NECESSARY CHANCES

Abstract: In this paper I propose a new way of thinking about natural necessity and a new way of thinking about biological laws. I suggest that much of the lack of progress in making a positive case for distinctively biological laws is that we've been looking for necessity in the wrong place. The trend has been to look for exceptionlessness at the level of the outcomes of biological processes and to build one's claims about necessity off of that. However, as Beatty (1995) observed, even when we are lucky enough to find a biological "rule" of some sort, that rule is apt to be a victim of "the rule-breaking capabilities of evolutionary change." If indeed no distinctively biological generalization — even an exceptionless one — is safe, we need to locate necessity elsewhere. A good place to start is, I think, precisely the point at which Beatty sees the possibility of lawhood as breaking down — namely, at the level of chances.

They all knew it was ridiculous to expect this one poor little bar of chocolate to have a magic ticket inside it, and they were trying as gently and as kindly as they could to prepare Charlie for the disappointment. But there was one other thing that the grown-ups also knew, and it was this: that however small the chance might be of striking lucky, the chance was there. The chance had to be there.

<div align="right">Roald Dahl (1964) Charlie and the Chocolate Factory (43)</div>

What is so fascinating about probability is that it lies neither in the domain of Laplacean determinism nor in that of Epicurean anarchy, but somewhere in between, where short term disorder and long term order meet.

<div align="right">Michael Strevens (2000) "Do Large Probabilities explain better?" (388)</div>

I. THE NECESSITY OBJECTION TO BIOLOGICAL LAWS

The living world is a very predictable place. We expect organisms to be well adapted to their environment, and they are (to an often remarkable degree). We expect offspring to very closely resemble their parents, and they almost always do. We expect the organisms that are better adapted to their environment to leave more descendants than those less so, and they usually do. We expect significant changes in an environment to be followed by changes in the composition of the populations occupying that environment, and they are. We expect the ratio of males to females in sexually reproducing species to be roughly 1:1, and it very often is. It is no wonder that, in the face of the predictability exhibited by the biological world, like that exhibited by the non-biological world, people have thought that it is a very *law-abiding* place.

Independently of the commonsense notion that biological phenomena are law-abiding phenomena, professional biologists often make references to specific biological laws. Frequent references are made

to, for example, the Hardy-Weinberg law, which "describes the consequences of random mating on allele and genotypic frequencies" (Gillespie 1998: 1). Dollo's law, the principle that there is no reversion to ancestral types, is a fundamental presupposition of phylogenetics (Gould 1970: 208).[1] The Principle of Natural Selection (PNS), of course, is also often referred to as a "law."[2] Indeed, within each branch of biology one can find researchers speaking fairly unconsciously about this or that "law," some of which are relevant to many different problems (and so appear in discussions across a range of disciplines), some of which are only of interest to biologists working on very specific problems (compare, for instance, Mendel's laws and various laws associated with viruses).

I think that these points — the appearances of the living world and the professional discourse within biology — provide all the justification one would need for inferring that there are biological laws. Despite the intuitive pull of this view, there are some deep problems that have proven difficult to get around. In particular, John Beatty's "Evolutionary Contingency Thesis" (Beatty 1995) has been a strong source of support for the view that, appearances notwithstanding, there simply could not be any such thing as a biological law. Beatty has argued that to the extent that a generalization is "distinctively biological" (i.e., not a truth about biota that can be expressed purely in the language of physics or chemistry [or any other discipline]), that generalization describes a state of affairs which is the product of the vicissitudes of evolutionary processes —an "evolutionarily contingent" outcome.

> What does it mean to say that such generalizations describe evolutionarily *contingent* states of affairs? This has to do with the *rule-breaking* capabilities of the agents of evolutionary change: the agents of evolution not only make, but also break the rules that pertain to the living world. More formally, to say that biological generalizations are evolutionarily contingent is to say that they are not laws of nature — they do not express any *natural necessity*; they may be true, but nothing in nature necessitates their truth (Beatty 1995: 51-52).

In sum, since "nature fails to necessitate" the truth of biological generalization, those generalizations fail to express laws of nature (*ibid.*: 53).

The ability to discharge the Necessity Objection is a constraint on any viable theory of biological lawhood. Chancy processes are the stock-in-trade in biology, and Beatty is surely right to use this fact

to undermine the intuition that the living world is a law-abiding place. For, in order for there to be laws for a domain there need to be necessities for that domain, and nothing about the biological world looks particularly necessary in light of Beatty's points.[3]

In this paper I propose a new way of thinking about necessity in biological contexts. I'd like to start off by suggesting that much of the lack of progress in making a positive case for distinctively biological laws is that we've been looking for necessity in the wrong place. The trend has been to look for exceptionlessness at the level of the *outcomes* of biological processes and to build one's claims about necessity off of that. However, as Beatty (1995) observed, even when we are lucky enough to find a biological "rule" of some sort, that rule is apt to be a victim of "the rule-breaking capabilities of evolutionary change." If indeed no generalization regarding the outcomes of biological processes is safe — even an exceptionless one — is safe (a point which I am willing to grant), we need to locate necessity elsewhere. A good place to start is, I think, precisely the point at which Beatty sees the possibility of lawhood as breaking down: at the level of *chances*.

