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Parsimony and the Fisher–Wright debate

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Abstract. In the past five years, there have been a series of papers in the journal *Evolution* debating the relative significance of two theories of evolution, a neo-Fisherian and a neo-Wrightian theory, where the neo-Fisherians make explicit appeal to parsimony. My aim in this paper is to determine how we can make sense of such an appeal. One interpretation of parsimony takes it that a theory that contains fewer entities or processes, (however we demarcate these) is more parsimonious. On the account that I defend here, parsimony is a 'local' virtue. Scientists' appeals to parsimony are not necessarily an appeal to a theory's simplicity in the sense of it's positing fewer mechanisms. Rather, parsimony may be proxy for greater probability or likelihood. I argue that the neo-Fisherians appeal is best understood on this interpretation. And indeed, if we interpret parsimony as either prior probability or likelihood, then we can make better sense of Coyne et al. argument that Wright's three phase process operates relatively infrequently.

Introduction

In 1914, Sturteyvant defended the view that linkage is best explained by the hypothesis that genes are aligned on a chromosome, as opposed to a view favored by Bateson and Castle, the 'reduplication' hypothesis.[1] Summing up his rationale, he wrote that 'the chief advantage of the chromosome hypothesis of linkage… *seems to be its simplicity*.'' In retrospect, we know that Sturteyvant was correct, but in this passage, his reasoning seems spurious. What does Sturteyvant mean when he suggests that the chromosomal hypothesis is 'simpler'? Why does the greater simplicity of a hypothesis count as a reason that favors it (perhaps defeasably) over its rival? Carlson, in his discussion of Sturteyvan'ts rationale, is skeptical of the virtue of simplicity as grounds for preferring one hypothesis to another, calling such appeals merely 'aesthetic' (Carlson 1966). Many philosophers have expressed similar skepticism.

This skepticism is often connected to a more general skepticism about the simplicity of nature. Why assume that the hypothesis that admits the fewest causes, entities, or processes, (however these are demarcated, and, all else being equal) is the more likely to be true? It would seem that such a view presupposes

[1] For details on the reduplication hypothesis, see Carlson, *The Gene: A Critical History*, 1966, p. 56. (The details of the theory are not essential to understanding this example.)

an ontological thesis. According to this thesis, we are to assume that nature is in fact simple, or that the natural world is governed by simple laws, a few fundamental forces, or, as Newton suggested, 'Nature does nothing in vain, and more is in vain where less will serve' (Newton 1729). In other words, if we assume that nature takes the shortest way, in every case where we are assessing competing explanations for some set of phenomena, we ought to choose that explanation which invokes fewer rather than more causes, entities, or processes.

But such reasoning seems spurious. If one understands simplicity, or, parsimony[2] as economy of process, it is tempting to dismiss appeals to parsimony by scientists, and especially appeals made by biologists. There seems to be no principled reason why one ought to assume that the biological world is simple, or that an explanation of that world which makes appeal to fewer entities or processes is better. Indeed, in the biological realm, there seem to be good reasons not to expect that nature will take 'shortest way.' Jacob (1977) and Gould and Lewontin (1979) have taught us well that 'nature is a tinkerer'; phylogenetic inertia, developmental constraints, chance, and the possibility of multiple solutions to the same adaptive problems are all at play in yielding extant morphology, distributions of traits in populations, and biogeographical distributions of species. At best, appeal to simplicity in this global sense is a heuristic virtue, insofar as simpler hypotheses are perhaps easier to test, on a some contruals of simplicity. But the parsimony of some thesis in this respect does not lend it greater credibility. The global ontological thesis seems hardly warranted in the case of biology. Sturteyvant is clearly unwarranted in taking simplicity *per se* as a reason to prefer the chromosomal theory.

However, is this what Sturteyvant meant to say when he argued that the chief virtue of the chromosomal theory its simplicity? In Sturteyvant's view, according to the alternative, 'reduplication' hypothesis:

> We are forced to assume an enormously complex series of cell divisions, many of them differential, proceeding with mathematical regularity and precision, but in a manner for which direct observation furnishes no basis. It seems to me that it is not desirable to assume such a complex series of events unless we have extremely strong reasons for doing so. I can see no sound reason for adopting the reduplication hypothesis. It *apparently rests on two discreditable hypotheses: somatic segregation, and the occurrence of members of the* 3:1, 7:1, 15:1, *etc., series of gametic ratios in more cases than would be expected from a chance distribution…*

[2] Twardy (personal communication) raises the question of whether simplicity and parsimony are one and the same virtue. Though they are often used interchangably, my claim in this paper is that parsimony, or rather, what scientists often mean by parsimony, is not simplicity, in the sense of fewer parameters in one's model or fewer mechanisms or processes invoked. So, I agree with Twardy that the two virtues may be pulled apart.

