Studies in History and Philosophy of Science 50 (2015) 48–58

Contents lists available at ScienceDirect

Studies in History and Philosophy of Science

journal homepage: www.elsevier.com/locate/shpsa

The early history of chance in evolution

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ARTICLE INFO

Article history:
Available online 29 October 2014

Keywords:
Chance;
Charles Darwin;
Evolution;
Francis Galton;
Karl Pearson;
Natural selection

ABSTRACT

Work throughout the history and philosophy of biology frequently employs 'chance', 'unpredictability', 'probability', and many similar terms. One common way of understanding how these concepts were introduced in evolution focuses on two central issues: the first use of statistical methods in evolution (Galton), and the first use of the concept of "objective chance" in evolution (Wright). I argue that while this approach has merit, it fails to fully capture interesting philosophical reflections on the role of chance expounded by two of Galton's students, Karl Pearson and W.F.R. Weldon. Considering a question more familiar from contemporary philosophy of biology—the relationship between our statistical theories of evolution and the processes in the world those theories describe—is, I claim, a more fruitful way to approach both these two historical actors and the broader development of chance in evolution.

1. Introduction

Our discussions of the history and philosophy of evolutionary biology continually make use of terms that may broadly be described as falling under the umbrella of 'chance': 'unpredictability', 'randomness', 'stochasticity', and 'probability' provide only a few examples. We find extensive discussion in the history of biology concerning the introduction of statistical *methods* in the life sciences (see, e.g., Porter, 1986; Sheynin, 1980). In the spirit of integrating the history and philosophy of science, however, it is notable that the corresponding question about these *concepts* often goes unanswered. How were the various notion of 'chance' now so prevalent in the biological literature introduced into evolutionary theorizing?

One of the only serious attempts to describe both facets of this historical transformation was advanced by Depew and Weber (1995), and has since been found in various places throughout the history and philosophy of biology. Their picture of the development of chance in evolution seeks to understand two crucial historical events. First, when and how did evolutionary theorizing become statistical? Second, when and how did such theories come to be taken to describe "genuinely chancy" processes in the world?[1]

Elucidating this standard view is the project of my second section. Francis Galton, it is generally recognized, is responsible for the first, methodological shift—it was Galton's work on the statistically derived law of ancestral heredity that introduced statistics into the study of evolution. The second, conceptual shift originates in Sewall Wright's shifting balance theory, which required a much more significant role for a chancy process of genetic drift than the theories which had come before it.

After introducing Depew and Weber's view, we will explore it in more detail. Section 3 will return to Darwin's own works, to establish the now-standard interpretation that Darwin believed evolution to be a *non*-statistical theory of *non*-objectively-chancy processes in the world. We then turn to Francis Galton in Section 4, where I describe his role in the development of the first statistical methods in the study of evolution. Rather than moving on to Wright, however, we will examine in Section 5 two of Galton's students at the end of the nineteenth century, Karl Pearson and

[1] The appropriate referent for "genuinely chancy" here is a very difficult problem, as various concepts of objective chance are often conflated in the (historical and present) literature on evolutionary theory. Thankfully, the point will not matter substantially for us, as I will not consider how the second question should be answered.

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http://dx.doi.org/10.1016/j.shpsa.2014.09.006
0039-3681/

W.F.R. Weldon. On Depew and Weber's view, these two would be minor characters.

Why, then, consider Pearson and Weldon at all? It is their work that will serve as our point of departure from considering the introduction of chance in terms of Depew and Weber's two focal historical moments. I will argue that if we are interested in the emergence of chance in evolution, Pearson and Weldon should indeed not be read as minor players. A vitally important distinction can be detected in Weldon and Pearson's writings on the philosophical justification for the use of concepts of chance. Suitably considered, that is, we can see Pearson and Weldon as innovators not merely in the use of statistical methodology, but in the philosophical grounding for the use of chance as well. If we focus only on the two events of the Depew and Weber view, we will entirely fail to recognize this aspect of their thought. We must look, then, for a new context for this historical development—a new driving question on which we are able to understand the eventual philosophical rift between Pearson and Weldon. I will argue that this distinction can be best exposed by considering the relationship between our *statistical theories* and the *processes* which those mathematical frameworks are intended to describe.

As regards this new question, then, a more mathematical, more positivist school of thought, with Pearson at its head, takes these statistics to be a tool for glossing over the (complex, possibly deterministic or indeterministic) causal details of biological systems. On the other side, a more empiricist, experimentally inclined school, with Weldon at its head, takes these statistics to be an essential way of grasping the full causal detail of biological systems. We can thus see here, I claim, a dramatic difference in the understanding of the connection between evolutionary theories and the evolutionary process, positions that are better comprehended not by way of the "reification" or "objectification" of chance, but by considering their differing views on the relationship between evolutionary theory and the biological world. And this question, as I will briefly argue in the conclusion, resonates strongly with contemporary work in the philosophy of biology.

2. Two focal events

We will begin, then, by discussing the view of the historical development of chance laid out in Depew and Weber's *Darwinism Evolving* (1995) and echoed throughout the subsequent literature in the history and philosophy of biology.[2] The second part of their book is devoted to describing the relationship between the advance of a new variety of Darwinism grounded in the developing science of genetics and what they call the "probability revolution"—the same broad historical process that Hacking called the "taming of chance" (Depew & Weber, 1995, p. 202). While they sometimes refer to this revolution as a singular event, they also helpfully subdivide it into two parts. The first is a "statistical revolution," the introduction of statistics as a tool "for collecting and analyzing quantifiable data," initially in the social and then in the scientific realm (Depew & Weber, 1995, p. 203). Later, with the addition of a robust probability theory, "the idea arose that probabilities [derived from these statistics] are based on objective propensities of real things" (Depew & Weber, 1995, p. 206). These two ingredients combined to make the probability revolution complete.

We see again, here, the distinction between the introduction of statistical methods into science and the corresponding introduction of the philosophical concepts that underlie these methods. Narrowing our view to the evolutionary realm, we are led to investigate the two historical events mentioned in the introduction: what was the first time that the statistical revolution was reflected in evolutionary theory (i.e., the first use of statistical methods), and what was the first time that probability in the genuine, objective sense was utilized (i.e., the first use of one particular philosophical conception of chance)?