I will argue that the chances associated with fitness, selection, and drift are necessities of a distinctively biological variety. After describing in more detail the chances in question, I argue that they are a species of natural necessity. Having established that these chances are necessary, I then go on to show (a) how those necessities ground laws of nature, and (b) what is distinctively biological about those laws. If these arguments are successful, an important part of Beatty's challenge will have been met, for we will have shown that there are certain biological generalizations whose truth is necessitated by nature in the appropriate way.

II. NECESSARY CHANCES

When we talk about certain laws associated with radioactive decay, such as its being a law that sodium-19 has a 50% chance of decaying within 40 nanoseconds, the necessity being invoked is of course not one concerning what *phenomena* must occur. It is a claim about the necessity of the *chances* associated with sodium-19's decay. Indeed it would be a contradiction to attribute the necessity to the

phenomena, since, after all, if it were necessary that each sodium-19 atom decay within 40 nanoseconds, then no such atom would have *any* chance of lasting longer than that, let alone a 50% chance (Lange 2006). In every world that shares our laws, all sodium-19 atoms have a 50% *chance* of decaying within 40 nanoseconds. But in only some of those worlds do all sodium-19 atoms *in fact* decay within 40 nanoseconds.

It is the idea of the assignment of a *necessary objective chance* of decay to an individual atom that is of interest here. The motivation for this idea, first proposed by Ernest Rutherford and Frederick Soddy (1903), was initiated by Rutherford's discovery that the rate of radioactive decay for single atoms of a given element was apparently invariant across all known types of manipulation of atomic processes. At the same time, Gigerenzer *et al* note,

> the disintegration processes occurring in different atoms of a macroscopic sample of radioactive material seemed to be somehow correlated with each other. The sample as a whole obeys a well-defined decay law: after a characteristic time (the half-life of the substance) half of the atoms of the radioactive element present at the beginning of the time interval will have decayed (Gigerenzer *et al* 1989: 180).

The explanation for the causal isolation of decay, combined with its coordinated regularity, was that the process was an inherently random one. And by 1910, enough data on the distribution of α-particles for particular time intervals had been amassed that Rutherford and Geiger could claim that "we may consequently conclude that the distribution of particles in time is in agreement with the laws of probability and that the α-particles are emitted at random" (Rutherford and Geiger 1910: 704).

Invariance across conditions is often thought to be indicative of necessity because it suggests that what *is* the case *has* to be the case. Indeed, Lange (2001, 2005a,b, 2009) has argued that necessity just *is* invariance across a certain range of conditions — namely, the set of conditions that are logically consistent with the candidate necessity (a property he calls *stability*). It seems to be just this sort of invariance that Rutherford had in mind when he used his various different types of failures to influence the

rate of atomic decay as a basis for inferring that an atom possessed its specific propensity to decay as a matter of necessity.

1.   *Necessary Chances: Random Drift*

There are illuminating parallels between atomic decay and random drift that are made particularly clear in the context of the dawn of the "neutral theory" of molecular evolution, which looks interestingly like the early studies of atomic decay. The neutral theory states that most allelic substitutions are neutral or effectively neutral with respect to their selective consequences, and therefore have most likely risen to fixation because of genetic drift. Motoo Kimura's initial observation that the rate of nucleotide substitution in the evolutionary history of mammals was extraordinarily high (about one nucleotide pair every two years) — a fact which

> can only be reconciled with the limit set by the substitutional load by assuming that most mutations produced by nucleotide replacement are almost neutral in natural selection (Kimura 1968: 625)[4] —

suggested that the mechanism responsible for most substitutions must be genetic drift, which meant that allelic substitutions were predominately random occurrences.   In addition, Kimura and Ohta's (1971) "Protein Polymorphism as a Phase of Molecular Evolution," the first fully developed expression of the theory (Gillespie 2004), begins by remarking that the

> strongest evidence for the theory is the remarkable uniformity for each protein molecule in the rate of mutant substitutions in the course of evolution. This is particularly evident in the evolutionary changes of haemoglobins, where, for example, the number of amino-acid substitutions is about the same in the line leading to man as in that leading to the carp from their common ancestor (Kimura and Ohta 1971: 467).

Just as Rutherford had reasoned from the fact that the rate of α-particle emission was constant across an exhausive range of conditions, the fact that the substitution rate remained constant for huge chunks of evolutionary time, spanning what was presumably an exhaustive range of environmental conditions, suggested that there was something *necessary* about the randomness. Whether or not the reasoning is

sound,[5] the correspondence in patterns of reasoning is suggestive. What we want to know now is how to get from here to some sort of biological law.

It is common to think of natural selection as a sampling process that is sensitive to certain physical differences among the individuals being sampled (Beatty 1984; Millstein 2002; Brandon 2005). Imagine a locus with two alleles: A_1, which causes spotted fur, and A_2, which leaves fur plain. If females in a given generation have preference of 2:1 to mate with spotted males, we expect the next generation, a sample of the parent generation, to exhibit a greater ratio of spotted males:plain males than the parent generation. Selection has occurred, because the sampling process in this round of sampling was sensitive to whether or not males possessed spots.

Part of what makes alleles A_1 and A_2 the targets of selection is that they result in different phenotypic traits. The environment's sensitivity to spots is what causes A_1 to spread and A_2 to decline. Contrast this case with another locus with two alleles: B_1 and B_2, both of which cause males to have a bushy tail, also preferred by females. Unlike A_1 and A_2, where the environment can influence their evolutionary trajectory by introducing a female mating preference for spots, there is nothing about the environment that can affect the frequency of B_1 relative to B_2 in future generations. Whether males have B_1 or B_2, they are going to have bushy tails. Since the distinction between B_1 males and B_2 males does not track any corresponding phenotypic difference, the sampling process will not be sensitive to whether males have B_1 or B_2.

