DARWINIAN THOUGHT EXPERIMENTS: A FUNCTION FOR JUST-SO STORIES

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IN the conclusion of the sixth [1872] edition of *On the Origin of Species*, Charles Darwin entered the following apologia:

> As a record of a former state of things, I have retained in the foregoing paragraphs...several sentences which imply that naturalists believe in the separate creation of each species; and I have been much censured for having thus expressed myself. But undoubtedly this was the general belief when the first edition of the present work appeared. ...Now things are wholly changed, and almost every naturalist admits the great principle of evolution. [*Origin* 751 (206.1.1-6)][1]

The unstated implication is that the *Origin* had a good deal to do with this change. It *is* a convincing work. Much has been written in recent years about how it carries conviction—its argument patterns and their relation to the philosophy of science both of Darwin's time and place and our own. Surprisingly little has been said, however, about a truly pervasive aspect of the argument of the *Origin*, an aspect which lies at the heart of its power to convince: its use of thought experiments.

The following discussion develops the concept of "Darwinian thought experiments" in three stages.

1. After some preliminary setting of context, it examines a crucial use of "imaginary illustrations" in *On the Origin of Species* and a critique of its central argument, by Fleeming Jenkin, which nonetheless also relies entirely on imaginary examples to make its point. Jenkin's argument nevertheless deeply impressed Darwin and our task is to better understand why. It is argued that this bit of historical dialectic reveals something about *the role thought experiments can play in the evaluation of a theory*.

2. From this historical case I derive a functional description of thought experiments in evolutionary biology—Darwinian Thought Experiments. I claim that thought experiments are intended as *tests*, not of the truth of the statements comprising the theory, but of the *explanatory potential* of the theory. They are designed either to display, or to challenge, a theory's *ability* to explain the full range of phenomena it claims for its domain. It is because they are designed to evaluate a theory's explanatory potential,

rather than its truth, that these "figments of the imagination" are able to perform a legitimate role in science.

3. Finally, I suggest that at least *some* of the imaginary narratives one finds throughout the history of evolutionary biology—sometimes disparagingly dubbed *just so stories*—are Darwinian Thought Experiments, and as such have an important, if limited, role to play in evolutionary biology at various stages of theory development and theory extension.

I. Darwin's Thought Experiments

The Lyellian Context.

Charles Lyell defined geology as "the science which investigates the successive changes that have taken place in the organic and inorganic kingdoms of nature; it inquires into the cause of these changes, and the influence which they have exerted in modifying the surface and external structure of our planet" [Lyell 1831 1]. In doing so, he placed causal inquiry into the history of life at the center of his science. His methodological *actualism* limited, on epistemological grounds, the search for causes of past geological events to processes now in operation. His *gradualism* permitted the use of our understanding of such processes in explanations of large scale changes. It is then not surprising that the second volume of the *Principles of Geology*—which Charles Darwin received when the Beagle anchored in Montevideo in November of 1832[2]—is devoted to what is known about existing species which might be relevant to understanding their history.

The fossil record makes it clear that there have been successive creations and extinctions of species, and the second volume of *Principles* opens with a consideration of the possibility that these creations are due to "indefinite modification through long course of generations" of already existing species. There is a lengthy and respectful consideration of the best argument for indefinite modification available at the time, that of the French systematist Jean Baptiste de Lamarck in his *Philosophie Zoologique*, and a careful critique leading to rejection of that possibility.

Charles Lyell thus makes the question of species origins—the question which John Herschel baptized "the mystery of mysteries" in a letter to Lyell in 1836—a central question for geology. A young naturalist tramping around the coastlines and offshore islands of South America is an early convert to Lyell's methodological principles. Lyell's dispassionate consideration of the idea of "descendants of common parents deviating indefinitely from the original type"—Lyell's words, not Darwin's—presented Darwin with transmutation as an actualistic solution to a fundamental geological problem, and with a carefully thought out list of objections to that solution.[3]

Darwin out-Lyelled Lyell on this issue; he achieved an actualist and gradualist theory of species origins. And this brings me to the central puzzle of this part of my discussion. Charles Darwin created a causal theory of species origins, which I will briefly characterize in a moment, a theory which refers, as a Lyellian theory ought, *only to states and processes now in operation*. Darwin is quite self-conscious of this debt. After having presented his "imaginary illustrations" of the action of Natural Selection he concludes:

> I am well aware that this doctrine of natural selection, exemplified in the above imaginary instances, is open to the same objections which were at first urged against Sir Charles Lyell's noble views on "the modern changes of the earth, as illustrative of geology;" but we now very seldom hear the action, for instance, of the coast-waves called a trifling and insignificant cause, when applied to the excavation of gigantic valleys or to the formation of the longest lines of inland cliffs. Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications, each profitable to the preserved being; and as modern geology has almost banished such views as the excavation of a great valley by a single diluvial wave, so will natural selection, if it be a true principle, banish the belief of the continued creation of new organic beings, or of any great and sudden modification in their structure. [*Origin* 185/95-96]

There are two distinct comparisons to Lyell, artfully woven together into a flattering tapestry. First, Darwin is comparing the *gradualism* of natural selection to the gradualism of the geological agencies to which Lyell referred geological change—great changes can be wrought by accumulating tiny modifications over long periods of time. Then there is a comparison with Lyell's *actualism*—Darwin is pointing out that the theory just presented refers only to causes now in operation, not to supposed miraculous events to which we in principle are denied access.

This is a *flattering* tapestry because Darwin is ignoring a significant difference between the status of Lyell's theories and his own. Lyell and many others on whom he relied, had painstakingly collected data on the actual short term operations of the mechanisms of erosion, deposition, subsidence, uplift and the like, and then projected their long term effects. In place of this, as Darwin here admits, he gives only imaginary illustrations.

The historical use of evolutionary theory depends entirely on the states and processes to which it refers being *historical invariants* of terrestrial life, having generated effects in the past as they do now. It would thus appear crucial that Darwin verify the short term operation of natural selection in wild populations and its subsequent effects on the make-up of those populations. A glance through the table of contents of the *Origin*'s first edition might lead you to expect that at least part of the twenty years between Darwin's *Species Notebooks* and the 1859 publication of the *Origin* had been spent on such a project. For once the theory is presented in full, Darwin turns to what he calls "Illustrations of the action of Natural Selection" [*Origin* 176/90-96], and then to "Circumstances favourable to Natural Selection" [*Origin* 191/101-111]. Reviews of the first edition indeed indicate that that is just what certain readers were expecting. What they got, however, were thought experiments.