Depew and Weber go on to describe what have come to be the standard explanations of these two events. For the first, they point to the work of Francis Galton. "Galton," they note, "contributed less to the continuity of the Darwinian tradition by his substantive views … than his conceptual and methodological ones" (Depew & Weber, 1995, p. 201). They make extensive use of the analysis of Hacking, who persuasively argued that Galton was the first not just to use a statistical law for the description of phenomena, but also as "autonomous," as a law "serviceable for explanation" of those phenomena by itself, without having to invoke a large array of supposed (but unobserved) underlying, small causes (Hacking, 1990, p. 186). Depew and Weber note that this, as well, is the first time that statistics is used in a positive manner for the support of Darwinian theory, rather than as a way to attack natural selection.[3]

In the case of the second event—the introduction of an objective, reified, or "genuine" notion of chance in evolution—Depew and Weber argue that "Sewall Wright opened up this Pandora's box" (1995, p. 287). Wright's turn toward chance, they write, was a way of enhancing the ability of the evolutionary process to create novelty, to provide "more openings for creative initiations" (Depew & Weber, 1995, p. 285). Wright, therefore, completes the probability revolution in the biological sciences. While Fisher, they argue, saw chance as merely a source of mathematical noise, a difficulty in theorizing which needed to be overcome and factored out, it was Wright who first argued that evolution invoked genuinely chancy processes—including random drift, the chanciness of which occasionally pushed organisms down an adaptive peak and enabled them to reach a higher neighboring optimum. On this view, we have a shift toward 'chance' precisely because chance is, for the first time, an active force which can be implicated in certain sorts of population change (namely, change which runs contrary to fitness gradients). The interpretation of Wright is, however, famously quite complicated (Hodge, 1992a, pp. 287–288), and for our purposes here I will leave the issue underdeveloped. As we will see, whether or not Wright was indeed the first to use an objective notion of chance is immaterial to my project.

Before continuing, I should note that by offering a new, third focus for our historical work on chance in evolution here, I do not at all intend to disparage either this pair of questions or the explanations offered for them. Indeed, both mark significant and important developments in the history of biology, ones which we are right to single out for extra scrutiny. I will argue, however, that if we restrict ourselves to only looking at the development of chance through these lenses, we run the risk of missing significant and important developments in the way that chance was

[2] Both questions are found, at least, in Hodge (1987) and Morrison (2002). Galton's role in the first shift has been discussed by Hacking (1990), as we will see later. Sheynin (1980) covers the first shift extensively as well. The second question is explored by Morizot (2012). Philosophically, many works—such as Brandon and Carson (1996), Millstein (2000), Rosenberg (2001), or Pence and Ramsey (2013)—implicitly rely on this distinction between the (assumed) statistical nature of evolutionary theory and the (contested) "chanciness" of biological processes.

[3] The same analysis is offered by Provine (1971, pp. 22–23), Gayon (1998, p. 105), Porter (1986, pp. 135, 284–285), and Radick (2011, p. 133).

understood by practicing biologists.[4] It is this worry—and the example of the philosophical work of Pearson and Weldon, which clearly fails to fit within these categories—that drives me toward producing a novel approach to understanding the development of chance in evolution.

3. Darwin's view

Now, let us rewind and consider Darwin's position with respect to the two primary historical events laid out above: is Darwin's own theory statistical, and does it purport to describe objectively chancy processes?

3.1. Darwin on statistics

Darwin's relationship to statistics is fairly clear. While Darwin did have a copy of Quetelet's *Sur l'homme et le développement de ses facultés* in his library (Rutherford, 1908, p. 69), he did not directly utilize statistical methods in his own work. As Manier notes, Darwin seemed to be unable to apply even a slightly statistical conclusion, as in his reference to the distribution of general adaptations in birds arriving in a new environment (Darwin, 1837, B 55e), "without deprecating it as a facade which concealed our ignorance" (Manier, 1978, pp. 122–123). Porter rightly notes that Darwin's work "can only in retrospect be construed as statistical" (1986, p. 134). He goes on to describe a series of letters between Karl Pearson and Francis Galton (with input from several of Darwin's descendants). Pearson had hoped to show that Darwin's own work ought truly be considered to be statistical (in line with Pearson's own predilections), but Galton, after consulting with the Darwins, replied that "I fear you must take it as a fact that Darwin had no liking for statistics" (Porter, 1986, pp. 134–135*nn.*).

Thus we have, throughout the *Origin,* the pervasive feeling that natural selection is intended to be a theory that utilizes only traditional, non-statistical, even largely deterministic sorts of explanations—explanations that are justifiable by Herschel's Newtonian-derived *vera causa* standard. Several authors, particularly Jon Hodge, have argued that Darwin's theory was explicitly modeled on the ideal for scientific theorizing depicted in Herschel's *Preliminary Discourse.*[5] It is for this reason that Darwin was especially stung by Herschel's dismissal of the *Origin.* "I have heard," Darwin wrote in a letter, "by a round-about channel, that Herschel says my book 'is the law of higgeldy-piggeldy.' What exactly this means I do not know, but it is evidently very contemptuous. If true this is a great blow and discouragement" (Hull, 1973, p. 7). Darwin was no radical on this score—he had hoped that his theory would be fully legitimate by Herschel's largely Newtonian and deterministic lights.

3.2. Darwin on chance

What about Darwin's relationship to some sort of concept of objective chance? Within the evolutionary process, Darwin identifies two loci where chance might operate. The first is the role of chance in the generation of the variation upon which natural selection is supposed to act. Frequently, Darwin argues for the existence of this variation by extrapolation from our experience with domesticated plants and animals. "Can it, then, be thought improbable," he asks, "seeing that variations useful to man have undoubtedly occurred, that other variations useful to some being in the great and complex battle of life, should *sometimes* occur in the course of thousands of generations?" (Darwin, 1859, p. 80, emphasis added). Elsewhere he notes that horticulture, throughout the ages, "has consisted in always cultivating the best known variety, sowing its seeds, and, when a slightly better variety has *chanced to appear,* selecting it, and so onwards" (Darwin, 1859, p. 37, emphasis added).

He seems, however, to be uncomfortable with the prominent role of chance here. At one point in the notebooks, discussing strength in blacksmiths, he writes that in addition to the inheritance of acquired characters, "the other principle of those children, which *chance?* produced with strong arms, outliving the weaker ones, may be applicable to the formation of instincts, independently of habits" (Darwin, 1838b, N 42). The emphasis here is Darwin's own—he seems to be a bit incredulous that chance can be the proper explanation for the appearance of variation, though he at the time has no better story to offer. Throughout the development of evolutionary theory it is "[m]ere chance, as we may call it, [that] might cause one variety to differ in some character from its parents" (Darwin, 1859, p. 111).