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> … the chief advantage of the chromosome hypothesis of linkage… seems to be its simplicity. In addition, it *appeals to a known mechanism*… It explains everything that any of the forms of the reduplication hypothesis does and in addition *offers a simple mechanical explanation for the fact that 'secondary series' are always smaller than Trow's special hypothesis calls for them to be*. On the reduplication hypothesis this fact must merely be accepted, for, I think, it can not be explained (Sturteyvant, in Carlson 1966).

Once we examine Sturteyvant's argument in closer detail, we can see that he is not suggesting that we ought to prefer the chromosomal hypothesis solely on the grounds that it has a greater economy of process. Moreover, the argument does not appear so obviously misguided. Indeed, once one examines Sturteyvant's reasoning behind the claim that the 'simpler' theory is preferable, the argument begins to look quite persuasive. Sturteyvant claims, first, that on the alternative view, we have to posit events that we have no independent evidence for. Second, he claims that the alternative view 'rests on' or presupposes hypotheses that are 'discreditable.' Third, his preferred chromosomal hypothesis makes use of a mechanism whose operation is well understood. Fourth and finally, there are phenomena that the alternative hypothesis cannot explain and the chromosomal hypothesis can. Thus, in Sturteyvant's view, we ought to prefer the chromosomal hypothesis because it operates via a known mechanism, does not presuppose questionable hypotheses, and can explain phenomena that the alternative hypothesis leaves mysterious. In other words, the chromosomal hypothesis is 'simpler,' by which he means, makes better sense of the evidence to hand.

I wish to suggest that appeals to simplicity or parsimony in the biological context are often shorthand for more elaborate and well-grounded rationales, once one unpacks the argument carefully. This is the case in the paper by Coyne et al. where they claim that mass selection is a more parsimonious hypothesis than Wright's three phase shifting balance process. Thus, my interpretation is at odds with that of Skipper, who argues (Skipper 2002) that we ought to interpret the neo-Fisherian's appeals to parsimony in the same vein as I originally interpreted Sturteyvant above. In other words, Skipper argues that by 'parsimony', the neo-Fisherians meant 'economy of process.' His summary of the neo-Fisherian position is as follows, 'If the evolution of populations can be explained adequately via a theory that postulates a small economy of entities and processes, there is no need to invoke a theory with a larger economy of entities and processes' (p. 360). Skipper contends that this view is an instance of a naïve appeal to parsimony, one which sacrifices realism and precision for generality. The neo-Fisherians, he argues, ascribe to a 'Newtonian' ideal, according to which there is one theory (what Skipper calls Fisher's 'large size theory'), that explains all of the phenomena in some domain. 'However,' Skipper warns us, 'considerable care must be taken in drawing a close connection between explanatory adequacy, generality, and

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parsimony because explanatory adequacy need not be so closely connected with generality' (p. 361).

I agree with Skipper that we should certainly take care in assuming that there is a close connection between explanatory adequacy, generality and parsimony. In other words, a more explanatory theory is not necessarily a more general one (though, this will depend in part upon the request for explanation, or, the pragmatic dimensions of the why-question). Moreover, I agree heartily with Skipper that the theory which posits fewer mechanisms, entities, or processes (however we count these), all else being equal, is not necessarily more likely to be true. However, this is not what the neo-Fisherians were suggesting. Just as in the case of the example of Sturteyvant's argument for the chromosomal theory, once we examine the neo-Fisherian's appeal to parsimony more closely, it is not so obviously misguided. In claiming that mass selection is 'more parsimonious,' Coyne et al. (1997) are claiming not that it is more general or more simple in the sense of invoking fewer entities or processes. Rather, by 'more parsimonious' they mean that mass selection operates via a known mechanism which is empirically well-established, does not depend upon presuppositions that are questionable, and finally, that the evidence tells against the alternative hypothesized mechanism as operating very frequently.

Moreover, their argument is not that the Fisherian model is more explanatory simply because it is more general. In those cases where the Wrightian three phase process is occurring, the Wrightian model would certainly be the best explanation. However, they claim that there are good empirical and theoretical grounds for these cases being rather rare. And thus, we should expect more requests for explanation of this or that adaptation to be satisfied by the Fisherian model. In other words, it does not explain more because it is more general; rather it is more general because it explains more.

Before I defend this thesis, I wish to make clear what I am not attempting in this paper. My aim is not to provide an overview of the debate between the neo-Wrightians and the neo-Fisherians. Rather, my aim is to clarify what is meant by 'parsimony' by Coyne et al. and in the process, to defend an account of parsimony that takes it to be a genuinely epistemic, and not merely aesthetic or pragmatic virtue. I take my cue from Sober, in a paper titled 'Let's Razor Ockham's Razor' (1990) and *Reconstructing the Past* (1988). He claims that by giving close attention the specific context in which appeals to parsimony are made by scientists, one may come to understand that these appeals may sometimes be understood as appeals to either higher prior probabilities or higher likelihood. Sober's model for unpacking appeals to simplicity employs Bayes' Theorem.[3]

[3] The model is 'Bayesian' in the sense that it uses Bayes' theorem, an uncontroversial theorem in the probability calculus. It does not commit one to a particular view on reconditionialization, subjective probabilities, etc.. I.e., one does not need to subscribe to Bayesianism (whatever that means; reasonable people disagree) in order see why Bayes's rule is a useful way to elucidate scientific inference in cases such as these involving competing hypotheses. I wish to emphasize that I am not committed here to any theses about whether or not probabilities are best understood as degrees of belief.