The Arguments of the Origin

During the summary of chapter four of the *Origin*, Darwin makes the following remark.

> Whether natural selection has really thus acted in nature, in modifying and adapting the various forms of life to their several conditions and stations, must be judged of by the general tenour and balance of evidence given in the following chapters. [*Origin* 271-272/127]

The clear implication of this statement is that, whatever else Darwin was doing in the first four chapters, he was not establishing that natural selection had operated as he claimed in nature.[4] This is a strange disclaimer to make at the close of a chapter which includes a section entitled "Illustrations of the action of Natural Selection." If those illustrations are not intended to help confirm the operation of natural selection, what are they intended to do? To answer this question, we need briefly to trace the argument up to that point.

An outline of chapters 1-4

An important clue to the nature of Darwin's argument for the theory of natural selection is found at the beginning of the second chapter.

> Before applying *the principles arrived at in the last chapter* to organic beings in a state of nature, we must briefly discuss whether these latter are subject to any variation. [*Origin* 120/ 44; emphasis added]

This suggests that more is accomplished in chapter one than its title (*Variation under Domestication*), or most discussions of it, lead one to believe. The argument of that chapter establishes five claims crucial to Darwin's argument.

1. Many so-called domestic varieties are so different from one another that, if found in nature, they would likely be ranked as distinct species, and in some cases we know these to be derived from a single, natural stock. Indeed, virtually every well-marked domestic variety has occasionally been classified as a distinct species.

2. These well-marked varieties are derived from a common ancestral stock by means of the accumulation of slight, successive, heritable differences in certain directions.

3. Such individual differences or slight variations are greatly increased, in number and diversity, by changes in the conditions of life, which seem to produce variation "indirectly" by effecting the reproductive machinery.

4. The intention of producing a new variety is an inessential feature of this accumulative selection mechanism. As Darwin takes us through a series of cases where human purpose plays a progressively smaller role in the production of new varieties, he sends a quiet message: *new varieties*

are produced by the selective retention, and reproductive transmission, of certain differences rather than others. That is all there is to it.

5. The conditions which are most favorable to selection producing distinct varieties/species are a high degree of variability over many characters, a large population (increasing the probabilities that appropriate variations will appear), methods for isolating the favored brood stock, and careful attention to variation by breeders. In the section of chapter 4 entitled "Circumstances Favourable to Natural Selection" all but the fourth condition is repeated for natural populations.

In essence, then, the first chapter has supplied us with a *general selection theory* abstracted from Darwin's reflections on the literature devoted to the production of varieties of domesticated organisms.

The main purpose of the second chapter is to press the conclusion that "species are only strongly-marked and well-defined varieties" [55] in the case of natural kinds as well, so that if accumulative selection can produce strongly-marked varieties, the question of the origin of species is a *fait accompli*.

And thus, having in chapter three provided evidence that every organism in a state of nature is involved in a constant struggle for existence, Darwin opens chapter four with the following question:

> How will the struggle for existence, discussed too briefly in the last chapter, act in regard to variation? Can the principle of selection, which we have seen is so potent in the hands of man, apply in nature? [*Origin* 163/80]

Can selection, established as potent when applied, consciously or not, by man operate in nature? Darwin, throughout chapter four, is going to be arguing, not that it does, but that it *can*. Humans, whether intending to produce distinct varieties or not, play some role in the selective accumulation of differences which add up to a new variety. Darwin is now asking us to consider whether it is possible that the Malthusian struggle for existence could lead to a parallel selection in natural populations. Darwin wants to convince us that it could. To answer the questions with which Darwin opens chapter four—the struggle for existence can act on heritable variation *selectively*, tending to retain and transmit those which are of greater value in the struggle more frequently than those which are of lesser value. The most basic realization Darwin comes to is that the differences in the character traits of members of a species are not only *descriptive*—they are also *normative*. The difference between two wolves with legs of different lengths is both a measurable difference in length and a measurable difference in survival value in a specified environment.

Darwin has provided an abstract description of an elaborate causal mechanism here. He identifies a number of universal (or nearly universal) features of living nature—reproductive superfecundity, character variability, the inheritance of variation, the active struggle for self-maintenance and the constant search (among sexual organisms) for reproductive partners. Darwin has made considerable headway in support of the existence of each of these features. But that is not enough. There will be natural selection leading to indefinite descent with modification only if each of these states and processes operate and interact in the ways Darwin's model describes. How will Darwin convince us of this?

One way is by showing us how many "general classes of facts" from all the domains of natural history are best accounted for by the explanatory patterns associated with this theory.[5] This Darwin does in chapters 10-13. But this strategy will only work for Darwin once his readers have been convinced that the theory laid out in the first four chapters has explanatory potential. There are two steps to establishing this. The first is to establish the reasonableness of the primary explanatory pattern(s) associated with the theory. This step can be viewed as a response to a very general challenge of the sort expressed in the demand, "Show me exactly how it would work in a real case." The second step is to demonstrate the theory's ability to explain—in principle—facts which are prima facie problems for the theory, the subject of chapters 6-9.

While the argument of this paper will only establish the slightest hint of evidence for this wider claim, it is worth making it: I don't believe the Newtonian strategy which Darwin follows is chapters 10-13 could possibly work without the "imaginary illustrations" that I am about to discuss. Darwin seldom stops to consider how the "Darwinian narrative" explanation would generate the expected outcome in those later chapters. But that is because he has already done so.

On the view of argued here, the later sections of chapter four, and much of chapters 6-8, serve to demonstrate and defend the explanatory potential of the theory, its ability to deal with facts it claims to explain, and which it might seem to be incapable of explaining. And it is here that the use of thought experiment dominates.

Here are the opening lines of the section which is supposed to provide illustrations of the actions of natural selection.