The second role Darwin sees for chance in the process of evolution derives from the fact that natural selection is not a perfect discriminator—it is merely the case that a profitable variation "will *tend* to the preservation of that individual" which bears it, and this will lead that individual's offspring to "thus have a *better chance* of surviving" (Darwin, 1859, p. 61, emphasis added). It must surely be the case, he argues, that "individuals having any advantage, however slight, over others, would have the *best chance* of surviving and of procreating their kind" (Darwin, 1859, p. 81, emphasis added).[6] Nothing, however, guarantees a particular individual's success—the best the evolutionary process has to offer is the promise of higher fitness. In a passage which nicely exhibits both of Darwin's senses of chance, he writes that natural selection is the process by which "every slight modification, which in the course of ages *chanced to arise,* and which in any way favoured the individuals of any of the species, by better adapting them to their altered conditions, would *tend to be preserved*" (Darwin, 1859, p. 82, emphasis added).

What does Darwin actually *mean* by the term 'chance' in these two invocations? Excepting some mentions of something like the law of large numbers,[7] Darwin rarely discusses what he takes the correct interpretation of chance to be. One of his only sustained considerations of the issue, at the beginning of the fourth chapter of the *Origin,* is commonly cited:

> I have hitherto sometimes spoken as if the variations—so common and multiform in organic beings under domestication, and in a lesser degree in those in a state of nature—had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation. (Darwin, 1859, p. 131)

This is as direct an expression of a subjective, unpredictability, or ignorance interpretation of chance as we might hope to find.

[4] I also do not claim that Depew and Weber themselves argued that our focus should be exclusive in this way, or that they failed to notice the problems that would result. They even come close to foreshadowing the account I will develop in Section 6 when they claim that "what was at stake in the conflict between Fisher and Wright was how many of the conceptual resources of statistical models are relevant to causal explanations of biological processes" (1995, p. 286).

[5] Hodge's contribution is a remarkable series of papers: (1977; 1987; 1989; 1992b; 2000; Hodge and Radick, 2009). For others, see also Lennox (2005); Lewens (2009); Waters (2009); Hull (2009).

[6] References to organisms' "chance of surviving" or "chance of leaving offspring" are one of Darwin's most frequent refrains, and are *incredibly* common throughout Darwin's work. For only a small (!) cross-section of examples, see Darwin (1838a, E 137), Darwin (1859, pp. 5, 88, 90–92, 104, 109, 114, 127, 136, 176, 235, 388), Darwin (1871, pp. 161, 265, 319–320, 406, 414).

[7] See, e.g., Darwin (1871, p. 316), Darwin (1837, B 55e).

Darwin explains that whenever he makes reference to “chance,” it is merely an indication that we lack knowledge or predictive power with respect to the particular causes of the phenomenon at issue. He goes on to note that one might ascribe the source of variation to the reproductive system, the conditions of life of the parents, climate, food, and so forth. All of these are, that is, possible *true* causes of variation—we simply lack the precision to determine which is genuinely responsible for variation in a given case (or even in the majority of cases).[8]

Finally, we have Darwin’s famous discussion of chance from the *Variation.* He considers the objection, by that point quite familiar, that “selection explains nothing, because we know not the cause of each individual difference in the structure of each being” (Darwin, 1875, p. 427). To reply to this objection, Darwin asks us to consider an analogy. When rock falls from the face of a cliff, he argues, we might call the shape of the fragments that result accidental,

> but this is not strictly correct; for the shape of each depends on a long sequence of events, all obeying natural laws; on the nature of the rock, on the lines of deposition or cleavage, on the form of the mountain, which depends on its upheaval and subsequent denudation, and lastly on the storm or earthquake which throws down the fragments. (Darwin, 1875, p. 427)

We then imagine assembling a structure from these stone fragments. Of course, Darwin argues, an omniscient creator could foresee all these events. But ought we really infer that all the natural laws that caused the stone to take its current shape exist *for the sake of* the structure that the builder builds? Clearly not, he implies. It is in this sense that the shape of the stones is *accidental.* And natural selection works in the same way. Many of the variations in organisms are not useful or pleasing to either man or to the animal itself (and many of the artifically selected variations which are pleasing to man are deleterious to the organisms). They are the result of lawlike causal processes, but there is no sense—divine or otherwise—in which the laws are the way they are *for the sake of* the development of some particular character in some particular organism. There is no overarching pattern to find, and for this reason, and only in this sense, can we view the evolutionary process as “chancy.”

All these examples are traditionally cited when discussing Darwin’s understanding of chance, and the standard reading of Darwin summarizes them by claiming that he held an ignorance interpretation of chance.[9] But this agreement masks the interesting depth of Darwin’s thought on the matter. We see throughout these quotes an interplay of three distinct ways of understanding chance. First is simple subjective unpredictability, as he invokes in the case of variation—the inability of a given observer with a given set of evidence to predict the precise outcome of some system. Second, and much more important for Darwin, is the concept of ‘accident’, which we see in the discussion of the stone arch—the lack of any sort of overarching design, any “for the sake of which” or final cause. Finally we have objective chance, which Darwin consistently interprets as some sort of *lack of causation.*

This last sense—objective chance—is categorically rejected by Darwin. It is clear that Manier is correct when he states that Darwin “attributed no causal force to chance itself” (1978, p. 121). All causes, in Darwin’s view, are still perfectly Newtonian; both the stone building example in the *Variation* and the discussion of variation in the sixth edition of the *Origin* are very clear about this position. Variation, in general, is more about unpredictability for Darwin—it is the bulk material, viewed throughout the *Origin* as a black box, a fact that provides a necessary and empirically well-confirmed (if inexplicable) *input* to the evolutionary process.

When Darwin discusses the possibility of chance in the process of natural selection, on the other hand, his worry is with *design,* and hence he is primarily concerned in this arena with chance in the sense of *accident.* The particular sequence of variations which any particular population undergoes lacks any master plan, and is thus to this extent a matter of chance. While it is therefore a consequence of selection that many features of organisms are accidental, Darwin still rejected objective chance as applied to the process of selection. To return to our original question, then—whether or not Darwin thought the evolutionary process was objectively chancy—we have ample evidence to answer it firmly in the negative. Evolution does not involve objectively chancy processes for Darwin.

Such, then, is the state of affairs as of 1859. Darwin has proposed the theory of evolution by natural selection, a non-statistical theory of non-objectively-chancy processes in nature. Complex processes, to be sure—processes the details of which may forever escape our knowledge. But the theory itself is intended to conform to Herschel’s *vera causa* ideal, which, according to Herschel, grounds the explanatory power and prowess of Newtonian mechanics. While Darwin may have been far more willing to appeal to (again, his sense of) chance than many of his contemporaries, and while he may have placed much more of the living world under the guidance of an accidental process free of final causes than those who had come before him, we don’t see a drastic shift in the role of either statistical theorizing or objective chance in Darwin’s work. As of yet, we have seen neither of the historical events for which we are searching. Let us then move forward to Francis Galton.