Now, since the sampling process is not sensitive to whether males have B_1 or B_2, each male in the offspring generation is just as likely to have B_1 as he is to have B_2. Because of their causal isolation, B_1 and B_2 are, in a sense, *emitted at random* from one generation into the next. For the same reasons that we assign a necessary objective chance of .5 to a sodium-19 atom's decay during a particular 40 nanosecond time interval (in particular, the causal isolation of the event), we assign the same chance of .5 to a particular male offspring's possession of (say) B_1. We therefore expect the B_1:B_2 ratio to change for no other reason than chance.[6]

Robert Brandon (2006) has recently defended the view that drift should be considered the zero-force law in evolutionary theory. When there are no evolutionary forces (selection, mutation, migration, or nonrandom mating) affecting the eventual composition of an offspring generation, there will still be drift. In Brandon's Newtonian formulation (designed to reflect the analogy between his Principle of Drift [PD] and the zero-force law in Newtonian mechanics [the Law of Inertia]): "A population at equilibrium will tend to drift from that equilibrium unless acted on by an evolutionary force" (Brandon 2006: 10).

Brandon's argument for the PD's lawhood depends on the universality of drift and on the theoretical isomorphy between the PD in evolutionary theory and the Law of Inertia in Newtonian mechanics. This seems to me a very strong argument, but it can be made stronger still. Brandon is careful to qualify the PD by emphasizing that drift will *tend* to occur, rather than occur necessarily. In particular, he points out that there are some cases in which drift is impossible — cases in which "all of the fitnesses of the competing entities [in the population] equal either 1 or 0," what he calls a *Maximal Probability Difference* (*ibid*: 8). If the PD is a law of biology, then there has to be some necessity associated with it. Drawing on the parallel between drift and atomic decay, I want to argue that the associated necessity is not *drift itself*, but rather the *chances of drift*.

The necessity of the chances of drift can best be appreciated by thinking about drift more generally in terms of sampling error. In general, there is no guarantee that the frequency distributions of samples will deviate from those of the original population.[7] But for each sample size *n*, there will be a particular chance of sampling error with which it is associated, with the chances of sampling error decreasing as the sample size increases. Conceptually speaking, since sampling error is the difference between the frequency distribution of the sample and that of the original population, the *chance* of sampling error is merely the chance that the frequency distribution of the sample will deviate from that of the original population (1 - *p*, where *p* is the probability that the sample's frequency distribution will equal the frequency distribution of the original population). Suppose an urn contains 1,000 balls, half red and half

black.[8] In a sample of 10 balls, the modal outcome is that 5 balls will be red and 5 balls will be black. However the chance of the distribution turning out 50:50 is only about .25, meaning that the there is about a .75 chance that the sample distribution will deviate from that of the original population — i.e., a .75 chance of sampling error.

Returning to drift, we are now in a position to locate the necessity associated with the PD. The laws of probability will always be able to tell us the chance that the frequency distribution of a random sample of organisms will or will not mirror that of the population from which it is drawn. The chance that the sample's distribution will *not* mirror that of the parent population is the chance of evolutionary drift. This chance, being a consequence of the laws of probability, is a necessary one, at least according to the analyses of necessity with which I am familiar. Of course, as mentioned above, in a population of 1,000 organisms, half type-*A* and half type-*B*, about one out of every four random samples (size *n* = 10) will have an *A*:*B* ratio identical to the parent population, and so there will have been no evolutionary drift in these cases. But the PD's necessity is unscathed in these cases, since for each case in which the sample's distribution turns out to mirror that of the parent population, there was still a necessary chance of about .75 that the sample's distribution would drift.[9]

A final point on the PD's lawhood. One intuitive source of difficulty for the claim that there are laws in biology (one that, for example, has functioned in arguments against the existence of a human nature and biological kinds more generally) is the myriad individual differences among organisms. Do such differences undermine the PD's lawhood? No, they do not. The PD describes the zero-force state for evolutionary systems (Brandon 2006: 11, 13, 16). The absence of evolutionary forces implies that the sampling process involved in producing the next generation is *not* sensitive to the differences among individual organisms; sampling is *indiscriminate* (Beatty 1984; Millstein 2002). Taken as a zero-force law, then, the PD obtains regardless of the ways in which organisms are differentiated.

Indeed, there is a rather obvious way in which differences among individual organisms *amplify* the chances of drift. There are two key factors involved in the production of sampling error when sampling is random. One of them, sample size, has already been mentioned. The other factor is the amount of variation present in the population being sampled. Sampling error is much more likely to occur when the population being sampled is 20% *A*s, 20% *B*s, 5% *C*s, 16% *D*s, and 29% *E*s than when it is just half *A*s and half *B*s (or for that matter, all *A*s). Thus, the more variation there is among organisms in a population, the less likely a sample will be to reflect that population's composition. So rather than being undone by the differences among organisms, the PD is significantly strengthened.

