traits by adverting to a statistical property of populations (2015, p. 50). According to many historians, Francis Galton in 1887 was the first to provide statistical explanation for why inheritance over the course of generations preserves the distribution of characters in conformity to the law of error (according to Quetelet's "law of deviation").[28] Galton's insight led him to develop "regression". As Stigler describes it, "the movement from the population center toward the extremes [is] balanced by the movement back, due to the fact that much of the variation carrying toward the extreme is transient excursions *from the much more populous middle*". Stigler concludes: "The problem that Galton had identified was not a problem after all, but was instead due to a statistical effect that *no one had identified before*". (p. 130) Yet, it appears Charles (with George's help) made the point sixteen years earlier. The statistical property that in part explains why the diminutive character that was eliminated in the previous generation reappears in the next generation is the frequency distribution of characters. Most of the mates available for the smallish individuals (that weren't too small to be eliminated) are going to be larger than they are. That's a simple fact about the (skewed) bell-shaped distribution of characters with a peak at the mean. The offspring of these mating pairs will preserve the distribution of characters (according to Quetelet's conjecture).

[28] For a longer discussion of Galton's regression and its importance to the Modern Synthesis see Stigler (1986, 2016). For a longer discussion of Galton's regression and its importance to the philosophy of scientific explanation, see Hacking (1990), Sober (1980), and Ariew et al. (2015).

Aware that thought experiments are insufficient to assuage his skeptic interlocutor, Darwin makes an appeal to naturalistic observations: "No doubt the process would take place with excessive slowness; but this result agrees perfectly with what we see in nature; for the number of forms possessing the merest traces of various organs is immense". George went further and promised that his father would perform an experiment "next summer" and publish the results. I do not know if Darwin ever performed the experiment.

Darwin ends his 1873 letter with a repeat of his disclaimer: "I have ventured to make these hypothetical remarks solely for the sake of calling attention to the subject". What Darwin did in 1873 is significant—it shows Darwin capable of applying statistical thinking to an evolutionary explanation. His explanation involved two distinct statistical applications. First, Darwin recognized that law of error was an appropriate model for the character distribution for individuals undergoing the biological processes of development, selection, and intercrossing. The insight led him to explain how diminutive characters could have evolved as the aggregate effect of the variety of ways individuals experience the biological processes. Second, part of Darwin's explanation why selection doesn't eliminate the diminutive characters averts to a statistical fact about the frequency of distributions. So much for Darwin having a "non-statistical mind".

4. Conclusion

The claims I offer in this essay about Darwin's statistical work and how it contributed to the development of his theories of evolution is in several ways relevant to Mayr's remarks about Darwin's population thinking. The first concerns Mayr's original claim (concerning metaphysics) that Darwin replaced typological thinking with population thinking. In our first case we will see how Darwin's statistical work was responsible for his theory about new species originating as varieties. Since it is this very theory about speciation to which Mayr attributes Darwin's revolutionary anti-essentialism, we could relish in the irony: Darwin's methodological statistical thinking was responsible for his renowned metaphysical population thinking about species.

Second, Mayr's original motivation for his claims about Darwin being a population thinker was to identify areas where Darwin made significant contributions to the biological sciences. The subsequent literature on methodological population thinking has narrowed its concern to how Darwin treats variational change in the Origin of Species, where he comes up short. In this essay, I preserve Mayr's intent by considering Darwin's methodological contributions to biology more broadly, in terms of how he used statistical methodologies over the entire course of his career, to develop his ideas about evolution. In highlighting how Darwin employed statistical thinking throughout his career we not only transform our understanding about how Darwin came to develop his ideas about evolution we also gain a new understanding about how statistics and probability were used to for scientific inquiry. Darwin's cases show that statistics provide powerful tools for scientific research, especially when coupled with probability theory. Among other possible applications, they allow investigators to analyze large-scale patterns that would otherwise be undetected at the level of individuals, provide empirical tests for hypotheses, and even explain large-scale trends. With his botanical arithmetic Darwin constructed tables of data drawn from zoological catalogs to identify relationships between frequencies of varieties, species and genera. In this instance Darwin used statistics to identify ensemble-level properties that would have otherwise gone undetected when regarding individuals. Darwin's application of the rule of three was for hypothesis testing. He wanted to test whether a small genus is small because it is beginning to grow species or because it is losing species to extinction ("aberrance"). Darwin hypothesized that a growing genus would contain a number of species that is proportional to a large genus. The arithmetic rule of three allowed him to consider what those values would be so that he could compare them to the actual number of species. Darwin's botanical work contributed to the construction of his theory of taxa formation, including his Principle of Divergence. Recall that population In the second case, in 1873 Darwin applied statistics to explain the ensemble-level dynamics by averting to a statistical law.