4. Statistical theories: Francis Galton

What was the main driving force behind the introduction of statistics into the theory of evolution by natural selection? As it turns out, it was an old problem. As early as the “Sketch” of 1842, Darwin was worried about *blending inheritance.* He writes that “if in any country or district all animals of one species be allowed freely to cross, any small tendency in them to vary will be constantly counteracted” (Darwin, 1909, p. 3), destroying the power of natural selection to alter the species. The point was made far more serious in the review of the *Origin* by the engineer Fleeming Jenkin (1867).

Gayon notes that the thrust of this paper is often misunderstood (1998, pp. 96–97). Jenkin is not merely concerned with the apparent reliance of Darwin’s theory on “sports,” or large deviations of characters from parent to offspring. Rather, he notes the following two interrelated (and much more complex and significant) problems with Darwin’s theory as expressed in the *Origin.* First, how is variation distributed? If the distribution is continuous, then we must use statistics to describe it. If, on the other hand, it is not a continuous, populational sort of variation, but rather individual and isolated instances, these instances must be measured, and the odds of some particular variation being eliminated by chance must be determined. Second, what is the method of transmission of characters to offspring? If offspring carry a mixture of the characters of their parents, as Darwin and most others assumed, how can the problem of regression to the mean be avoided?

Depew and Weber argue that Darwin’s own response to this problem is highly unsatisfactory. In the last two editions of the *Origin,* all he does to respond to this charge is to posit the existence of more continuous variation and fewer “sports”—as Depew and Weber note, “by fiat,” changing the singular nouns referring to

[8] This discussion is even more explicit in the sixth edition of the *Origin* (Darwin, 1876, pp. 6–8).

[9] Commentators to argue for such a view include Hull (1973, pp. 62, 426–427), Hodge (1987, p. 243), Depew and Weber (1995, p. 113), and Beatty (2006, p. 630).

variation to plurals (1995, p. 196). Given that Darwin's response here was so unsatisfying, what was to be done about the problems that Jenkin raised? The long-term solution, of course, was the rejection of the blending model of inheritance. But this would have to wait for the "rediscovery" of Mendel's paper and the birth of genetics, almost thirty years after Darwin's death (Druery & Bateson, 1901).

In the meanwhile, defenders of Darwin's theory sought refuge in statistics—establishing how natural selection could work in a gradualist, statistical manner on populational, continuous variation. The most prominent early defender was Darwin's cousin Francis Galton. The publication of Darwin's *Origin* sparked in him a deep interest in breeding—particularly in eugenics and the heredity of human intelligence and other abilities. To that end, Galton found two things unsettling about the trouble with blending inheritance. First was the potential undermining of his cousin's theory of evolution by natural selection, which Galton had described in a letter to Darwin as engendering "a feeling that one rarely experiences after boyish days, of having been initiated into an entirely new province of knowledge which, nevertheless, connects itself with other things in a thousand ways" (Galton & Darwin, 1859). But second, and more importantly, were the eugenic implications of the blending argument. Unless heredity and variation work in precisely the right way, it remains possible that the eugenic program is a failure before it begins: that *even with* the aid of severe eugenic programs, we will still be unable to preserve "superior" characters within the families that are entitled to them.

Thus was the problem of blending inheritance doubly magnified for Galton. How did he propose to resolve it? He began with a radically different view of the way in which inheritance operates. Relatively early during his study of heredity, Galton shifted to a population-based, statistical view of the transmission of characters from parents to offspring (Porter, 1986, p. 136). Galton used this perspective to develop a view of particulate inheritance on which many small heritable factors—some "latent" and some "developed" or "patent" in the adult—combine and compete for a small number of "places" within the offspring. The closest metaphor we can create for such inheritance, Galton writes, is this. Consider "an urn containing a great number of balls, marked in various ways, and a handful to be drawn out of them at random as a sample: this sample would represent the person of a parent [his or her developed characters]." Then we mix another, similarly sized urn in with the first, representing the contribution of the other parent, and draw out a second sample. "There can be no nearer connexion justly conceived to subsist between the parent and child than between the two samples" (Galton, 1872, p. 400).

The very foundations of heredity, therefore, can now be considered statistically—as a vast, population-level urn-drawing experiment. Heredity thus was, from the time of Galton's first articles on the subject, best dealt with at the statistical level. From here, we can turn toward mathematizing the relationship between parent and offspring.

The primary mathematical contribution to evolutionary theorizing made by Galton himself, the law of ancestral heredity, describes the extent to which the contribution of heritable characters in ancestors influences the characters of offspring—"the integration of *all* hereditary phenomena in a single conceptual framework or expression," in the words of Gayon (1998, p. 132). In *Natural Inheritance,* Galton describes the law as follows:

> [T]he influence, pure and simple, of the Mid-Parent [the average of the mother and father] may be taken as 1/2 and that of the Mid-Grand-Parent [the average of all four grandparents] as 1/4, and so on. Consequently the influence of the individual Parent would be 1/4, and of the individual Grand-Parent 1/16, and so on. (Galton, 1889, p. 136)

Galton is attempting to do the following. Consider the characters of an offspring. We know that there is a strong force of regression to the mean, so the interesting question becomes: at what fidelity are the characters of parents (and earlier ancestors) transmitted to their offspring? Galton first determined empirically that the coefficient of correlation between sons and 'mid-parents' was 2/3. However, this correlation includes not only characters from the parents themselves, but also some from the grandparents passed on to the parents and then the offspring—we have to "factor out" this grandparental contribution if we want to determine the "pure" contribution of the parent. By two separate estimations (one assuming a constant diminution of transmission in all generations and one assuming a diminution that increases over time), Galton arrives at the value of 1/2 for the mid-parent contribution.

Galton's technical conclusions aside, we can clearly see the tools and methods of statistics deeply embedded in his work. The value upon which the entire derivation of the law of ancestral heredity rests, the mid-parent to offspring correlation of 2/3, was determined empirically via regression on measurements of height, and Galton sought to confirm it via statistical measurement of moth populations, human eye-color, artistic talent, disease, and so forth. Galton has, indisputably, brought statistics to a central component of evolution, and statistics proved to be here to stay. We thus very clearly find in the work of Galton the first historical event for which we have been searching—evolutionary theorizing now involves statistical methods.

But note the depth of the use of statistics—Galton's concern with eugenics and breeding means that we only have this statistical viewpoint in heredity, not in any other, related biological theories. Galton at times gestures at a statistical view of natural selection (e.g., Galton, 1877b, p. 533), but not in anything like a robust or empirically grounded way. The thorough integration of statistics into further areas of evolution would be executed by Pearson and Weldon, to whom we will turn below.