> In order to make it clear how, as I believe, natural selection acts, I must beg permission to give one or two imaginary illustrations. Let us take the case of a wolf, which preys on various animals, securing some by craft, some by strength, some by fleetness; and let us suppose that the fleetest prey, a deer for instance, had from any change in the country increased in numbers, or that other prey had decreased in numbers, during the season of the year when the wolf is hardest pressed for food. I can under such circumstances see no reason to doubt that the swiftest and slimmest wolves would have the best chance of surviving, and so be preserved or selected. [*Origin* 176/90]

A little further on he expands the example:

> Now if any slight innate change of habit or of structure benefited an individual wolf, it would have the best chance of surviving and of leaving offspring. Some of its young would probably inherit the same habits or structure, and by the

repetition of this process, a new variety might be formed which would either supplant or coexist with the parent-form of wolf. [*Origin* 177/91]

He then goes on to discuss a more complex coevolutionary example involving a nectar feeding insect and the flowers it frequents.

What are those illustrations intended to accomplish? In calling them "thought experiments," I am claiming a certain role for them in the support of Darwin's theory. That role is to display in a vivid and concrete way that, *if* each of the mechanisms and processes referred to by Darwin's theory were to interact in particular ways, there *would* occur an accumulation of minute, random variations in a particular direction, culminating in distinct varieties and, eventually, new species. In order to accomplish this, Darwin's "imaginary illustrations," besides being "imaginary," must possess three additional features.

1. The objects and processes referred to must be *concrete*.

2. The illustrations must be *plausible*.

3. The relation of the concretes to the abstract terms of the theory must be clear.

Concreteness is what gives these illustrations the feeling of "experimentation."[6] Experiments must, as theorizing need not, involve the manipulation and observation of concrete objects, their properties, their changes, and their interactions. If Darwin were to have simply described the process of selection, as he imagines it to take place, in abstract terms, that would simply be to repeat the theory one more time.

Plausibility is provided by making use of familiar objects doing things we expect them to under realistic conditions. Wolf packs, deer herds, seasonal fluctuations in prey, mountain *vs.* lowland environments, young being born with different body types and leg lengths—none of this requires a *stretch* of the imagination. It all could happen, in a fairly robust sense of "could." If Darwin were able to illustrate the operation of the theory only by making up a wild science fiction scenario, it would hardly count as support for his theory. Darwin makes two additional moves toward plausibility in this case: he refers to a familiar analogue outcome due to selection in dog-breeding; and he mentions a case (which may well have been the source of this thought experiment) of a population of wolves coming in two varieties apparently correlated with differences in prey.[7]

Finally, if the imaginary illustration is to provide support for Darwin's theory, the crucial elements of the theory must be instantiated in the concrete illustration. Darwin does this [a] by imagining a relative or absolute increase in the fleetest prey at the point when the wolf pack is hardest pressed for food—this allows us to see, concretely, the idea of a struggle for limited resources; [b] by translating this struggle into a concrete example of differential survival/preservation/selection—the swiftest wolves are at an advantage in the struggle; and finally [c] by reminding us that this struggle will produce a new variety of wolf only if the advantageous habit or structure be inherited by the swift wolf's young, and this same process be repeated over and over again.[8]

As we have seen, Darwin doesn't see these examples as supplying confirmatory evidence of the operation of selection in nature; nor, because they are imaginary, can they hope to supply further evidence, beyond what has already been offered, of the existence of the component entities of his theory. Are they, then, expendable bits of rhetoric, fraudulent stand-ins for the evidence Darwin didn't have? The evidence against this is clear—Darwin tells us openly that there is no evidence in the first four chapters for the operations of natural selection in nature; and he refers to these repeatedly as imaginary, hardly the act of one who is trying to pass figments of his imagination off for the real thing. No. Darwin tells us what he is doing; all we need to do is read his modal operators clearly. He is illustrating how the struggle for existence *could* produce a variety by means of selection.

Thought experiments are intended to provide evidence for or against a theory's explanatory potential. As we will see, many of the most powerful challenges Darwin had to meet were to the effect that the theory presented in the *Origin could not possibly* explain the things he thought it could.

The Jenkin Dilemma: Selection cannot create a species

Darwin, in using thought experiments, left himself especially vulnerable to a certain kind of attack. Fleeming Jenkin's critique of this section of the *Origin* and Darwin's subtle response show the power of thought experiment in the articulation of a new theory.

Jenkin mounts his attack against Darwin's argument on many fronts. In every case his arguments are effective either because they make explicit assumptions of Darwin's argument which Darwin hadn't recognized or because they draw out consequences of Darwin's model which are contrary to those Darwin desires. I shall focus attention on the section of Jenkin's review which he heads "Efficiency of Natural Selection."

Jenkin's strategy is to accept natural selection as a given, and focus on the nature of variation and inheritance. He summarizes his argument in the form of a dilemma.

Assume that variations are either the common slight differences we see among the individuals of any population, or the rare "sports" where entirely new structures or habits appear "all at once." Jenkin argues that there is no evidence that variations of the first sort ever give rise to enough difference to create a new species. On the other hand, a rare sport might. So he considers two possible ways in which a rare "macromutation" might be inherited: assuming a rare sport mates with an ordinary member of the population, the offspring [a] might be thought to be intermediate, or [b] at least some might be thought to be a faithful reproduction of the original mutant. If we choose [a] then it is certain that such a rare sporting variation will be swamped out of existence, even if it bestows a very significant selective advantage on its possessor. On the other hand, if we choose [b], we may have a theory of species origins, but selection plays no essential role in that theory. (Figure 1.)

Figure 1: The Jenkin Dilemma

I. *The Possibilities*

Trait Frequency \ Trait Type	Sport	Slight Variation	Inheritance Type
Rare	A1	B1	Blending
	A2	B2	Sorting
Common	C1	D1	Blending
	C2	D2	Sorting

II. *Consequences for the Efficiency of Selection*

1. If [A.1.] or [B.1.] even strong selection will be swamped by blending.
2. If [A.2.] natural selection will play no role in the creation of new species.
3. If [B.2.] [D.1.] or [D.2.] natural selection can effect only slight changes in already existent features.
4. [C.1.] and [C.2.] are taken, by both Darwin and Jenkin, to be empirically excluded.

Jenkin took it that he had shown that, no matter what notions of variation and inheritance Darwin is operating with, the theory of evolution by natural selection is nonviable.