This last instance of Darwin's application of statistical explanation is particularly telling against the common view that Darwin was not a statistical thinker about evolution. According to Sober, statistical thinking is a distinctive means of making sense of the blooming, buzzing, confusion of individual variation. Typologists accomplish this by identifying a particular natural tendency shared by each individual within a population. Statistical thinkers, on the other hand, identify statistical properties of populations. By this definition, Darwin's evolutionary explanation for rudimentary characters in his 1873 letter is an instance of statistical thinking.

Most philosophical treatments of Darwin's philosophy of science single out Darwin's arguments against creationism, his application of Baconian empirical methods (Cowles, 2020), his use of inference to the best explanation (Lewens, 2006), or his adherence of John Herschel's *vera causa* method (Hodge, 1992) for distinguishing natural selection as a true cause. Yet, few recognize the extent to which Darwin broadened the development of evolutionary biology through applications of statistical methodology. Yet, Darwin did not merely make natural selection "ripe" for statistical thinking, the early development (1850s) of his profound anti-essentialist ideas about species were in part based upon statistical considerations.

Uncited reference

Darwin, 1859, Endler, 1986, Galton, 1877, Hodge, 1986, , Ospovat, 1979, , , .

References

Ariew, A. (2007). *Under the influence of Malthus's law of population growth Darwin eschews the statistical techniques of Aldolphe Quetelet. Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, *38*(1), 1–19.

Ariew, A. (2008). Population thinking. In D., Hull, & M., Ruse (Eds.), *Oxford companion to philosophy of biology* (pp. 64–86). Oxford U. Press.

Ariew, A., Rice, C., & Rohwer, Y. (2015). *Autonomous statistical explanations and natural selection. The British Journal for the Philosophy of Science*, *66*(3), 605–634.

Browne, J. (1980). *Darwin's botanical arithmetic and the 'principle of divergence,' 1854-1858. Journal of the History of Biology*, *13*(1), 53–89.

Chung, C. (2003). *On the origin of the typological/population distinction in Ernst Mayr's changing views of species, 1942–1959. Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, *34*(2), 277–296. https://doi.org/10.1016/S1369-8486(03)00026-8.

Cowles, H.M. (2020). *The scientific method: An evolution of thinking from Darwin to Dewey*. Cambridge, Massachusetts: Harvard University Press.

Darwin, C. (2022a). *Correspondence Project* Letter no. 2123. https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-2123.xml. 1857a. (Accessed 4 March 2022).

Darwin, C. (2022b). *Darwin Correspondence Project* Letter no. 2130. https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-2130.xml. 1857b. (Accessed 4 March 2022).

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life* (1st ed.). London: John Murray. http://darwin-online.org.uk/content/frameset?itemID=F373&viewtype=text&pageseq=1.

Darwin, C. (2022a). *Darwin Correspondence Project* Letter no. 9085. https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-9085.xml. 1873a. (Accessed 4 March 2022).

Darwin, C. (1873b). *On the males and complemental males of certain Cirripedes, and on rudimentary structures*. *Nature*, *8*, 431–432. https://doi.org/10.1038/008431b0.

Darwin, G. (1874a). *Science at Cambridge*. *Nature*, *10*, 286. https://doi.org/10.1038/010286a0.