2.   *Necessary Chances: Fitness*

The considerations regarding invariance are also involved, I argue, in discussions of biological fitness. According to one popular conception, *fitness* is the objective chance of a certain number of offspring Q, given an organism O in a certain environment E. This chance obtains in virtue of the way in which O is physically related to E, and is often treated as a *propensity* for an organism-environment dyad to result in a certain number of offspring (Brandon 1978; Mills and Beatty 1979). On this conception, we can gauge an organism's fitness by measuring its basic physical capacities and the sorts of things those capacities allow it to do in its environment, in the same way we might gauge a substance's propensity to dissolve in water by studying its basic molecular structure. The result of our analysis is an estimate, for a range of different numbers of offspring, of its chances of producing that number of offspring.

Fitness values function in evolutionary theory as descriptions of the dynamics of the evolutionary sampling process for a given population and allow us to make predictions regarding how a population will change over time. An organism O_1 is assigned a fitness value based on how probable it is that a particular bundle of physical properties associated with O_1 will be represented in a sample of the population.[10] When physical differences between O_1 and another organism O_2 cause O_1 to be better

than O_2 at reproducing in a given environment, O_1 is assigned a higher fitness value; the physical differences between O_1 and O_2 make it more probable that O_1 will appear in a future sample of the population.

How are fitnesses able to dodge the long arm of evolution, in a way that the distinctively biological facts that Beatty has in mind (e.g., those expressed by functional generalizations) are not? We can start to differentiate fitnesses from other types of biological facts by thinking about the ways in which fitnesses avoid the disruptive influences to which other, evolutionarily *contingent* facts are subject. Beatty cites random mutation as a regularity disrupter *par excellence* (Beatty 1995: 57-59). Mutations can disrupt biological regularities by introducing novel solutions to environmental problems, or, say, by introducing a trait that is desirable to the opposite sex. In general, the ability of mutations to *affect individual phenotypes* is what makes lots of distinctively biological facts evolutionarily contingent.

How do potential effects of mutations relate to fitnesses? One intuition is to assert that mutations can affect the fitness of some organism-environment dyad whenever those mutations change either an organism's phenotypic properties or the properties of something in its environment. What makes this suggestion plausible is the fact that an organism's reproductive success is a function of the highly complex interaction between it and its environment. The intrusion of mutations can threaten the sanctity of this interaction in a multitude of ways, most of which will be deleterious to the organism; if you mess with the organism, you mess with its chances of reproductive success.

But, in fact, this suggestion is a red herring, since any change in organism shifts our attention from one organism-environment dyad, O_1E_1, to another, O_2E_1 — the dyad consisting of the old environment plus the organism produced by the mutant allele (*mutatis mutandis* for any change in the environment). There has no more been a change of fitness in this case than in the case where we go from talking about the fitness of male lions of the Serengeti to male salamanders of the Oregon shore. To produce a change in the fitness of a particular organism-environment dyad would require something more fun-

damental than a change in the biological facts themselves (besides those to which fitness values refer), and since Beatty's evolutionary contingency thesis applies only to distinctively biological facts, fitnesses are preserved across any rule-breaking devices that the agents of evolutionary change can produce. Indeed, one might go even further than that. For, if we are to count the actual physical laws as part of the environment (which, intuitively, we should — think what would happen to birds in flight if we suddenly changed the gravitational constant), then fitnesses are preserved even across the set of physically possible states of affairs. Now that's necessity! (Proof: if fitnesses are not necessary, then there are two possible worlds p and q which are identical in their physical facts but in which organism O_p and O_q differ with respect to their probability of reproducing a certain number of offspring. If p and q share their physical facts, then O_p is physically identical to O_q. If O_p is physically identical to O_q, then no evolutionary sampling process can differentiate between O_p and O_q. If no evolutionary sampling process can differentiate between O_p and O_q, then O_p and O_q will have the same probability of reproducing a certain number of offspring. Therefore, if fitnesses are not necessary, then O_p and O_q both have and do not have the same probability of reproducing a certain number of offspring — Contradiction!).

Like water solubility, then, I'm suggesting that fitness values are treated as necessary features of the organisms to which they're assigned: given that organism in that environment, there *has* to be that specific chance of a certain level of reproductive success. If fitness values are assigned on the basis of a particular arrangment of physical properties O_1E_1, then those values should remain constant as long as that arrangement of physical properties remains constant in the relevant ways. This sentiment is widespread in the biological literature, for example, as reflected in descriptions of the concept of fitness as a "characteristic reproductive success" (Brandon 1990: 147) or "a consistent relationship" between a trait "and mating ability, fertilizing ability, fertility, fecundity, and, or, survivorship," (Endler 1986: 4); that is, the sort of relationship in which the trait and a "characteristic reproductive success" do not dissociate.[11]