Fisher vs. Wright

R.A. Fisher and Sewall Wright were two theoretical population geneticists working in the early twentieth century who placed different emphasis on different factors in the evolutionary process. According to Wright, selection alone is not sufficient to generate adaptive novelty. By 'novelty' here, I mean to emphasize that according to Wright, selection alone could not suffice for major adaptive changes due to radical changes in the genetic constitution of a population. Wright did not deny that selection could yield adaptative evolution. However, he thought that there must be a 'balance' of 'forces' at play in evolution (selection, drift, etc.), or a population would eventually become 'stuck' atop adaptive peaks. This is because selection acts on genes in combination, and, according to Wright, there is pervasive epistasis for fitness (or, breaking up such gene combinations may be maladaptive). Unless a population is subdivided, novel adaptive gene combinations will not come about, and populations of organisms may become 'stuck' atop suboptimal peaks in the 'adaptive landscape.'

The adaptive landscape is a model of the relative fitness of different gene combinations, with the horizontal axes representing different genotypes, and the vertical axis representing relative fitness. For Wright, the problem of how to move from suboptimal to higher 'adaptive peaks' in the field of gene combinations was *the* key problem that theoretical biologists must solve, for the reasons I stated above. Wright wrote, 'The problem of evolution as I see it is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field' (1932). In other words, Wright's question was, 'How could one shift from one "balanced" gene combination to another, across what must be deep valleys of low fitness?' According to Wright, the most effective means of traversing such peaks is via a three phase 'shifting balance' process of isolation of small subpopulations, intrademic (within group) and interdemic (between group) selection. Wright believed this three phase process to be the main means of generating adaptation, and perhaps also, many cases of speciation.

If the reader has already begun to worry about the epistemic or ontological status of adaptive landscapes, then she (or he) is not alone. Indeed, there has been a flurry of papers in the evolution literature recently about the status and shape of the 'adaptive landscape.'[4] Philosophers like Ruse (1993) have expressed skepticism about the way in which the adaptive landscape metaphor misleads scientists. Fisher (letter to Wright, in Provine 1986 ■Au: AQ: Citation Provine (1986) is not in list please add to list.■) was one of the first to raise concerns about the landscape. Was it indeed three dimensional? Or, as we consider a greater and greater number of genes in combination, could the landscape that describes relative fitness of different genotypes become multidimensional? Is the landscape 'rugged' in the way Wright suggested? Arethe

[4] See especially, Gavrilets (1996, 1997).

'peaks' static, or could there be 'ridges' arising between peaks over time, either due to assortative mating, or changes in the environment, such that epistasis for fitness is not necessarily a barrier to adaptive evolution and genuine evolutionary novelty? These are exactly the worries that Coyne et al. the modern neo-Fisherians have raised. Some might argue that one is stacking the deck against Wright by arguing that by adopting the adaptive landscape metaphor, his model makes presuppositions which are questionable. Surely we should first look at the empirical evidence for or against those presuppositions? Indeed, this is what Coyne et al. (1997) do at length.

As mentioned above, Fisher did not agree with Wright's presuppositions about either the extent of genetic epistasis for fitness, nor the metaphorical adaptive landscape which depends upon this assumption. Fisher suspected that the landscape was not three dimensional, but rather multidimensional, such that adaptive evolution could occur along any of several trajectories of gene frequency change. Epistasis, according to Fisher, was not so pervasive that populations must become 'stuck' atop adaptive peaks. Moreover, Fisher pointed out that while populations may well be structured in nature, migration every generation between groups makes questionable the effectiveness of drift as a way isolating novel gene combinations and thus of 'peak-shifting'. This is not to say that Fisher thought that drift did not operate in evolution. Rather, Fisher thought it unlikely that drift played an important role in *adaptive* evolution. Fisher also infamously believed that one could treat effective population size as the entire breeding population, which he assumed to be quite large (on the order of infinity!). And since selection is more effective than drift in populations of large size (where $4Ns > 1$ (N = population size, s = selection coefficient), selection must be the main factor in adaptive evolution.