In arguing against possibilities [A.1.] and [B.1.] Jenkin resorts to thought experiments. These imaginary illustrations are designed to *test the power of Darwin's theory* assuming that variations differentially favored do occur, but occur only rarely and are significant deviations from the norm for the species; but allowing Darwin *either* a blending or a non-blending theory of inheritance.

The first test imagines the appearance of a rare "burrowing hare" in a non-burrowing species. "Let us consider," says Jenkin, "whether a few hares in a century saving themselves by this process could, in some indefinite time, make a burrowing species of hare" [Jenkin/Hull 1973 314]. He begins with a population of a million hares, supposes 10,000 survive to reproductive age, supposes there to be one burrower in the million with a 2:1 survival advantage over any other particular individual in virtue of its burrowing ability. Nevertheless, Jenkin notes, the odds are "enormously in favor of *some* average individual." The burrower's chances improve from 100:1 against being one of the survivors to 50:1 against, because of the selective advantage of burrowing. But even granting an unrealistic selective advantage, the chance of the burrowing hare surviving to contribute its variation to the next generation is 1:50.

Suppose, nevertheless, he beats the odds. On the assumption that sexual reproduction operates by a blending of parental traits in each of the offspring, Jenkin supposes the selective advantage of 100 offspring of our burrowing hare to be reduced from his 2:1 to 1.5:1; thus any individual's odds of surviving to reproductive age goes down, but because the burrowers now constitute a slightly greater segment of the population, Jenkin allows that the chances of one burrower surviving will improve slightly. Thus at each generation the odds against the variation being preserved are considerable, and the inevitable consequence of beating the odds is reducing the survival advantage of the variation in question.

Jenkin further illustrates the effects of blending with a more easily visible characteristic—skin color. Playing a variation on the theme of Robinson Crusoe, he imagines a "shipwrecked hero" with "every advantage which we can conceive a white to possess over a native" [Jenkin/Hull 1973 315]. He becomes king, takes many wives, kills many of the black males, and prevents many others from contributing to the gene pool. He has every physical advantage. Jenkin then imagines the results.

> In the first generation there will be some dozens of intelligent young mulattoes, much superior in average intelligence to the negroes. We might expect the throne for some generations to be occupied by a more or less yellow king; but can any one believe that the whole island will gradually acquire a white, or even a yellow population.....? [Jenkin/Hull 1973 316]

Shifting to this example shifts attention from the issue of the low probability of survival in a large population to the effects of blending on the survivor—for in this case, the survival and reproductive superiority of the pale-skinned variant are granted for the sake of argument.

Jenkin now states Darwin's take home lesson. "Darwin says that in the struggle for life a grain may turn the balance in favour of a given structure, which will then be preserved. But one of the weights in the scale of nature is due to the number of a given tribe." The chances of a trait having evolutionary significance, Jenkin is pointing out, is a product of its adaptive advantage *and* its frequency.

Now up to this point a natural reaction for someone familiar with Darwin's theory is that it is immune to Jenkin's dilemma. Darwin insisted that it is the slight, individual variations that are the material for natural selection—not differences of the burrowing/non-burrowing, white/black variety on which Jenkin's argument depends. To the extent that Jenkin's argument presupposes that such differences are the material for selective survival and transmission, it would seem to leave Darwin untouched. How odd, then, that Darwin took the critique so seriously.

Darwin, however, read his reviews carefully. For, as Jenkin now goes on to say, his argument applies to all types of variation.

> If it is impossible that any sport or accidental variation in a single individual, however favourable to life, should be preserved and transmitted by natural selection, still less can slight and imperceptible variations occurring in single individuals be garnered up and transmitted to continually increasing numbers...... [Jenkin/Hull 1973 316]

This amounts to the extension of the dilemma from [A.1.] to [B.1.]. It was in making this extension explicit that Jenkin's review had its impact on Darwin.

Most scholars have missed the significance of this part of Jenkin's review for Darwin.[9] While he did not see it as a devastating criticism, it *did* point out a dangerous ambiguity in his theory. It is clear that, insofar as Jenkin's imaginary advantageous variants are rare sports, they don't represent the selective materials of Darwin's theory—if he is adamant about anything, it is that natural selection is a sifting of slight, individual differences. But the fact that Jenkin claims the same point is even more telling against slight variations shows that the real issue at hand is the *frequency* of the variations upon which selection acts.

Jenkin has succeeded in uncovering two ambiguities lurking in Darwin's own imaginary examples.

1. Inheritance is often treated as a process whereby an individual passes on traits *undiluted* to offspring. Yet when he explicitly discusses intercrossing, he assumes the product of crossing two different traits of a character will be an intermediate trait.[10]

2. A single individual with a selective advantage is often treated as the major player on the evolutionary stage, and yet passages in which he discusses circumstances favorable to natural selection show him sensitive to the importance of the frequency of the favored variant in increasing the probability of its selection.

Look back to Darwin's wolf illustration, and you will see a tension that is not immediately obvious. Initially we are asked to imagine a competition favoring "the swiftest and slimmest wolves" [IOrigin 176/90]; but a few lines later it is suggested that "if any slight innate change of habit or structure benefited *an individual wolf*, it would have the best chance of surviving and of leaving offspring. Some of its young would probably inherit *the same* habits and structures..." [*Origin* 177/91]. Jenkin rightly points out that if it is a slight change in an *individual* its chances of being inherited at all are extremely slight—and supposing it beats the odds, if the trait is transmitted by a cross with an animal lacking the advantageous variation, on the assumption of blending inheritance, the offspring will not inherit *the advantageous* trait, and nothing so significant as a new variety of organism will ever be formed by such a process.

Darwin was thus forced to make a number of choices between alternatives latent within the first edition theory. He opted to stick with a theory of the struggle for survival differentially favoring slight individual differences and adding these up slowly over time. But he now realized that the theory had to be stated in a way which [a] significantly *increased* the odds of merely slightly favorable variations being preserved and passed on and [b] significantly *decreased* the odds of the slight advantage being quickly swamped by intercrossing. In the fifth edition of the *Origin*, the reference to the individual wolf is dropped—but not quietly. Darwin explains—

> It should be observed that, in the above illustration, I speak of the slimmest individual wolves, and not of any single strongly-marked variation having been preserved. In former editions of this work I sometimes spoke as if this latter alternative had frequently occurred. [Origin178 (95.1-3:e)]

He notes that, while he had always, thanks to his knowledge of domestic breeding, focused on individual differences, it was not until reading Jenkin's review that he appreciated "how rarely single variations, *whether slight or strongly marked*, could be perpetuated" [*Origin* 178/95.4-6:e]. After reviewing and conceding Jenkin's point, he demonstrates how the cleaned up theory handles Jenkin's dilemma. Again, it is explanatory potential he wants to demonstrate, and thus a new thought experiment will do the trick.