4.1. Galton on chance

What about the role of objective chance in Galton's theorizing? He is nearly silent on this issue, but we can divine two conclusions. First, return to Galton's discussion of his statistical theory of heredity. Galton sees both the transmission of elements to offspring and the development of organisms as complex but necessarily strictly Newtonian or mechanistic causal processes. He describes "segregation" as a straightforward process of competition (which Radick (2011) has likened to natural selection), saying that "for each place [in an organism's set of developed characters] there have been many unsuccessful but qualified competitors" (Galton, 1872, p. 395). On development, he says that if we had sufficient information, "statistical experiences would no doubt enable us to predict the average value of the form into which they would become developed … but the individual variation of each case would of course be great, owing to the *large number of variable influences* concerned in the process of development" (Galton, 1872, p. 396, emphasis added). This sounds much like Quetelet's view of social statistics as the result of the aggregation of a myriad small, non-statistical causes.

Second, we can consider Galton's famous use of the quincunx device. Consider the outcome of dropping a handful of shot into the top of the device in Fig. 1. The shot falls through the series of pins set in the board, and collects at the bottom in a series of bins. The shot will, Galton notes, pile up in these bins in precisely the distribution described by the normal curve (shown at the bottom of the device). Importantly for us, consider Galton's description of how the device approximates the law of errors:

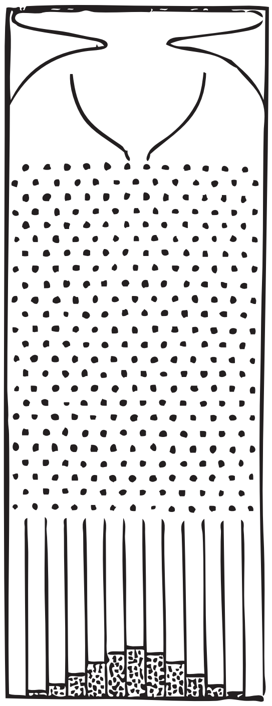

Fig. 1. Galton's quincunx device used to demonstrate the normal curve. Figure 7 from Galton (1889, p. 63).

> The principle on which the action of the apparatus depends is, that a number of small and independent accidents befall each shot in its career. In rare cases, a long run of luck continues to favour the course of a particular shot towards either outside place, but in the large majority of instances the number of accidents that cause Deviation to the right, balance in a greater or less degree those that cause Deviation to the left. […] This illustrates and explains why mediocrity is so common. (Galton, 1889, pp. 64–65)

Setting aside, for our purposes, the moral overtone present in Galton's invocation of 'mediocrity', here we have another instance of precisely the same sense of chance we saw expressed by Darwin. The law of errors is nothing more or less than the record of a very large number of small, deterministic causes acting on the same system over time—and it is merely our ignorance, or our inability to follow those "runs of luck," that makes the use of statistics necessary.

But the full tale of Galton's view of chance must be slightly more complicated than this. For the analogy between the quincunx and the "large number of variable influences" in heredity is not a perfect one. The most common way of describing the law of errors in Galton's day comes from Quetelet, who, Galton was right to note, believed that the "essence" of the law of errors "is that differences should be wholly due to the collective actions of a host of independent *petty* influences in various combinations, as was represented by the teeth of the harrow [in the quincunx]" (Galton, 1877a, p. 512). Quetelet, that is, had argued that a normal distribution arises by subjecting an object (be it a piece of shot or a person) to a long sequence of minor (or "petty"), independent causes, leading to the pattern of "runs of luck" and "balance" that Galton described.[10]

But this cannot be the full explanation of heredity, despite the fact that heredity produces normal distributions. "[A]lthough characteristics of plants and animals conform to the law [of errors]," he argues, "the reason of their doing so is as yet totally unexplained," because the processes of heredity "are not petty influences, but very important ones" (Galton, 1877a, p. 512). Far from the minor tweaks to the direction of the shot applied by the teeth of the quincunx, the influences of heredity dramatically shape the course of an organism's life. Thus, we are forced to conclude "that the processes of heredity must work harmoniously with the law of deviation, and be themselves in some sense conformable to it" (Galton, 1877a, p. 512). While Galton does not therefore believe the statistical account of heredity is a *direct* analog of the behavior of the quincunx, we must explain the fact that the various non-statistical and decidedly *non*-petty processes of heredity are "conformable" to statistical explanation.

Whatever the account of this coincidence, we clearly have no cause for inferring anything other than an interpretation of chance as unpredictability for Galton. The laws derived for the various processes of heredity, he argues, "may never be exactly correct in any one case, but at the same time they will always be approximately true and always serviceable for explanation" (Galton, 1877b, p. 532). It is clear that it is merely our ignorance of the precise details of these processes that makes higher-level statistical laws necessary and particularly "serviceable." If we are looking for the first invocation of objective chance, we are not to find it in the work of Galton.

5. Pearson and Weldon: minor characters?

Following the narrative of Depew and Weber, we would now move our focus forward to the work of Sewall Wright, where we would find the first instance of chancy evolutionary processes in his shifting-balance theory. Wright argued that (as one of the phases of the shifting-balance process) the chancy influence of genetic drift could produce novelty by driving a population *down* a fitness gradient, against the direction of selection, moving it across a "valley" of lower fitness to a new local optimum. We will not here, however, evaluate this second historical event—Depew and Weber may well be quite correct that the first instance of objectively chancy theories is found in the work of Wright. Rather, I want to advance a much shorter increment, to two of Galton's students—Karl Pearson and W.F.R. Weldon.

Pearson, whose life has been masterfully detailed by Porter (2004), was a particularly interesting character. He studied at Cambridge, and after having received his degree with Mathematical Honors, departed for Germany, becoming deeply affected by the Romantic tradition and publishing and lecturing on German history.[11] He developed an intense interest in socialist politics as well as women's rights. Finally, upon returning to England, he was appointed chair of Applied Mathematics and Mechanics at University College, London, where he was primarily occupied with teaching mathematics to students of engineering. His work there, which included teaching geometry and drawing, would have a substantial influence on the significant visual aspect of his later work in statistics.

His completion of William Kingdon Clifford's *Common Sense of the Exact Sciences* (1885) provided an early glimpse of Pearson's philosophy of the physical sciences. Broadly positivist in nature—that is, emphasizing the importance of mathematical formulas in the development of scientific knowledge and espousing a strict

[10] Quetelet himself called these "accidental causes," which "only manifest themselves fortuitously and act indifferently in any direction" (Quetelet in 1846, quoted in Hankins, 1908, p. 129). It is these causes that produce the variance seen in a normally distributed quantity, by contrast with "constant" causes, which set the mean.