In 1997, Coyne et al. assessed the empirical and theoretical support for the Wrightian vs. Fisherian model in the journal *Evolution*. They concluded that there was relatively little evidence that *Wright's particular three-phase process* plays a significant role in the evolution of adaptations. They were not questioning the fact of Wright's influence and contributions, or that one or another phase of the process might be important in adaptive change (e.g. group selection), *only* that the three phase shifting balance process in particular was a major mode of adaptive change. Moreover, they were not suggesting (with Fisher), that the effective population size of most populations was the entire breeding population, or that this was on the order of infinity. Rather, they drew the more modest conclusion that selection ought to be preferred as the more 'parsimonious' explanation for adaptation over the three phase shifting balance model. In reply, Wade and Goodnight defend Wright, and attacked the neo-Fisherians for their naïve commitment to parsimony as a theoretical virtue. Lewontin has argued that biology is an 'epistemologists' paradise' exactly because of arguments of this sort; we have two theories, both seemingly able to account for the same phenomena: which do we choose?

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Parsimony: not what you thought it was

At first glance, it may seem plausible that when Coyne et al. claim that the Fisherian view is more parsimonious, they mean that it has the greatest economy of process. Fisher's mass selection is 'less complicated' than Wright's three phase process because one mechanism (selection) is operating as opposed to four or five, depending upon how you count (isolation, drift, intra- and interdemic selection, migration). I wish to counter this interpretation. The view that they defend is not that Fisher's theory is preferable because it involves fewer processes. Rather, it is that the Fisherian process has a higher prior and likelihood than Wright's three phase process. More specifically, their claim is that given the body of evidence at hand, the chance of shifting balance playing a significant role in adaptive evolution is low relative to the alternative, because the conditions required for it to operate are not very likely to be met in nature.

In short, the neo-Fisherian model

*Operates via known mechanisms

*Does not depend on questionable presuppositions

[i.e. uses presuppositions we accord a higher prior, hence has a higher prior]

*Fits the data better than Wright.

[Hence higher likelihood.] In short, it has a higher likelihood and prior than the alternative shifting balance theory.

The Bayesian way

In a (1990) essay, and again in his (1988) book, Elliot Sober gives careful scrutiny to the notion of parsimony.[5] Below, I will sketch Sober's analysis of parsimony and suggest that this is one useful way to understand what is meant by 'parsimony' in the Fisher–Wright debate. As Sober himself points out, one need not subscribe to Bayesianism in order to see the use of Bayes's rule as one way of making sense of how scientists revise their views.

First, some terminological distinctions. Sober points out that Bayes's theorem provides a useful way of characterizing the considerations that might affect one's assessment of a hypothesis' plausibility. The theorem says that the conditional probability of some hypothesis H ($\mathrm{Pr}(H/e)$) is:

$$\mathrm{Pr}(e/H)\mathrm{Pr}(H)]/\mathrm{Pr}(e)$$

So, when comparing two hypotheses, *H1* and *H2*, their posterior probability is influenced by two factors: their priors and their likelihoods:

$$\text{Or}, \mathrm{Pr}(H1/e) > \mathrm{Pr}(H2/e) \text{ iff } \mathrm{Pr}(e/H1)\mathrm{Pr}(H1) > \mathrm{P}(e/H2)\mathrm{P}(H2)$$

What does all this mean?

[5] Though, more recently, (Sober and Wilson 1998) Sober and Wilson demarcate several different forms of appeal to parsimony by Williams (1966), ■Au: AQ: Citation Williams (1966) is not in list please add to list.■ not all of which are epistemic.

$Pr(H1)$ is the prior probability of H. $Pr(e/H1)$ is $H1$'s likelihood. What is likelihood? For one theory to have a higher likelihood, roughly, the evidence will be more likely obtain than on the alternative theory. Likelihood is not the same, however, as explanatory power. For example, if $H1$ is 'rain tomorrow' and e is 'today's barometric reading is 29 torr,' then, $H1$ would have a high likelihood relative to the evidence, but it would not explain the evidence.

One way of thinking about what scientists do when they're assessing the explanatoriness of two competing hypotheses is that they're evaluating their relative likelihoods, and/or antecedent plausibility. According to Sober, the appeal to parsimony in such contexts are not necessarily appeals to greater economy of process (though he does not rule out that they could be, given certain background assumptions and in certain contexts). Philosophers, he says, have 'hypostatized' parsimony. In other words, they have assumed that appeals to parsimony mean the same thing in every context. Instead, he suggests that when a scientist appeals to parsimony, his or her appeal has a distinct meaning relative to a specific context and specific background assumptions. Appeals to parsimony may thus be appeals to a theory's greater plausibility, given either its greater likelihood, and prior probability, or a combination of both. In his words, 'parsimony is a virtue that does not speak its name.' So, appeals to parsimony in the assessment of competing hypotheses, may in fact be appeals to something 'more fundamental' – namely, the greater likelihood, or prior probability of some theory, relative to the evidence and our background beliefs. There is no reason to adopt Occam's razor, in the sense of 'fewest entities and/or processes' as a general principle for all of science all of the time. Rather, the nature and relevance of considerations of parsimony are context dependent. In Sober's terms, parsimony is not a 'global,' but a 'local,' virtue of theories.