> ...but there *can hardly be any doubt*....that this result [the production of a new variety] *would* follow from the preservation during many generations of a large number of individuals with more or less curved beaks, and from the destruction of a still larger number with the straightest beaks. [*Origin* 179/97.7-11:e; emphasis added]

Darwin, in this edition, carefully goes through and corrects singulars to plurals in all his examples—one example can stand for many. During the course of his co-evolutionary discussion of nectar-feeding insects and nectar-producing plants there is a passage which in the first edition runs:

> Bearing such facts in mind, I can see *no reason to doubt* that an accidental deviation in the size and form of the body, or in the curvature and length of the proboscis, &c., far too slight to be appreciated by us, *might* profit a bee or other insect, so than an individual so characterised *would* be able to obtain its food more quickly, and so have a better chance of living and leaving descendants. [*Origin* 117/94; emphasis added]

In the fifth edition, on the other hand, we read:

> Bearing such facts in mind, it may be believed that under certain circumstances *individual differences* in the curvature or length of the proboscis, &c., too slight to be appreciated by us, might profit a bee or other insect, so that *certain individuals* would be able to obtain *their* food more quickly than others; and thus *the communities to which they belonged* would flourish and throw off many swarms inheriting the same peculiarities. [Origin 183/117+8:e]

Darwin also consistently views traits in a population as *continuously varying* between most and least advantageous forms. This means that *selective advantage is also a continuum*; individuals are favored *more or less* depending on where they fall on a "value" continuum. This makes the concept of fitness relative, for whether a variation is to be viewed as more or less advantageous than another depends entirely on where each falls on the continuum. Using Darwin's example, a nearly straight proboscis confers some advantage compared to a completely straight one, but is disadvantageous compared to all those which are more curved.

This move handles the "rarity of perpetuation" side of Jenkin's dilemma—but now what about the effects of free intercrossing? There would seem to be an objection, which later Darwinians faced as well, that free intercrossing of organisms with the more favored trait and those with the less favored will counteract the action of selection.

In his presentation of the "Circumstances favorable to Natural Selection"—what we would call his discussion of models of speciation—Darwin agonizes over the fact that the set of circumstances he sees as most favorable for natural selection are also most favorable to free intercrossing. Darwin tends to see free intercrossing as a force opposed to the production of distinct varieties, and thus as a counter-evolutionary force. Thus, the fact that he thinks large populations of free-ranging, rapidly reproducing organisms are optimal both for selection and intercrossing means that these two opposing forces are in danger of cancelling each other out. But at least in one place in that discussion he states, as clearly as he anywhere does, how viewing variation as constituting a value continuum overcomes this problem as well. Its worth quoting in full:

> In man's methodical selection, a breeder selects for some definite object, and free intercrossing will wholly stop his work. But when many men, without intending to alter the breed, have a nearly common standard of perfection, and all try to get and breed from the best animals, much improvement and modification surely but slowly follows from this unconscious process of selection, notwithstanding a large amount of crossing with inferior animals. Thus it will be in nature; for within a confined area, with some place in its polity not so perfectly occupied as might be, natural selection will always tend to preserve *all the individuals varying in the right direction, though in different degrees*, so as better to fill up the unoccupied place. [*Origin* 193/102; emphasis added]

If selection of different degrees favors all the organisms tending to vary from the mean in a direction appropriate for the exploitation of an unoccupied or imperfectly occupied niche, there should be enough crosses of these organisms with each other to overcome the effects of occasional crosses with those varying in the other direction. Darwin also occasionally suggests that those organisms varying in ways allowing them to exploit various opportunities will, for that very reason, tend naturally to spend more time in close proximity to one another, and thus will cross more often [*Origin* 194-195/103]. This discussion, one of the most rich and least studied in the *Origin*, is carried on almost entirely in the concrete yet hypothetical mode of the thought experiment.

Let us step back now and ask ourselves what the nature of these imaginary illustrations is, and what role they have played in Darwin's defense, and Jenkin's criticisms, of the theory of species descent by natural selection.

II. Thought Experiments[11]

I now want to argue that these imaginary illustrations, used both by Darwin and Jenkin, can be usefully thought of as thought experiments.[12] The first step in the argument is to specify, in functional terms, what I mean by the expression "thought experiment."

Thought experiments are:

[a] tests of a theory's explanatory potential which
[b] posit hypothetical or counterfactual test conditions and
[c] invoke particulars which are irrelevant to the generality of the theory, and which
[d] are selected to instantiate features of the theory under special consideration.

By viewing thought experiments as tests of the explanatory potential of theories, one returns to one of Thomas Kuhn's initial insights in the paper my title makes glancing reference to, that *thought experiments are functionally experiments*, and do what experiments generally do.[13] Kuhn's description of that role has an implicitly Popperian slant, in that he sees thought experiments are essentially valuable in showing ways in which current theories fail;[14] but the more general point is important and worth preserving.

The above characterization also accounts, in a non-Kuhnian way, for another curious fact about thought experiments—their crucial role in major conceptual revisions within a scientific domain. On the view set out here, the reason for this is clear. Thought experiments are especially important when the issue at hand is the theory's *potential* to explain *as*, and *what*, it claims it will. In the Darwinian case, the abstract characterization of the theory of natural selection in the first fifteen pages of chapter four of the *Origin* is then hypothetically instantiated in two imaginary ecological settings—e.g. how a change in available food supplies would quickly shift the advantage in the direction of wolves built for speed. This is Darwin providing us with *a concrete, if hypothetical*, realization of how the causal interactions described in the theory could accumulate variations in a certain direction. He makes it look like it's worth checking out!