[11] This brief biography follows that presented by Pearson's son in Pearson (1936).

form of empiricism—he would go on to develop this philosophy of science in his widely known *magnum opus,* the *Grammar of Science,* first published in 1892 and later revised and expanded (with more material on evolution) in 1900.

W.F.R. Weldon, known as Raphael, was born in 1860.[12] He attended University College and later King's College, studying biology under Lankester and Balfour. After obtaining his degree, he worked at both the Naples Zoological Station and Cambridge, finally being appointed as Lecturer in Invertebrate Morphology at University College, London, in 1884. He became quite active in the Marine Biological Laboratory at Plymouth after its completion in 1888, eventually running several large-scale experiments there.

In 1890, Weldon was appointed to the Jodrell Professorship of Zoology at University College, London, and Weldon and Pearson quickly formed a friendship. Pearson had been driven to the study of biology by reading Galton's *Natural Inheritance,* which had been published the year before (Pearson, 1936, pp. 210–211), and, early in 1890, Weldon had published his first work applying statistics to biology (Weldon, 1890). The mathematics in Weldon's paper had been prepared under the direct tutelage of Galton himself, who was sent the paper as a referee (Pearson, 1906, p. 17). A bit later, in November 1891, Pearson delivered the first of the Gresham College Lectures in Geometry. He would go on to deliver thirty lectures in this series on the subject of chance and statistics—in particular, focusing on visual aids and graphical representations of various kinds to make the material accessible to a broad student audience (Porter, 2004, pp. 235–236). As time went on, however, evolution featured ever more strongly in the lecture content. We can see, Porter notes, "a vision … taking form, even as he wrote his lectures, that evolution by natural selection could be comprehended statistically" (Porter, 2004, p. 238).

By this point, then, the collaboration between Pearson and Weldon was off to the races. Nearly all of Weldon's papers from 1893 until his untimely death from pneumonia in 1906 involved statistical collaboration with Pearson, and Pearson would publish a series of some twelve papers titled "Mathematical Contributions to the Theory of Evolution," describing various applications of statistical methodology to the evolutionary process. With Weldon's death and the increasingly hostile climate of the battle between the biometricians and Mendelians, Pearson would largely abandon the study of biology after 1906, taking over the directorship of Galton's Eugenics Laboratory at University College (Pearson, 1936; Magnello, 1999a, b).

Let us now consider how Pearson and Weldon fare as regards the two historical events that have formed our framework here: do they utilize statistical methods for the study of evolution, and do they consider this to be undergirded by an objective notion of chance extant in the world? We will discover that, on Depew and Weber's view, Pearson and Weldon are relatively garden-variety: their situation with respect to our two focal questions is identical with their mentor Galton's.

As far as the statistical nature of evolutionary theorizing, whereas Galton deployed statistical methods primarily within the study of heredity, Pearson and Weldon also brought statistics to the study of variation, inheritance, correlation, and natural and sexual selection—a much broader swath of biological theories. While Galton, as we mentioned above, viewed *portions* of evolutionary theory statistically, *much more* of evolution was to be studied statistically for Pearson and Weldon. Pearson, for example, in the second edition of his *Grammar of Science,* claims that only the growth of the statistical picture of evolution had made it possible to provide a "precise definition of fundamental biological concepts" (1900, p. 372). We thus have the introduction of a thoroughgoing statistical methodology in portions of evolutionary theorizing where Galton's use of statistics had only been cursory. Pearson and Weldon's combination of mathematics and experiment was exceptionally productive.

What about their views on the role of an objective notion of chance in biology? Because of the positivist bent in Pearson's work, he did not believe, nor could he consistently have believed, that our scientific theories somehow latch onto objective chance in the world. Objective, reified chance is an inhabitant of the realm of things-in-themselves, which Pearson barred from his philosophy. He thus offers an ignorance interpretation of the scientific use of probabilities, just as Galton and Darwin had before him. In a section titled "The Bases of Laplace's Theory lie in an Experience as to Ignorance" (Pearson, 1892, p. 171), he argues that the underlying justification behind the use of probabilistic claims in science is an equiprobability assumption, and this equiprobability assumption is justified as the best course of action in the face of ignorance: "In our ignorance we ought to consider before experience that nature may consist of all routines, all anomalies, or a mixture of the two in any proportion whatever, and that all such are equiprobable" (Pearson, 1892, p. 172). He goes on to offer an extensive justification of why our past experience with situations of incomplete information does indeed justify the use of equiprobability as a canon of legitimate inference.

Weldon, as well, affirms a straightforward interpretation of chance as subjective unpredictability. In a lecture he delivered the year before his death (to which we will return later), he argued that "all experience, which we are obliged to deal with statistically, is experience of results which depend upon a great number of complicated conditions, so many and so difficult to observe that we cannot tell in any given case what their effect will be" (Weldon, 1906, p. 97). Weldon, again, follows Darwin, Galton, and Pearson in adopting a notion of chance grounded entirely in ignorance. The introduction of an objective notion of chance in evolution is not to be found in the work of either Pearson or Weldon.

6. A new question

The explanation given by the standard history of the early development of chance in evolution is relatively straightforward. We begin with Darwin, who develops a non-statistical theory of non-objectively-chancy biological systems. Galton, endeavoring to respond to the troubles of blending inheritance, statisticalizes the theory of heredity. Pearson and Weldon expand this usage of statistics to selection itself, making them only methodological innovators. Neither Galton nor his students discard Darwin's ignorance interpretation of chance in the objective biological world—this was Sewall Wright's doing, introducing objective chance in the context of his shifting balance theory.

If we consider merely the two events brought out in Depew and Weber's analysis, it is not obvious why Pearson and Weldon are even worthy of mention at all, much less of a systematic development of their views on chance. Pearson and Weldon innovate only in terms of the use of statistical methodology to understand evolution—they have nothing new to offer in terms of their conceptual or philosophical views. On the contrary, the case of Pearson and Weldon, I argue, is an excellent example for use in teasing apart more thoroughly the history of the introduction of concepts of chance in evolutionary theorizing. Most worryingly, if we adopt Depew and Weber's focus on objective chance, two issues make it difficult even to frame the question of Pearson and Weldon's use of such a concept. First, as with all examinations of the conceptual entailments of biological theories, we are hampered by biologists'

[12] This brief biography follows Pearson's memorial of Weldon (Pearson, 1906). No scholarly biography of Weldon has as yet been prepared.

uncertain attitude toward the metaphysical or ontological claims of their theories (see, e.g., Waters, 2011, on 'toolbox' theorizing). Second, despite the fact that some early work on chance in the late nineteenth and early twentieth centuries did make room for the possibility of genuine indeterminism in the sense that Depew and Weber consider, we have no evidence that 'chance' in this sense was a concept entertained by any of the authors whose work we have considered here.[13]

Pearson and Weldon, however, were far from silent on the proper role of and philosophical justification for the use of concepts of chance in evolution. A schism that developed between the two men, often unremarked-upon in the historical literature, reveals that they were engaged in a serious, long-standing debate over precisely this issue. What problem, then, drove them to develop well-considered justifications for the role and utility of chance?