Darwin, G. (2022b). *Correspondence Project* Letter no. 9084. https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-9084.xml. 1874b. (Accessed 4 March 2022).

Darwin, C. *Darwin Correspondence Project*. https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-1686.xml. 1855.

Darwin, C. *The Autobiography of Charles Darwin*. http://darwin-online.org.uk/content/frameset?viewtype=text&itemID=F1497&pageseq=1. 1958.

Endler, J.A. (1986). *Natural selection in the wild*: *Vol. 21*. Princeton University Press.

Fisher, R.A. (1953). *The expansion of statistics*. *Journal of the Royal Statistical Society. Series*

A (General), *116*, 1–10.
Galton, F. (1877). *Typical laws of heredity*. *Proceedings of the Royal Institute of Great Britain*, *8*, 282–301.
Gigerenzer, G., Swijtink, Z., Porter, T., Daston, L., & Kruger, L. (1990). *The empire of chance: How probability changed science and everyday life*: *Vol. 12*. Cambridge University Press.
Hacking, I. (1990). *The Taming of Chance* (1st ed.). Cambridge England; New York: Cambridge University Press.
Hodge, M.J.S. (1986). *Law, cause, chance, adaptation and species in Darwinian theory in the 1830s, with a postscript on the 1930s*. *Probability Since*, 287–329.
Hodge, M.J.S. (1992). *Darwin's argument in the origin*. *Philosophy of Science*, *59*(3), 461–464.
Kohn, D. (2009). Darwin's keystone: The principle of divergence. In M., Ruse, & R.J., Richards (Eds.), *The Cambridge companion to the origin of species* (pp. 87–108). Cambridge: Cambridge: University Press.
Lewens, T. (2006). *Darwin* (1st ed.). London; New York: Routledge.
Lewens, T. (2009). *What is wrong with typological thinking? Philosophy of Science*, *76*(3), 355–371. https://doi.org/10.1086/649810.
Love, A.C. (2002). *Darwin and Cirripedia prior to 1846: Exploring the origins of the barnacle research*. *Journal of the History of Biology*, *35*, 251–289. https://doi.org/10.1023/A:1016020816265.
Magnello, M.E. (1996). *Karl Pearson's Gresham lectures: W. F. R. Weldon, speciation, and the origins of Pearsonian statistics*. *British Journal for the History of Science*, *29*(1), 43–63.
Mayr, E. (1959). *Darwin and the evolutionary theory in biology. Reprinted as: typological versus population thinking*. *Evolution and the Diversity of Life. Selected Essays*, 26–29.
Ospovat, D. (1979). *Darwin after Malthus*. *Journal of the History of Biology*, *12*(2), 211–230. https://doi.org/10.1007/BF00124192.
Porter, T.M. (1986). *The rise of statistical thinking, 1820–1900*. Princeton University Press.
Sheynin, O.B. (1980). *On the history of the statistical method in biology*. *Archive for History of Exact Sciences*, *22*(4), 323–371.
Sober, E. (1980). *Evolution, population thinking, and essentialism*. *Philosophy of Science*, *47*(3), 350–383. https://doi.org/10.1086/288942.
Stigler, S.M. (1986). *The history of statistics: The measurement of uncertainty before 1900*. Harvard University Press.
Stigler, S.M. (2016). *The seven pillars of statistical wisdom* (Illustrated edition). Cambridge, Massachusetts: Harvard University Press.
Tamborini, M. (2015). *Paleontology and Darwin's theory of evolution: The subversive role of statistics at the end of the 19th century*. *Journal of the History of Biology*, *48*(4), 575–612.
Walsh, D.M. (2015). *Organisms, agency, and evolution*. Cambridge: Cambridge University Press.
Weisberg, M. (2007). *Who is a modeler? The British Journal for the Philosophy of Science*, *58*(2), 207–233.
Wilkins, J.S. (2009). *Species: A history of the idea*. University of California Press.