Let me briefly note the need for (a), (b) and (c) in the above characterization. (a) The concreteness of the "illustration" gives it the character of observational and/or experimental data. Without this character, we would have simply a restatement of the theory. (b) The hypothetical character of the "illustration" gives it its "thought-like" character, to borrow John Norton's formulation (see Appendix). But not just any random imaginary concrete will do. Thought experiments are characteristically designed to support or undermine specific aspects of a theory, and as such those which are chosen in specific discussions are chosen to illustrate the theory's capabilities (or problems) for the specific issue at hand. Jenkin's review is illustrative here—his shift from the burrowing hare to dominant Caucasian is due to a shift in the problem he is attending to. The burrowing hare nicely illustrates the problem of the low probability of a rare variant being passed on and of how little difference selective advantage will make. When he wishes to shift to the issue of blending inheritance, the crossing of skin color is a more vivid and obvious illustration.

Jenkin's review is helpful for two reasons. First, it shows a virtue in Darwin using these thought experiments at this point—it provided enough concrete information about how the theory's causal processes were supposed to produce a new species that flaws were much easier to spot. Thus Jenkin's critical task was rendered much easier. Furthermore, it shows how the same technique can be used to illustrate problems that must be overcome if the theory is to be at all interesting. It is crucial to Jenkin's attack that he plug in *concrete—if hypothetical*—values for selective advantages, populations sizes, frequency of favored trait and so on. Once this was done, Darwin was able to see that he had to be quite explicit in the presentation of his theory about the kind and quantity of variation, and about mechanisms for overcoming the swamping effects of free intercrossing.

The epistemic appropriateness of using thought experiments seems to depend on there being reasons why an actual empirical test—via controlled observation or experimentation—is either unnecessary or out of the question. There have been literally thousands of tests of the operations of selection mechanisms on natural populations, both in the wild and in artificial laboratory situations, in this century.[15] Such tests, while perhaps of a less sophisticated form, were certainly possible in Darwin's time. So I don't imagine Darwin used thought experiment because empirical tests were out of the question. What I want to claim is that this historical example reveals a function for thought experiment which is independent of empirical support of a theory's truth.

Further support for this suggestion derives from chapters 6-9 of the *Origin*, in which Darwin tries to head off certain objections to his theory. A look at these problems shows that Darwin was worried about arguments that attempted to show his theory's inability to explain certain well-known facts of natural history. That is, Darwin saw it as his primary task in these chapters to show that a process of descent with modification directed primarily by natural selection *could* in principle account for various "broad classes of facts."

For example, Darwin's theory implies the slow, gradual development of highly complex and coadapted structures and behavior patterns, by the process of selection "adding up" slight variations in a certain direction. Darwin was prepared for a counter-argument based on this implication. The counter-argument claims that such organs would not be advantageous until they achieved a certain threshold level of "perfection." But in order for selection to operate as Darwin said it did, every slight modification, including those at the most rudimentary stages of such a structure's history, would need to confer an advantage on their possessor. And what is more, as complex organs such as the vertebrate eye are composed of a number of structures, all of which must develop in a coordinated fashion if the organ is to work, the theory would have to posit a host of such changes occurring at the same time and rate. It does not seem, the critic concludes, that such a gradual production of such structures is possible. In order to respond to such an argument, Darwin needed only to show that a Darwinian/selectionist explanation of such structures and behaviors was *possible*. He is quite clear about this.

> If it could be demonstrated that any complex organ existed, which *could not possibly* have been formed by numerous, successive, slight modifications, my theory would absolutely break down. [Origin 334/189; emphasis added]

What follows in these chapters includes much unsupported story telling.[16] But that is a perfectly acceptable technique for the purpose at hand. Darwin wants to show people that what they think is impossible is perfectly possible. It could have happened, first appearances to the contrary notwithstanding.

To his surprise, many reviewers granted these possibility arguments without blinking an eye—and went on to insist that Darwin's primary problem was turning "the could haves" into "dids."[17] They missed the point.

And it has ever been the case! Throughout evolutionary biology's history, some of its greatest triumphs began as thought experiments showing that the explanation of a certain phenomenon was within the explanatory resources of the theory.

III. A Legitimate Function for Just-So Stories

Critics of the Panglossian Paradigm, as the adaptationist explanatory program is sometimes disparagingly called, have done an important service as the private detectives of evolutionary biology, searching out fraudulent uses of plausible stories posing as confirmed explanations. In the programmatic remarks that follow I want to suggest that Just-So Stories may have a number of legitimate roles to play in evolutionary biology, one being the important role of thought experiment. Three cases where I believe they did play such a role are mentioned, chosen from many that come to mind.

1. One major theoretical advance achieved by the work of people like R. A. Fisher and J. B. S. Haldane, was to show that, given the nature of genetic

recombination and mutation, a variation conferring a very slight advantage on an individual would nonetheless spread through a large, panmictic population at a surprising rate. Here is a different response to the Jenkin Dilemma, one which accepts *rare* slight variations as possible targets of selection, but operates with a well confirmed non-blending theory of inheritance. The early population geneticists showed that a central plank of Darwin's version of evolutionary change—selection acting on small heritable variations—was theoretically acceptable within the new Mendelian framework. In a context where a variety of critics were claiming this was impossible, this was a crucial advance. The use of imaginary tests of the theory's ability played a crucial role in demonstrations of the new theory's power.[18] Similarly, a major dispute was played out entirely in the language of thought experiment between Fisher and Sewall Wright over the sufficiency of such a process for the generation of new species.[19] Today computer simulations would no doubt play a significant role in such disputes—these being the latest form of laboratory equipment for thought experiment.