This, I claim, is precisely the impetus we need to develop a new way of understanding the role of chance in the early development of evolution. The two historical events of the Depew and Weber view do not capture the philosophical work of Pearson and Weldon, so it is beholden upon us to find a way of framing the issues that allows us to recognize and comprehend it. The best candidate for this new question, I argue, is this: *What is the relationship between biological systems and the statistical theories used to describe them?* This question lets us most clearly see the subtle difference between Weldon and Pearson's views, and enables us to better explore this facet of the early history of chance in evolution.

6.1. *Pearson contra Weldon*

Let's return to Pearson's philosophy of science. Though the two men were unknown to each other at the time, we can recognize what we would now call a "Machian" view of physics as much of the motivation for Pearson's *Grammar*—indeed, Mach would write to Pearson in 1897, plaintively noting "how useful would it have been for me to know back in 1872 that I didn't stand *alone* in my efforts."[14] Pearson focuses extensively on the usefulness of science for the economy of thought, denigrates the speculative use of 'metaphysics' in science, and extensively praises an austere form of empiricism.

In the *Grammar of Science,* for example, he writes that the last step of the scientific method is

> the discovery by aid of the disciplined imagination of a brief statement or formula, which in a few words resumes the whole range of facts. Such a formula … is termed a scientific law. The object served by the discovery of such laws is the economy of thought. (Pearson, 1892, p. 93)

Further, the discovery of these simplified laws of nature must remain the central focus of our work in the biological sciences in particular. In the second edition of Pearson's *Grammar,* he notes that the advance of statistical biology "enables me to define several of these conceptions much more accurately than was possible in 1892" (Pearson, 1900, pp. viii–ix). Statistics has finally endowed us with the ability to demonstrate evolution's action quantitatively. After discussing the various types of selection that have been proposed, Pearson writes that "before we can accept [any cause of progressive change] as a factor we must not only have shown its plausibility, but if possible have demonstrated its quantitative validity" (Pearson, 1900, p. 380).

And when such a focus on statistics has failed to hold (in particular, in the study of variation) it has led to a stagnation in biology—in Pearson's words,

> largely owing to a certain prevalence of almost metaphysical speculation as to the causes of heredity, which have usurped the place of that careful collection and elaborate experiment by which alone sufficient data might have been accumulated, with a view to ultimately narrowing and specialising the circumstances under which correlation was measured. (Pearson, 1896a, p. 255)

We can thus see a profound trend in Pearson's thought, reinforced throughout his work both in the general philosophy of science and specifically in biometry. For him, laws of nature are nothing more than brief formulas describing a trend in observed data, useful first and foremost for economizing thought and enabling prediction. The same is true for causes, as well—he argues that causation is nothing more than the experience "that a certain sequence has occurred and recurred in the past" (Pearson, 1892, p. 136), such sequences being described, of course, by mathematized laws of nature.

Now, let's turn to Weldon. As I mentioned briefly above, in 1906, a lecture by Weldon on the topic of inheritance (delivered the previous year) was published in a volume of *Lectures on the Method of Science.* While the bulk of the lecture is relatively uninteresting (if not downright confusing), Weldon begins by offering a conceptual defense of his use of statistical methods.

In physics, he argues, we have two uses for statistical inference. First, it averages over errors in measurement. Weldon gives the example of the determination of the latitude of the Radcliffe Observatory—even though highly skilled workers are responsible for its measurement, the values obtained fall into a range, in terms of the observatory's position, of about thirty-four yards (Weldon, 1906, p. 86). One function of taking a single number and declaring it *the* latitude of the observatory, then, is to average over small errors in these various measurements. Second, statistics generates values that we wish to utilize in calculations. Weldon notes that even though it may be the case that there *is no single value* for the latitude of the observatory (due to, for example, changes over time in the position of the equator), we still may use statistics for "attributing to the latitude of the Radcliffe telescope a constancy it does not really possess" (Weldon, 1906, p. 88).

The ideal, then, in the physical sciences, is to be able to use a method which can separate these two sorts of discrepancy—which can describe all of the results thus far obtained, discarding human error in measurement *without* discarding the genuine variability in the data. Should we apply statistics to biology in precisely the same way? No, Weldon argues. The variation in the biological case is too great. "[I]f I tell you," he writes, "that Englishmen are 5 feet 7(1/2) inches high, you remember your father who is five feet ten, and your cousin who is over six feet, and you think I am talking nonsense" (Weldon, 1906, p. 94). The kind of simplifying use of statistics deployed in the physical sciences doesn't work in biology. Rather, we need a way to capture *all* of the variation in biological systems—we need to collect and preserve statistical data in its entirety, in order to come up with a complete description of our observations. He writes

> If we want to make a statement about the stature of Englishmen, we must find a way of describing our whole experience; we must find some simple way of describing our whole experience, so that we can easily remember and communicate to others how

[13] For various objective uses of chance *prior* to the introduction of quantum mechanics, see, for example, Stöltzner (2008) on the Exner school in physics, Beatty (1984) for a brief mention of the relationship between Darwin and Peirce's tychism, or Dale (1999, p. 399) for John Venn's frequentist theory of probability.

[14] "Wie werthvoll wäre es mir gewesen schon 1872 zu wissen, dass ich mit meinen Bestrebungen nicht *allein* stehe." Ernst Mach to Karl Pearson, Jul. 12, 1897, published in Thiele (1969, p. 537).

> many men of any given height we find among a thousand Englishmen. We must give up the attempt to replace our experiences by a simple average value and try to describe the whole series of results our observation has yielded. (Weldon, 1906, p. 94)

Here, I think, we see the first glimmer of a profound difference between Pearson and Weldon. Statistics in biometry, as described here, is most emphatically *not* useful for the economization of thought or the simplification of phenomena, as we saw in Pearson above. Statistics is a way of describing *all* the results which we have obtained thus far, of preserving *all* our experience, not simplifying it. Weldon brings statistics to biometry, then, to preserve diversity—very nearly the *opposite* of Pearson's motivation.