Sober's argument for this claim comes in two stages. First, he notes that if we understand hypothesis evaluation using Bayesian framework, appeals to parsimony make better sense of these arguments if we understand them in terms of likelihoods and priors. Second, he argues that several cases of scientist's appeal to parsimony are best interpreted in this way. Let's consider an example Sober uses to illustrate his point. Williams argued that Wright's three phase shifting balance process is not very likely; he then extends this argument to argue that group-level selection in general is unlikely (1966, pp. 111–117).

Sober rationally reconstructs Williams' argument along Bayesian lines.[6] Let us designate group level selection hypotheses as HG, and individual level selection hypotheses as HI. First, Williams concedes that the phenomena (say, a herd of fleet deer) could be equally well be a product of group-level selection as individual-level selection. I.e. they have equal likelihoods.

[6] As my purposes here are expository, it is not relevant to this discussion whether Sober's reconstruction is faithful to the text. Indeed, Williams offers at least three (Sober and Wilson 1998) different rationales for the greater parsimony of lower-level selection hypotheses. The argument that moves from a critique of Wright's model to a critique of group selection is only one of several.

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$$\Pr(e/\mathrm{HG}) = \mathrm{P}(e/\mathrm{HI})$$

What he must mean, according to Sober, when he claims that lower level selection hypotheses are more parsimonious is that they have different priors, or $\Pr(\mathrm{HG}/e) < \Pr(\mathrm{HI}/e)$.

Williams argues that group selection requires a number of restrictive assumptions about population structure: there must be sufficient variation among groups, and rates of colonization and extinction must be sufficiently high. These facts, (which have since been contested) are the reasons he gives for the claim that lower level selection hypotheses are more parsimonious. I.e. they have higher priors, in light of the evidence concerning variation among groups and rates of colonization. According to Sober, Williams is not arguing that group selection never happens, he's simply suggesting that it's highly implausible that it does. According to Williams, the conditions for the possibility of group selection rarely hold, so:

$$\Pr(\mathrm{HI}/e) > \Pr(\mathrm{HG}/e) \text{ because } \Pr(\mathrm{HI} > \Pr(\mathrm{HG})$$

So, using the Bayesian framework, we can understand Williams's claims for the greater parsimoniousness of individual selection hypotheses as claims about the prior probability of individual selection being higher; where, prior probability here is simply understood as the probability, given our background beliefs about what conditions obtain in nature and which conditions are required for group vs. individual selection.

My (and Sober's) point here is not that Williams was correct.[7] Rather, the point is that this is one way of reconstructing scientists' appeals to parsimony that does not make them appear to be simple-minded (some humor). Sometimes, of course, scientists make flawed arguments, and appeals to parsimony can be ad hoc justifications. Several of Williams arguments do fall under this category. However, his argument against Wright follows the same structure as that above, and the very same rationale is offered by Coyne et al. except with the advantage of 50 years of theoretical and empirical work on shifting balance. Ultimately, whether or not a theory is understood to be more or less parsimonious may be understood as an argument over whether it has a higher likelihood, or a higher prior probability, or a combination of the two. In this case, the claim is simply that 'prior probability' is, in the Williams' context, a matter of plausibility of the conditions required for some process to occur. One might argue that it is dangerous to introduce formal tools when they simply cannot be defined suitably in these informal contexts, and that Sober does this to his detriment. It would be better, the objection goes, if Sober admitted that the Williams is not talking about probabilities *per se* but rather *judgments* of plausibility or truth. However, this is to miss the point of the exercize. Sober's claim is not that in fact scientists assign quantitative values to prior proba-

[7] Indeed, Sober has offered considerable argument to the contrary, see Sober and Wilson 1999.

bilities to this or that hypothesis, or that they in fact conditionalize using a Bayesian model. Rather, the point is that we may use a Bayesian framework to unpack the reasoning at work in judgments regarding competing hypotheses. And, if we do so, then appeals to parsimony do not seem to be merely matters of subjective opinion. Instead, they are judgments of plausibility based upon empirical data and background theory.

So, now let's turn to an analysis of the neo-Fisherians' argument and see whether this approach to parsimony can be helpful. When Coyne et al. say that Fisher's theory is more parsimonious than Wright's, what could they mean? First, they say that the presuppositions that Wright makes about the problem of adaptive evolution, those very ones which make shifting balance seem to provide a solution, are false. Second, they argue that the conditions required for all three phases in Wright's three phase process to operate in conjunction are not very often met in nature. Third, they claim that there is ample evidence that selection has generated adaptation, and, the conditions required for it to operate are not at all restrictive (All one requires is additive genetic variance, which they claim is amply available, and where $4Ns > 1$, selection must be the main factor in adaptive evolution).