Earlier I argued that the necessity of the chances associated with drift makes the PD a law of nature. I now want to make a similar argument for the PNS. As with drift, it is not necessary that selec-

tion occur — i.e., that better adapted types outreproduce more poorly adapted ones. Even Darwin saw this. But for any population composed of types *A* and *B*, if *A*s are fitter than *B*s, then there will be some chance that *A*s will outreproduce *B*s. This chance — what I'm calling the chance of selection — is a function of the difference in fitness between *A*s and *B*s, in the same way that the chance of drift is a function of the difference in fitness (or lack thereof) between different forms in a population. When the difference in fitness between *A*s and *B*s is very high, the chance of selection will also be high; when those differences are very low, the chance of drift will be very high (Brandon 2005: 168-169; see Figure 1). Whether high or low, those differences don't change because the fitnesses associated with *A*s and *B*s don't change, and so the chances of selection occurring in a population composed of *A*s and *B*s will remain similarly stable.
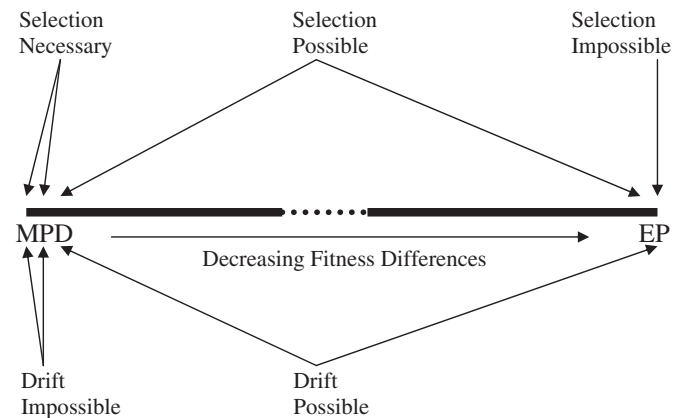
Figure 1: The heavy horizontal line, with dotted center section, represents the infinite number of possible fitness distributions from Maximal Probability Differences (MPD—all fitness = 0 or = 1, with some of both) on the left to the Equiprobable Distribution (EP—all fitness the same) on the right. The arrows emanating from the different descriptions of the modalities of selection and drift indicate the areas of the distribution falling under these descriptions. Source: Brandon 2006: 327

How does this bear on the lawhood of the PNS? Drawing on Brandon (1990: 11), let us expresses the PNS as follows:

> If *a* is better adapted than *b* in environment *E*, then (probably) *a* will have
> greater reproductive success than *b* in *E*.

In what way does this express a law of nature? And how does its lawhood reside in the necessity of the chance of selection?

Assume that *A*s are 3x as fit as *B*s. In this case, there is a 3:1 chance that selection will occur — i.e., there is a 3:1 chance that *A*s will actually outreproduce *B*s. Now suppose that, as a matter of fact, *B*s end up outreproducing *A*s after one round of sampling. How is the nomic status of the PNS preserved in this case? As everyone knows (and as some have worried) the fact that *B*s outreproduce *A*s on occa-

sion does not disrupt the truth of the PNS, because even in the case where *B*s outreproduce *A*s, the *chance* of selection occurring was still 3:1. This chance is preserved across any and all states of affairs (at least, those with which it is logically consistent), because its source — the difference in fitness between *A* and *B* — is preserved across all such states. Thus, the PNS expresses a necessity because it still would have held no matter what else had been the case: if *A*s are fitter than *B*s, then — no matter what — *A*s will probably outreproduce *B*s.

III. NECESSARY CHANCES AND THE LAWHOOD OF THE PNS: HISTORICAL CONSIDERATIONS

> The law of the succession of types, although subject to some remarkable exceptions, must possess the highest interest to every *philosophical* naturalist" (Darwin 1839: 210)

The PNS's lawhood resides in the fact that relationship between (a) being fitter and (b) (probably) having greater reproductive success would still have held, no matter what. I would now like to argue this model of the PNS's lawhood is confirmed by the way in which Darwin conceived of his own principle of natural selection. However, what Darwin giveth with one hand, he taketh away with the other. As our analysis of Darwin's own conception will make clear, what allows the PNS to achieve the rank of Law of Nature is precisely what has been perceived as robbing it of its distinctively biological status.

In a famous 1860 letter to Asa Gray, Darwin proclaimed that he was "inclined to look at everything as resulting from designed laws, with the details . . . left to the working out of what we may call chance." Among the "designed laws" numbered natural selection, and among the "details" numbered the occurrent biological facts such as organismal form and distribution. For Darwin, "chance" enters the picture in two prominent ways: (1) as the agent responsible for the menu of materials from which nature can select (this is the sense employed in his correspondence with Gray, brought out vividly in his "architect" analogy at the end of *Variations*) – call this *chance$_1$*; and (2) as the explanation for why some individuals leave more descendants than others – call this *chance$_2$*. What I want to do in the remainder of this paper is show how each of these two senses of "chance" functions in Darwin, how they are related, and

how, on this understanding, exceptions to biological regularities don't pose a problem for biological laws.

1. Chance₁: The "Chance" of "Exceptions"

The Darwin aboard the *Beagle* knew, as did other naturalists, that a region's extant forms sometimes fail to resemble its extinct forms – cases of what were in his words "exceptions" to the law of succession of types. These "exceptions" were thought to be the product of the sort of "chance" events in which Darwin took particular rhetorical delight, such as when the occasional bird's nest sits upon a detached bit of iceberg, destined for shores unknown, or when the occasional land-bird is blown clear "across the whole Atlantic Ocean, from North America to Ireland or England;" where

> seeds could be transported by these wanderers only by one means, namely, in dirt sticking to their feet, which is in itself a rare accident. Even in this case, how small would the chance be of a seed falling on favourable soil, and coming to maturity! But it would be a great error to argue that because a well-stocked island, like Great Britain, has not, as far as is known (and it would be very difficult to prove this), received within the last few centuries, through occasional means of transport, immigrants from Europe or any other continent, that a poorly-stocked island, though standing more remote from the mainland, would not receive colonists by similar means (*Origin* I: 364-365).