2. A basic issue in the "Group Selection" controversy of the early and mid-1960's, which eventually gave rise to much theoretical discussion about the nature, units, targets, and levels, of selection, was whether certain phenomena which seem to have individual costs but only "group level benefits" *could possibly* arise by means of Darwinian selection. Models of kin selection and the concept of inclusive fitness were then developed to show that indeed such phenomena as "altruistic" behavior patterns could be accounted for on orthodox neo-Darwinian principles. Again the initial issue was the *possibility* of Darwinian explanation against the background of an initial concern that there were certain phenomena that these explanations could not possibly handle.[20]

3. Finally, consider an example where the possibility of a Darwinian explanation remains the issue in question. This is the issue of the evolution of sexual reproduction. The problem is nicely put by George Williams:

> Consider a population with two female genotypes. At a certain stage in the life history, genotype A_1A_2 produces unreduced eggs that develop into genetic replicas of the mother. Genotype A_3A_4 produces reduced eggs that must be fertilized. An A-allele from a sperm can be called A_m. Thus an offspring of the sexual parent is either A_3A_m or A_4A_m. It has one, not both of the maternal genes. All the offspring of the parthenogenetic parent have the full maternal genotype A_1A_2. Unless something causes a difference in the numbers of offspring, the asexual parent has double the genetic representation of the sexual in the offspring generation. [Williams 1975 8]

As Williams later notes, "the primary task for anyone wishing to show favorable selection of sex is to find a previously unsuspected 50% advantage to balance the 50% cost of meiosis" [Williams 1975 11]. The paradox is fairly clear—any trait with that sort of disadvantage would disappear from a population with breathtaking speed. Yet there are many examples of organic populations that maintain, over long periods of time, a balance of sexual and asexual methods of reproduction. Again quoting Williams "that which must surely be false, by the method of deductive analysis, must surely be true by comparative evidence..." [11-12].

Notice that the above passage is a thought experiment; it asks us to consider a hypothetical but quite concrete breeding population with particular genetic characteristics especially relevant to the problem under consideration. The critical method of test used here, drawing out implications of the case embarrassing to the Darwinian, is remarkable similar to that found in the Jenkin review over a hundred years earlier.

Here is a case where the implications of orthodox Darwinian selection theory seem to rule out something which is manifestly the case. Or to put it the other way around, a Darwinian explanation for an extremely pervasive feature of the living world seems not to be possible. Once more the basic issue at stake is not what precisely the explanation of the evolution of sexual reproduction in a given population actually is, but rather whether *any* explanation which is Darwinian in form is even *possible*. Thought experiments intended to test the possibility are in order, and indeed might be useful as guides to the kinds of natural situations to look to for evidence that sexuality has actually evolved as an adaptation of a specific sort.

Darwin's "imaginative illustrations" are thought experiments—they are also what some biologists and philosophers derisively refer to as "Panglossian" or "just so stories" [Gould and Lewontin 1979; Kitcher 1982 60; 1985b 226]—without the redeeming literary merits of Voltaire or Kipling. Here is an unabashed example from an unabashed Adaptationist, chosen because it is remarkably like Darwin's own both in content and purpose. After describing the behavior of pit-digging in "antlions," Richard Dawkins goes on:

> Pit-digging is a complex behaviour pattern. It costs time and energy, and satisfies the most exacting criteria for recognition as an adaptation (Williams 1966; Curio 1973). It must, then, have evolved by natural selection. How might this have happened? The details don't matter for the moral I want to draw. Probably an ancestral antlion existed which did not dig a pit but simply lurked just beneath the sand surface waiting for prey to blunder over it. Indeed some species still do this. Later, behavior leading to the creation of a shallow depression in the sand probably was favoured by selection because the depression marginally impeded escaping prey. By gradual degrees over many generations the behavior changed so that what was a shallow depression became deeper and wider. [Dawkins 1982 20]

Out of context, this sounds like a fairy tale posing as a scientific explanation. But of course it is not. Dawkins doesn't much care whether the details of the above narrative are true, and he admits happily that neither he nor anyone else has tried very hard to find out. Like Darwin, he is illustrating the explanatory power of the theory, not providing an explanation of pit-digging behavior.

That is not to say that there are no such stories posing as evidence of natural selection. What Philip Kitcher [1985b] refers to as Pop Sociobiology is one grand pose. Nonetheless there are *legitimate* roles for such stories to play within evolutionary biology, and thought experiment is one.

The message of history on these narratives seems to be this. There are clear functions for them in the context of exploring a theory's capabilities. They should not be mistaken for evidence that the world actually does or does not operate as the theory claims, either by their users or their critics. The criticisms of Darwinian thought experiments are valid when directed against stories of how natural selection *could* have produced a certain result which masquerade as evidence of how it actually *did*.

APPENDIX

The characterization of thought experiments on p. 210 of this paper is modelled on that given by my colleague John Norton in another paper in this volume (pp. 103-18). It will facilitate the following remarks to have the two accounts before us.

John Norton's Characterization

Thought experiments are

[a] arguments which
[b] posit hypothetical or counterfactual states of affairs and which
[c] invoke particulars which are irrelevant to the generality of the argument's conclusion.

James Lennox's Characterization

Thought experiments are:

[a] tests of a theory's explanatory potential which
[b] posit hypothetical or counterfactual test conditions and
[c] invoke particulars which are irrelevant to the generality of the theory, and which
[d] are selected to instantiate features of the theory under special consideration.

Basically, then, I agree with Norton entirely on conditions [b] and [c]. Condition [d] is added to dispel any thought that the force of [c] is that the particulars invoked are chosen simply at random with respect to the theory, which is not, in my experience, the case.

Our primary disagreement is over Norton's characterization of thought experiments as arguments. I reject this suggestion for two reasons. First, even as a description of the *reconstruction* of these imaginary examples, it is only when the hypothetical and particular description of a situation is embedded in a proposed explanation or conjoined with a theoretical principle that anything like an argument emerges. That is, properly reconstructed, written presentations of thought experiments might play a role within an argument—in the examples Norton discusses they are often *parts* of reductios—but they are *not by themselves* arguments.

Second, I find I have to do very little reconstruction to see Darwin's and Jenkin's use of imaginative examples as tests of the explanatory possibilities of Darwin's proposed causal mechanism. Darwin is attempting to make clear how the proposed natural selection mechanism could lead to distinct varieties, and Jenkin is just as surely attempting to show that when you plug in plausible concrete values for certain of the theory's variables, Darwin's results fail to fall out. There is an argument here, but the literary presentation of the thought experiment is only part of it.

That we are looking at the written presentation of the thought experiment is perhaps obvious. The implications of this fact are not always obvious, however. I think the tendency to think of explanation and confirmation in terms of relationships between sentences of various kinds is behind Norton's insistence that thought experiments must be arguments. After all, as he has on occasion said to me, what else could they be?