Coyne et al.'s parsimony argument is not that Fisher's theory is preferable insofar as it invokes fewer mechanisms or processes. Rather, it is that the conditions required for the specific combination of mechanisms that makes possible Wright's model are unlikely to obtain. They are not suggesting that populations are not often subdivided, that drift plays no role in evolution, or that epistatic interactions between genes never occur. Rather, they are suggesting that the specific 'concatenation' of isolation, drift, intra- and interdemic selection required by shifting balance does not often obtain, and so it is unlikely that Wright's model explains many (if any) adaptations in nature.

Coyne et al.'s argument is not simply an argument against the plausibility of shifting balance. It is additionally a prudential argument. In other words, given the implausibility of shifting balance, they claim that it is prudential to adopt selection as our working hypothesis, should we come across some apparent adaptation in our investigations. Ample empirical and theoretical evidence exists in favor of selection, so there is no question that it occurs. In contrast, while there is some evidence for at least two phases of Wright's three-phase process, the evidence in support of all three phases occurring in sequence is rather slim, or so they claim.

In my view, this is an instance where Sober's defense of a 'local' notion of parsimony coincides with the actual practice of appeals to parsimony in the sciences.[8]

[8] Note Coyne's comments (personal communication). He writes: I think you are correct in your interpretation… We say several times, I believe, that the SBT requires the concatentaion of improbable circumstances AND that it is also untestable in many cases.

Why Wright might not have been right

Now, I'll discuss briefly some of the key points of Coyne et al.'s argument, and then turn to issues of prudence in choice of research program in conclusion. Their argument comes in three stages: first, they question the presuppositions that led Wright to formulate his model. According to Coyne et al. the problem as posed by Wright, of finding a 'trial and error' mechanism 'by which the species may find its way from lower to higher peaks' was confused. Second, they argue that each stage of the Shifting Balance individually is implausible, for both empirical and theoretical reasons. Third, they claim that the conditions required for all three stages to follow one upon another are restrictive and unlikely to hold in nature.

What was the purported problem that Wright set out to solve? Wright was motivated to develop the shifting balance theory in reply to what he saw as a serious problem for adaptive evolution: the problem of escaping highly adaptive 'peaks' in the field of gene combinations. Wright had been a student of Castle at the Bussey institute; where the research program was focused on the inheritance of traits due to multiple genes in interaction. Most of his graduate work and his first job for the USDA were concerned with the inheritance of complex traits, such as coat color, or milk yield. So, Wright was impressed with the fact that many traits were influenced by multiple genetic factors. Moreover, he was impressed with biogeographical work that seemed to show that the differences between species did not appear to be adaptive (Provine 1985 ■Au: AQ: Citation Provine (1985) is not in list please add to list.■). He concluded from these observations that major transitions between species could not possibly be the result of selection alone. The view that selection alone was not sufficient to generate novel species is an old argument in biology and one which found its way into textbooks popular at the time Wright began his studies in biology (see, for instance, Kellogg 1903, one of the first texts Wright read in his first courses in biology).

According to Wright, complex traits, in particular, adaptive traits, are most likely the result of genes that are more or less fit in combination – i.e. that there is pervasive epistasis for fitness. If there is pervasive epistasis for fitness, then it is not possible for highly adaptive gene combinations to be broken up without a population losing fitness. So, on this view, major adaptive changes in a population require that a population traverse an 'adaptive valley' via drift. Dobzhansky gives a vivid description of the adaptive landscape as follows:

> The field of gene combinations may, then, be visualized most simply in a form of a topographical map, in which the contours symbolize the adaptive values of various combinations. Groups of related combinations of genes, which make the organisms that possess them able to occupy certain ecological niches, are then, represented by the adaptive peaks situated in different parts of the field. The unfavorable combinations of

> genes which make their carriers unfit to live in any existing environment are represented by the 'adaptive valleys' which lie between the peaks (Dobzhansky 1951, pp. 8–9 ■Au: AQ: Citation Dobzhansky (1951) is not in list please add to list.■).

According to Wright, it is necessary for a population's complex of genes to be altered by sampling, or drift, in order for it to move to a more highly adapted state. Since adaptation is a product of genes in combination, 'novel gene combinations' are necessary for novel adaptations. If simply under the control of selection, a species will ultimately come to rest on a suboptimal peak. Notice that the above argument is an inference from an number of observations to a rather wide-ranging conclusion about adaptation and evolution as a whole.

Here's Wright's statement of the problem that he sought to solve with the shifting balance theory:

> The problem of evolution as I see it is that of a mechanism by which the species may continually find its way from lower to higher peaks. … in order that this may occur, there must be some trial and error mechanism on a grand scale by which the species may explore the regions surrounding the small portion of the field which it occupies. To evolve, the species must not be under the strict control of selection (Wright 1932, pp. 163–164 ■Au: AQ: Citation Wright (1932) is not in list please add to list.■).