"Chance" events like these were tremendously important for Darwin's later theorizing, and for his argument in the *Origin*. For it is "chance" events that produce the variations from which nature selects.[12] Now, the variation in this passage is generated by a particular type of "chance" event – *viz.*, "chance" migration. But it fits into a much more general and deeply sophisticated conception of the respect in which variations are "accidental" or the product of "chance."

To get a better handle on Darwin's understanding of *chance₁*, let us first turn to the *Origin*, for it is here that we find the beginning of what would become a decade-long effort to explicate the precise sense in which variation is the result of "chance." The first line of Chapter 5 – "The Laws of Variation" – begins with this:

> I HAVE hitherto sometimes spoken as if the variations—so common and multiform in organic beings under domestication, and in a lesser degree in

those in a state of nature—had been due to chance. *This, of course, is a wholly incorrect expression*, but it serves to acknowledge plainly our ignorance of the cause of each particular variation (Darwin 1859: 131, my emphasis).

Later, in volume II of *The Variations of Animals and Plants Under Domestication*, Darwin would provide a vivid explanation of why his use of the word "chance," while "wholly incorrect," was more than apt:

Let an architect be compelled to build an edifice with uncut stones, fallen from a precipice. The shape of each fragment may be called accidental; yet the shape of each has been determined by the force of gravity, the nature of the rock, and the slope of the precipice,—events and circumstances, all of which depend on natural laws; but there is no relation between these laws and the purpose for which each fragment is used by the builder. In the same manner the variations of each creature are determined by fixed and immutable laws; but these bear no relation to the living structure which is slowly built up through the power of selection, whether this be natural or artificial selection.

The analogy reappears in the last couple of pages of *Variations* (vol II), where Darwin further clarifies the notion of *chance*$_1$ and its relation to natural law:

Now, the fragments of stone, though indispensable to the architect, bear to the edifice built by him the same relation which the fluctuating variations of each organic being bear to the varied and admirable structures ultimately acquired by its modified descendants … The shape of the fragments of stone at the base of our precipice may be called accidental, but this is not strictly correct; for the shape of each depends on a long sequence of events, all obeying natural laws; on the nature of the rock, on the lines of deposition or cleavage, on the form of the mountain which depends on its upheaval and subsequent denudation, and lastly on the storm or earthquake which threw down the fragments. But in regard to the use to which the fragments may be put, their shape may be strictly said to be accidental (Darwin 1868: 430-431).[13]

The "chance" or "accidental" nature of variation is not *brute* chance, much less a genuine "accident of nature." Rather, variation is accidental *with respect to* the uses to which it is put by natural selection. It is unquestionably law-governed, but the laws of nature that produce variation operate independently of the law which governs the fate of different organismal forms. Darwin's reference to "exceptions," then, is best understood as a reference to *chance*$_1$ events, events that *are law-governed* but *accidental with respect to* the law of succession of types.

2. Chance₂: "Better Chances"

We can distinguish *chance₁* from another important sense of "chance" found throughout Darwin's work, one to which he appeals when he refers to organisms in certain situations having a "better chance" than others of surviving and reproducing, such as when he suggests that "the extreme varieties and extreme species will have a better chance of surviving or escaping extinction" (Darwin and Stauffer 1975: 238), or that

> forms existing in larger numbers will always have a better chance, within any
> given period, of presenting further favourable variations for natural selection
> to seize on, than will the rarer forms which exist in lesser numbers (Darwin
> 1859: 177).

It is "better chances" that translate into a *tendency* for such-and-such to happen, as reflected in the conclusion which follows the preceding quote: "Hence, the more common forms, in the race for life, will *tend* to beat and supplant the less common forms, for these will be more slowly modified and improved" (*ibid*: 177, my emphasis).

Here, then, is clear evidence that Darwin thought of natural selection as a causing a *tendency* in nature – a tendency for forms with better *chances* of survival and reproduction to *actually* outreproduce other forms. We can amplify this point by appreciating the relationship between *chance₁* ("chance events") and *chance₂* ("better chances" of survival and reproduction). Jonathan Hodge has phrased the relation this way:

> (i) it is 'a matter of chance' as to what what variations are generated in any
> environmental conditions; but (ii) it is not a 'matter of chance' as to which are
> more or less successful, in those conditions, in contributing offspring to sub-
> sequent generations (Hodge 1983: 287).

In other words, variation is accidental (with respect to environmental conditions). But the relationship between "better chances" of survival and reproduction and a *tendency* "to beat and supplant" other forms of life is, for Darwin, no accident. In contrast to the "accidental" connection between variations and the environmental conditions in which they arise, what connects "better chances" with "tendencies to beat and supplant" other forms of life is "not a 'matter of chance'" – the connection is a *necessary* one.

The reason the existence of a *law* of natural selection is important here is because we can imagine a world where some individuals, due to their better adaptedness, have a better chance of surviving and

reproducing but in which those individuals quickly die or fail to leave relatively many descendants (in the same way we can imagine a world where an individual buys almost all the lottery tickets and still loses, or in which all sodium-19 atoms last beyond their half-life of 40 nanoseconds). The law of natural selection governs what happens as a result of having "better chances" of survival and reproduction: under the influence of natural selection, "better chances" of survival and reproduction result in certain forms "tending to beat and supplant" others. Had natural selection not been included in the grand system of natural laws, better chances of survival and reproduction would not have resulted in a *tendency* for certain forms to beat and supplant others. Those forms with better chances would have done no better than chance (Consider: in the case where offspring do not resemble parents, better chances of surviving and reproducing might not have resulted in the tendency of some forms to beat and supplant others).[14]

Understood in this way, there may be "exceptions" to better adapted forms *actually* outreproducing those poorly adapted; such things can happen by chance$_1$. By contrast, there will never be an exception to forms with better chances of reproductive success *tending* to outreproduce those with worse chances of reproductive success.