Well, they could be precisely analogous to an actual experiment! A laboratory experiment is not a set of sentences (thought its published description sometimes is). It is a human activity intended to produce concrete, physical interactions of the kind which a theory claims will have certain effects and to observe whether the effects predicted by the theory result. Just as the written description of a laboratory experiment can become a premise in an inductive argument providing confirmation for a theory, so the written presentation of a *imaginary* concrete test situation can become a premise supporting a claim about the explanatory potential of the theory. In neither case should the written description be mistaken for the experiment itself.

NOTES

1. Because a central part of this discussion will involve changes that Darwin made in the *Origin* between earlier and later editions, the primary page references will be to Peckham's masterful Variorum edition [Peckham 1959]. Where necessary I will refer to the relevant line numbers in parentheses, as here. Where I am referring to material that appears in the first edition, I will also provide the page number of the Harvard facsimile of the first edition [Darwin 1859/1964]; for example [*Origin* 120/44] refers to p. 120 of the Variorum edition and p. 44 of the Harvard facsimile of the first edition.

2. Based on the inscription in his personal copy (preserved in the Darwin Library of the Cambridge University Library). The "box of valuable" referred to in a letter, sent from Monte Video, to sister Caroline dated October 24-November 24 [*Correspondence* Vol. 1 1985 276-279] may have contained it.

3. For the details of the influence of *Principles of Geology* on Darwin's early thinking about transmutation, see Kohn 1980, Hodge 1983, Gruber 1985 15-18, in Kohn ed. 1985.

4. Kitcher 1985 is certainly correct that the reference here to "the following chapters" includes arguments designed to show the power of Darwin's explanatory pattern to account for, and thereby unify, a host of previously unexplained facts from a wide range of domains. But also among "the following chapters" are those dealing with "problems of the theory" (especially chapters 6-9). Darwin's reference to the "tenour and balance of evidence" therefore likely includes evidence of the theory's ability to explain facts that critics might think beyond its grasp. Thought experiments are one of Darwin's primary tools for providing such evidence.

5. Cf. Kitcher 1985; Lloyd 1983; Recker 1987; Ruse 1971, 1975, 1979; Thagard 1978. I have found Kitcher's discussion of this aspect of Darwin's argument the most illuminating.

6. Compare the "irrelevant particular" condition on thought experiments in John Norton's paper in this volume. This paper owes much to numerous discussions between its author and John Norton on the topic of thought experiments. There is a brief appendix at the end of this paper which compares our accounts of thought experiments, pp. 215-16.

7. As the explicit description of Darwinian thought experiments below suggests, some thought experiments operate on hypothetical assumptions which are explicitly counterfactual (for example, Ronald Fisher's exploration of the implications of a population with three sexes, explored for the sake of understanding the virtues and limits of having two). Plausibility in these counterfactual cases is more like the plausibility of science fiction—given the highly unfamiliar presupposition of the thought experiment, the rest of the scenario must be consistent with it.

8. One common method used today to accomplish what Darwin is attempting to accomplish is the computerized simulation, which requires concrete and realistic, thought imaginary, values for the variables of one's theory to be plugged in. The method of imaginary computer simulation is simply a mechanically aided form of thought experiment.

9. The most notable exception is Peter Bowler 1984 198-199; the above discussion rejects the interpretations found in Vorzimmer 1970; Ruse 1979 210-211; and Mayr, 1982 512-515, 543, 740. Among these writers, only Bowler has noticed that Jenkin extends the argument to Darwin's favored case, that Darwin realizes this, and makes significant changes in his arguments to meet the problem created by Jenkin.

10. Actually, though the details can't be reviewed here, Darwin's discussion of the inheritance of variation in the *Origin* is much more complex than is usually assumed. He summarizes dozens of experimental and observational studies, occasionally mentioning hybrid crosses where all the first generation look exactly like one parent or the other, but with second generation offspring appearing like both parents[!]—and other less straightforward "non-blending" results. Thus, if there is a tendency to adopt blending as the norm, it is no more than a working hypothesis for Darwin. It is certainly not an unquestioned assumption.

11. It is just possible that someone might object to the use of this term on grounds that the imaginative illustrations used by Darwin in support of his theory and by Jenkin in undermining it are not imagined *experiments*, but imagined *observations.* I see very little epistemological difference between identifying a set of controlled observations of natural processes which could answer a well-formed scientific question and designing a set of controlled experiments for the same purpose. Both are observations, yet both have that controlled and question-driven character that separate them from "naive" observation. So I am content to keep using the language of thought experiment. On the other hand nothing important for my results turns on the word "experiment," so if a reader is bothered by it he may substitute "thought test" or "thought-evidence" as he reads.

12. A complementary discussion of this form of reasoning in evolutionary biology

is to be found in Brandon 1990, ch. 5. Brandon construes these illustrations as "how-possibly" explanations—i.e. as *displaying*, rather than testing, the explanatory possibilities of the theory. Our convergence on these issues was discovered when each of us presented papers on the topic at the 1989 meetings of the Society for the History, Philosophy and Social Studies of Biology in London, Ontario.

13. Kuhn 1964 307-334; repr. 1981 6-27.

14. Which means that on Kuhn's analysis, while Jenkin's imaginary examples could be thought experiments, Darwin's use of them in support of his theory could not be.

15. An excellent review can be found in Endler 1986.

16. A number of kinds of evidence are used for the first time in support of evolutionary hypotheses here, and used ever since by evolutionary biologists. For example, in countering the "not advantageous until perfected" argument, Darwin is able to show that eyes *currently* come in every degree of complexity from an optic nerve coated with pigment through to the vertebrate eye, and all seem suitably adapted to some environment or other [*Origin* 337-344/186-189]. Again, this does nothing toward confirming the actual evolutionary history of the vertebrate eye—but it does show that one argument against the possibility of such a history is flawed.

17. Among them, somewhat inconsistently, our friend Fleeming Jenkin; cf. Hull 1973 319, 339, 342, 343. This aspect of Jenkin's critique is clearly discussed in Kitcher 1985 127-190.

18. Cf. Fisher's fascinating discussion of the role of the imagination in mathematical physics and biology in the preface to *The Genetical Theory of Natural Selection*, viii-ix.

19. For an excellent account of the Wright-Fisher dispute, see Provine 1986, chs. 7-9.

20. Cf. Hamilton 1964; Williams 1966.

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