Wright's trial and error mechanism was drawn directly from the breeding program of the Duchess Shorthorn cattle, which he spent five years studying at the USDA. In order to improve the cattle stock, the following procedure was employed:

> The first step in any case should be selection of a vigorous foundation, approaching as closely as possible to the desired type. With such a foundation stock, one might practice the most intensive inbreeding in a large number of distinct lines, knowing that most lines would inevitably deteriorate greatly, but trusting that a few would be found in which desirable qualities would become fixed, and in which the deterioration in any vital respect would be so slight that they could be maintained successfully. By crossing such lines which have withstood this acid test of inbreeding, one might reasonably hope to recover more than the original vigor and retain those characters which had been fixed… This method, an alternation of intensive inbreeding with selection and crossbreeding of the few successful lines must naturally be done on a large scale… It is an important method and has some parallel in the general history of the breeds. Many of the early breeders practiced [it]. (Wright (1923b) ■Au: AQ: Cited reference Wright (1923b) is not in list please add to list.■, in Provine (1986), p. 46.)

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Here, in a 1923 discussion of cattle breeding, Wright gave a preliminary statement of what would become his three phase 'shifting balance' model of evolution:

> Phase I: Genetic drift causes local populations to temporarily lose fitness, shifting across adaptive valleys toward new, higher adaptive peaks.

> Phase II: Selection within demes places them atop new peaks.

> Phase III: Different adaptive peaks compete with one another, causing fitter peaks to spread through the entire population. Or, migration out from the most adaptive deme leads to the spread of the most adaptive.

In sum, given the pervasiveness of epistasis for fitness, which Wright witnessed in his experimental and USDA work, if strictly under the control of selection, a population could not make significant adaptive changes. (Note here that he's moving from the case of multi-genic traits in mammals to all traits in all species.) So, in order to escape suboptimal gene combinations, a population needs to be broken up into small subpopulations, which, after a period of isolation (during which drift and intrademic selection enable a population to 'escape' undesirable gene combinations), can then come into contact and compete.

Coyne et al. question the problem of evolution as set by Wright. Or, they question Wright's rationale as to why one must invoke explanations other than selection for adaptive evolution. Wright supposed that mass selection is too slow to explain diversity, that mutation is insufficient as source of variation, that cost of substitutions constrains the rate of adaptation, and that phenotypic change involves the appearance of maladaptive intermediates. In other words, he thought that the Darwinian paradigm, according to which selection acts in relatively large, panmictic populations, with mutations as the 'raw material', was not adequate to account for complex adaptations and the diversity of life. Some new story needed to be told that will explain how it is possible that new, more adaptive, gene combinations can come about.

Coyne et al. deny that all of these are legitimate worries. I'll focus on the last and one of the most longstanding objections: that phenotypic change involves the appearance of maladaptive intermediates, since this is what fueled Wright's idea of the adaptive landscape, and what ultimately lead to his shifting balance idea.

Wright's claim is that given the extent of epistatic interaction for fitness, we require some mechanism to explain how it is that a population can move from one highly adapted gene combination to another more adaptive combination. Crow (1990) ■Au: AQ: Citation Crow (1990) is not in list please add to list.■ describes the situation using a simple haploid model as follows:

> Suppose alleles a and b go well together, as do A and B, but A and b and a and B do not. Suppose further that the AB combination is better

> than the ab. If a population has a high frequency of a and b alleles it will not move to a state in which A and B are common, because to do so will produce a large number of inferior Ab and aB recombinants. We can think of this as a three-dimensional graph in which the two abscissas are the frequencies of the Ab and Ba alleles and the ordinate is the mean fitness of a population with this frequency combination. The surface will be saddle shaped, with a low peak where ab is common and a high one where AB is common. A population near the lower peak cannot get to the higher one without crossing a valley of lower fitness. (Crow 1990, p. 75)

Coyne et al. reply to this argument as follows. Wright imagines that the adaptive landscape is static, or, that the mean fitness of a population will be constant. However, there is good reason to think that this is false. First, a population may shift into an adaptive valley for any number of reasons other than drift – change in environment, for instance. A change in environment or a mutational change could change the mean fitness of a population, such that a population originally on a peak may come to rest on a valley, and simple selection could pull it up to a new peak. Moreover, ‘ridges’ can arise between adaptive peaks for one of several reasons. The fitness of a particular gene combination changes due to its relative frequency in a population, or because of the relative numbers of other individuals in the same environment. This phenomenon, that the fitness of a particular trait can change because of the relative frequency of individuals possessing this trait, is known as frequency dependence. Thus, particular genotypic combinations are not necessarily ‘stuck’ atop adaptive peaks. Indeed, phenomena like frequency dependence challenge the whole idea of a three dimensional landscape. If different individuals are more or less fit relative to the number other kinds of individuals in their cohort, then it does not make sense to speak of specific genotypes having specific fixed fitnesses. Not only will the adaptive landscape will be constantly changing because of the selection coefficient of some trait will change with frequency dependence, but if we consider the many dimensions in which we can measure an individual’s (or a population’s!) fitness, there are multiple ridges that an individual (or population) may traverse via selection. So, Coyne et al.’s first argument against Wright is that the problem of evolution as he describes it is not the problem he imagined.