I have been arguing that Darwin understood natural selection to be a law which governs the relationship between biological chances$_2$ and biological tendencies, and that this provides confirmation for the model of the PNS's lawhood outlined Section II: the PNS expresses a law of nature because when the chances of *A*'s reproducing exceed the chances of *B*'s reproducing, *A*s will (probably/tend to) outreproduce *B*s.

I think this is precisely the way in which the principle of natural selection is treated in contemporary biological science. Fitness values furnish us with (but are not equivalent to) expectations regarding a population's composition in future generations. When the population is very small and the actual composition of future generations deviates from those expectations, we don't mark it down as yet another exception to Darwin's principle of natural selection. Why? Because it does not impugn the lawful relationship between having a better chance of reproductive success, on the one hand, and tending to beat and supplant other forms of life, on the other. The nomic status of the PNS can tolerate the failure of better adapted types to become widespread in the population. What it cannot tolerate is that

such failure be *systematic* – i.e., that better adapted types *tend not* to become widespread in the population.

IV. But is it *biological*?

Have we, in our relentless pursuit of necessity, neglected to keep track of whether the necessities we've found have been "distinctively biological"? After all, necessity itself comes fairly cheap; there are as many logical and mathematical necessities as you like. There also appear to be a lot of physical necessities. Many of these have figured importantly in biological science. But Beatty's challenge has asked us for a specific variety of necessities — those with distinctively biological content, not "just mathematical, physical, or chemical generalizations (or the deductive consequences of mathematical, physical, or chemical generalizations)" (Beatty 1995: 46).

Beatty points out that Abner Shimony (1989) follows a pattern of reasoning similar to the one used above to establish the necessity of the chances associated with fitnesses and drift to argue that there is nothing distinctively biological about what we call "natural selection" — roughly, since the PNS just *is* a particularized statement about the effects of chances, there is no such thing as a distinctively biological *Principle of Natural Selection* (similarly for the PD). Rather, there are just instantiations of certain facts about chances, and Darwin happened to notice one of the biological instantiations of those facts. This view has recently been elaborated extensively by "Statisticalists" in a series articles which have argued that natural selection is not a biological phenomenon, but rather an abstract phenomenon that is a feature of all systems where there is variation in rates of increase.[15]

Given the centrality of the concepts of fitness, selection, and drift to biological science, the idea that they are not distinctively biological concepts strikes me as implausible. If fitness, selection, and drift don't qualify as distinctively biological phenomena, I can't imagine what would. Brandon (1990, Chapter 4) argues for this perspective when defending the biological status of the PNS through a detailed appeal to scientific practice. Beginning with the concession that "the PNS is simply a … rule that

allows one to connect propensities to observed frequencies" (aka the Principle of Direct Inference), he asks,

> why consider it a part (indeed a central part) of *biological* theory? Isn't it simply an application of a part of probability theory to a biological problem? Biologists, like other scientists, use inference rules from deductive and inductive logic. For instance, *modus ponens* … is frequently used by evolutionary biologists. Yet we do not feel compelled to treat *modus ponens* as a law of evolutionary biology. What is so special about the PNS? (*ibid*: 140)

In response, Brandon points to two crucial roles played by the PNS in biological science. First, he argues, the PNS unifies distinct instances of some better adapted organism outreproducing a more poorly adapted one. What unites two biological facts — e.g., (a) the superior reproductive tendencies of dark-colored moths in dark environments, and (b) the superior reproductive tendencies of heavy metal-tolerant plants in contaminated environments — is a deeper fact about biological systems generally, namely that the better adapted actually tend to have greater reproductive success. Second, he suggests that the PNS, and not the Principle of Direct Inference (PDI), is what serves as the central organizing principle for evolutionary biology, in that it alone directs us to the assessment of relative adaptedness with respect to a common selection environment (our "*E*" above). Elliot Sober signals a similar sentiment when he comments that Beatty's way of characterizing the "distinctively biological" constraint "has the curious result that biologists are not doing biology when they construct mathematical models of biological processes; rather, they are doing mathematics" (Sober 1997: S461).

The conflict here is between (i) the intuition (exploited by Beatty and Shimony) that a generalization cannot say something distinctive about biological systems if that generalization could also be true of non-biological systems, and (ii) the intuition (employed by Brandon, Sober, and myself) that the solutions to biological problems should be considered a proper part of biology. Since the PNS is just a special case of the PDI, how can it express a distinctively biological law? On the other hand, how can

its content *not* be distinctively biological, given that it solves that most distinctive of biological problems — viz., biological adaptation?