We can see this distinction between the two men confirmed elsewhere as well. An extended debate in the correspondence pages of *Nature* in 1895 and 1896 focused, in large part, on Weldon's own definition of causation. For Weldon, causation and correlation are *identical*. As the issue is reported by an incredulous E. Ray Lankester, Weldon describes Lankester as "illogical" for suggesting that we might declare the "cause" of survival in malarial regions to be due to some unknown property of the blood. "'It is,' said Prof. Weldon, 'impossible logically to separate these two correlated phenomena. The coloured skin is as much a cause of the survival of the dark man as is the germ-destroying property of his blood'" (Lankester, 1896, p. 245). For Weldon, that is, causation simply *is* correlation. And while we might later break these correlations by performing experiments or providing new data, until such tests are performed the complete causal picture of the scenario is encapsulated by the statistics. Oddly, Weldon seems to think that Hume would agree—he cites Hume's definition from the *Inquiry* of cause as constant conjunction in a later letter (Weldon, 1896, p. 294), implying that his appeal to statistical distributions would pass muster as a variety of Humean constant conjunction.

Perhaps most tellingly of all, Pearson responds to the fight between Weldon and Lankester—and sides with Lankester.

> On the second point [causation], surely Prof. Lankester is entirely in the right? It is not sufficient to show that there is a correlation between a certain frontal ratio and death-rate [in Weldon's experiments on crabs] in order to assert that the frontal ratio is a cause of death-rate. Very probably it may be, but the definition is not logically complete, or at any rate a definition of cause has been adopted which does not appear of much utility to science. (Pearson, 1896b, pp. 460–461)

The upshot of Pearson's response should be clear from our (admittedly brief) discussion of the two men's use of statistics, causation, and laws.[15] For Pearson, the sort of simple correlation described by Weldon is *too weak* a form of functional dependence to support the inference of causation. We need more data to make the description "logically complete"—to provide us with a more robust formula, something more closely resembling the functional laws of Newtonian mechanics.

While this distinction has been drawn quickly, we can see some general conclusions about the ways in which the two men approach the statistical method. For Pearson, science is a positivist enterprise aimed at the economy of thought, with statistics useful for simplification of data. Causation, then, to the extent that it remains a relevant concept at all, is cashed out in terms of laws of nature, which are precise instances of functional dependence (modeled after Newtonian mechanics). For Weldon, on the contrary, ideal science is the *complete* description of nature, and statistics is the best tool we have to capture the wide diversity of causal influences in biological cases. Causation just *is* correlation, and the purpose of experiment is to sharpen these correlations.

Most importantly, we can see that the two historical events described by the standard history do not give us any leverage on this distinction whatsoever. There's no hint of "objective" or "reified" chance in the work of either of these thinkers, as I argued in the last section—yet we still have an incredibly interesting scientific and philosophical difference between the two men which is worthy of study. What possible question might we ask that would allow us to take this distinction into account? Again, I claim that it is this: *what is the relationship between our statistical theories and the world those theories are intended to describe?*

On this axis, we can see that the two men are quite different. Pearson's positivist use of statistics as an intermediate step on the way to fully rigorized scientific knowledge entails that, for him, scientific theories are merely provisional, and, it would seem, necessarily acausal and anti-realist. Knowledge of biological processes "in the world" is meaningless for Pearson, and it is even doubtful that we would ever be able to provide sufficiently detailed theories in biology to qualify as fully rigorous law by Pearson's standards.

Weldon, on the other hand, nearly collapses the distinction between scientific theories and the corresponding processes in the world. The statistical descriptions deployed by the theory, for Weldon, *just are* descriptions of the systems' causal structure—the final aim of science for Weldon, it seems, is to construct a complete statistical picture of the world.

Approaching the case of Pearson and Weldon by considering the question of the relationship between statistical theories and biological processes, then, is incredibly fruitful. It lets us contextualize both the extensive work of the two authors in justifying the role of statistics in biological practice, and it enables us to see precisely where and why the two men disagreed when they did, on the matter of how we successfully obtain causal knowledge about a biological system.

7. Conclusion

Let me conclude a bit more speculatively. (If one is disinclined to countenance speculation, I also note that the historical claim for which I've argued above stands independently of the value of this closing idea.) For those who have been following contemporary philosophy of biology in the last decade, the novel question I posit here will not seem so novel after all. Precisely the same worry about the relationship between statistical theories and biological processes has been hotly debated, under the guise of the "causalist/statisticalist debate." On the one side, we have "causalists," who argue that natural selection and genetic drift describe causally efficacious processes (e.g., Abrams, 2009; Brandon, 1978; Hodge, 1987; Mills & Beatty, 1979; Otsuka, Turner, Allen, & Lloyd, 2011; Ramsey, 2006; Stephens, 2004). They are opposed by the "statisticalists," who claim on the contrary that these theories are merely statistical summaries of genuinely causal events at the level of the individual organism (e.g., Ariew & Ernst, 2009; Ariew & Lewontin, 2004; Krimbas, 2004; Matthen & Ariew, 2002; Walsh, 2007; Walsh, 2010; Walsh, Lewens, & Ariew, 2002).

While I lack the space to defend this claim in anything like the detail it deserves, it seems to me plausible that the question at work in the current debate is precisely that at issue between Pearson and Weldon: how are our statistical theories to relate to biological processes in the world? I do not mean to identify either Pearson or

[15] More detail on both the debate between Weldon, Pearson, and Lankester and the context of the 1906 Weldon lecture can be found in Pence (2011). Weldon's lecture is also discussed by Radick (2011). I can find no other citation or discussion of this lecture, so I have no evidence that it was read by Pearson and Weldon's contemporaries.

Weldon's views with either side in this debate, and we of course see nothing like the sophistication of today's propensity interpretations of fitness, population genetics, and so on in the 1890s. But this is certainly an interesting case—we have an instance where it seems that a historical case can be *better* understood by considering it in light of a contemporary philosophical question than by the common ways in which it is considered in the history of biology. That, I think, is a powerful argument for the integration of the history and philosophy of science.

Acknowledgments

Many thanks are due to Phil Sloan for his help throughout this project, and to Greg Radick for many helpful discussions about W.F.R. Weldon. This paper benefited from audiences at the Notre Dame HPS Graduate Workshop, at HOPOS 2012 (with special thanks to Erik Peterson), and, of course, at Integrated History and Philosophy of Science 4 (&HPS4, 2012), with special thanks to Don Howard, Theodore Arabatzis, and John Norton. An anonymous reviewer for the journal also offered helpful assistance. Finally, a talk by Greg Radick at ISHPSSB 2013 made me particularly aware of the extent to which my views on all these subjects have been informed by the work of Jon Hodge, to whom I (along with many of us in the history and philosophy of biology) owe a great debt.

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