Their second line of attack is to suggest that individually and in combination, each phase of the shifting balance process is unlikely to occur in nature, on both theoretical and empirical grounds. It is true that the chance of peak shifting by drift increases with decrease in population size. However, the chances of staying atop an adaptive peak for very small populations is very small. In other words, the smaller one’s reserve of variation, or, what is the same, the smaller the population size, the more likely that a population will drift into a valley or simply die out than that it will drift toward the vicinity of a new, more adaptive peak. This renders phase I implausible.

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Coyne et al. further point out that many processes besides drift that can move populations to different peaks (phase II). As mentioned above, local peaks could be converted to ridgesa, allowing adaptive advance by selection. And, of course, every case of natural selection is just a case of phase II.

Second, with respect to Phase III: peak shifts may occur only in sparsely populated parts of a species' range (i.e. the subpopulations would have to be so isolated as to have none or very little incoming variation); so it's difficult to see how novel peaks could spread, or, how more highly adapted groups could come into competition with other groups. Third, with respect to empirical evidence: they claim that for each example canvassed, phase I is infrequent, and only one known case shows convincing evidence for phase III. In sum, they suggest that theory shows that shifting balance can sometimes be an efficient mechanism in adaptive evolution, but only under restrictive conditions. And, empirical evidence suggests that there are very few cases, if any, where all three phases in sequence have actually occurred. Fisherian mass selection process is thus, they claim, ''more parsimonious'' than the shifting balance process.

Conclusions

What scientists mean by parsimony will vary relative to context, and, these different senses of parsimony can yield more or less epistemically sound grounds for adopting one or another theory or research program. Further, parsimony in the context of the Wright–Fisher debate is *not* greater simplicity in the sense of economy of process.[9] Rather, parsimony in this case amounts to plausibility, in this case, there is substantial evidence that Wright's presuppositions are false, and that his mechanism operates rarely in nature. In light of this interpretation of parsimony, I think that we can understand why Coyne et al. think we ought to be skeptical of the significance of shifting balance. They are offering an argument from what one might call prudence. Or, perhaps better, given the empirical evidence, we ought to be cautious as to whether shifting balance has played an important role in the evolutionary process. Caution or prudence are not words commonly used in scientific contexts; more often, scientist will appeal to a vague notion such as 'parsimony', which inevitably leads to confusion and conflation.

This is not to deny that there are many mechanisms at work in nature. The claim is not that there is no population structure, drift, or epistatic interactions between genes. All they are suggesting is that unless and until we are called upon to do otherwise, it's prudent to adopt the Fisherian model in attempting

[9] Though, of course, it is an open question what exactly we mean by 'economy of process'. Does the more economical process contain fewest kinds, fewest new kinds, or simply the fewest number of entities or processes? (Thanks to Marc Lange for this comment).

to explain some adaptation. The authors of these papers agree that there are a multiplicity of mechanisms at work in evolution. They agree that selection, drift, epistasis, etc. are all important factors in the process of evolution. What they disagree about is how often it is the case that one particular combination of these mechanisms obtains: namely, Wright's three phase shifting balance process.

Were Coyne et al. conflating explanatory power, generality and parsimony? No. Adopting Coyne et al.'s view does not require of us that we rule out drift, epistasis, or population structure as important factors in explaining evolutionary pattern or processes. We may still be pluralists about the many mechanisms and processes at work in generating evolutionary change. All it requires is being suspicious of one particular combination of these factors. Coyne et al. are not suggesting that mass selection is a *sufficient* explanation for adaptation, only that it is the a very likely candidate, barring evidence for isolation, drift, etc.

A nice analogy to this suggestion comes from Mayr's (and later, Sober's) discussion of the adapationist program. We can separate the question of whether we ought to adopt adaptationism as a research program from the question of whether natural selection is sufficient to explain any or all particular adaptations. Likewise, we may separate the question of whether we ought to adopt a Wrightian research program from whether in fact Wright's model explains any particular adaptation. There may be good reasons to reject the research program, but this is not to say that Wright's three phase process never occurs.

The kind of arguments I think that one might sensibly offer in support of adopting a research program will be very different from those offered in support of invoking a particular mechanism to explain some particular phenomena. Plausibility arguments of the sort I've just discussed will figure in the former discussions, but not in the latter. For any particular case, however, if the evidence isn't decisive, it's not clear that we much adopt one or the other. People can maintain two or three alternatives. Feynman has written that all the good physicists he knew kept about 3 models in their head all the time, and interpreted new evidence on each of them. Analogously, keeping in mind the roles of drift, mutation, migration, and various forms of selection (frequency dependent, intra- and inter-demic) is a good strategy. I think that we may consistently say that Fisherian mass selection is an important explanation for adaptation, without also committing ourselves to the view that mass selection is a sufficient explanation – or, that it suffices to explain every particular adaptation.

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