The argument from the premise that the PNS is a deductive consequence of the PDI to the conclusion that there is nothing distinctively biological about the PNS employs an unstated yet substantive conception of the semantic content of the PNS which assumes that all there is to the PNS is the more general commitment that we tend to view inferences from objective probabilities to frequencies as inductively well-founded. This view derives additional plausibility from the fact that evolutionary theory itself is thoroughly statistical, a feature to which I have appealed in this essay to demonstrate the lawhood of certain generalizations about the evolutionary trajectories of biological systems. While I do not find it hard to see why this view of the PNS's content would resonate with people, I do think that it misses something important and general about how scientific theories actually relate to one another. What it misses is the fact, familiar since Kuhn, that there is more to theoretical equivalence than merely showing that some theory T_2 can be logically derived from another T_1. Equally important for the content of theories are the meanings of theoretical terms, which depend on a range of contextual and historical factors which have a life of their own, one which will typically float free from the formalization of the theories themselves.[16] This is apparent even in contemporary evolutionary theory, and has been a part of that theory since its own formalization in the 1920s. Many evolutionary biologists conceive of natural selection as a sampling process. Others conceive of it as an optimization process. Biologists can agree on the family of models that characterizes evolutionary theory while disagreeing about the deeper implications of those models.

It is this general fact about how theories do and do not relate to one another which allows the PNS to retain its distinctively biological flavor while being formally derivable from the PDI. Earlier I said that the nomic status of the PNS can tolerate the failure of better adapted types to become widespread in the population, but *cannot* tolerate that such failure be *systematic* – i.e., that better adapted types *tend not* to become widespread in the population. Were we to find that better adapted types in general tend

not to become widespread in the population, we would abandon the PNS. We would abandon the PNS because it turned out not to be able to explain biological adaptation. But not being able to explain biological adaptation does not seem to be a problem for the PDI. That is, we would not abandon the PDI simply because better adapted types tend not to become widespread in the population; I'm sure we could find something else for the PDI to do (if it wasn't already doing a bunch of stuff independent of its influence on evolutionary theory, which it is). If the PNS were merely a deductive consequence of the PDI, abandoning the PNS would compel us to abandon the PDI (*modus tollens*). But I very much doubt we would feel any such compulsion. The explanation for our rejection of the PNS is its failure to solve biological problems. The general PDI is not charged with solving those problems, and so it is not threatened by the failure of the PNS. One response to this picture would be to say that retaining the PDI in the face of the PNS's failure is self-contradictory. That would be true if the content of the PNS is determined solely by the truth conditions for the PDI. Another, better view — the one I'm advocating — suggests that the PNS is not reducible to the PDI because the role of the PNS in biological science is partly constitutive of the PNS's semantic content.

V. CONCLUSION

I have argued that the Principle of Natural Selection and the Principle of Drift are distinctively biological laws of nature, because (a) they are distinctively biological, and (b) they possess the degree of necessity we expect from laws of nature, in virtue of the chances with which they are associated. Both of these conclusions have more or less been in the literature on biological laws for a while now. The virtue of my account, I think, lies in directing our attention to two key factors in explaining why the PNS and the PD appear to be *bona fide* laws of nature over which biological science can appropriately claim exclusive rights. Those two key factors are (i) the contextual determinants of meaning, which allow the PNS to exist independently from the Principle of Direct Inference, and (ii) the fact that necessity can reside at the level of chances (and tendencies) as well as occurrent phenomena. Both (i) and (ii) have an importance that generalizes beyond what they can explain about current biological science. (i) suggests

a general sense in which laws in autonomous special sciences might not be *reducible* to laws in lower-level disciplines, even if those special science laws are *derivable* from laws at lower levels. (ii) helps to explain why general trends are often taken as evidence of law-governed processes, even when the data exhibit nothing close to exceptionless regularities.

REFERENCES

Abrams, M. (2007) "Fitness and Propensity's Annulment." *Biology and Philosophy* **22**(1): 115-130.

— (2009) "The Unity of Fitness." *Philosophy of Science* **76**(5): 750-761.

Beatty, J. (1984). "Chance and Natural Selection." *Philosophy of Science* **51**(2): 183-211.

— (1995). "The Evolutionary Contingency Thesis." in G. Wolters and J. Lennox *(eds.) Concepts, Theories, and Rationality in the Biological Sciences.* Pittsburgh: University of Pittsburgh Press (45-81).

— (2008). "Chance Variation and Evolutionary Contingency: Darwin, Simpson, *The Simpsons*, and Gould" in Ruse (ed.) (2008): 189-210.

Bouchard, F. and Rosenberg, A. (2004) "Fitness, Probability and the Principles of Natural Selection." *The British Journal for the Philosophy of Science* **55**(4): 693-712.

Brandon. R.N. (1978). "Adaptation and Evolutionary Theory." *Studies in the History and Philosophy of Science* **9**(3): 181-206.

— (1990). *Adaptation and Environment.* Princeton: Princeton University Press.

— (2005). "The Difference Between Selection and Drift: A Reply to Millstein." *Biology and Philosophy* **20**(1): 153-170.

— (2006). "The Principle of Drift: Biology's First Law." *Journal of Philosophy* **103**: 319-336.

Brandon, R.N. and Carson, S. (1996). "The Indeterministic Character of Evolutionary Theory: No 'No Hidden Variables Proof' but No Room for Determinism Either." *Philosophy of Science* **63**(3): 315-337.

Collin, R. and Miglietta, M.P. (2008). "Reversing opinions on Dollo's Law." *Trends in Ecology & Evolution* **23**(11): 602-609.

Darwin, C. (1839). *Journal of Researches into the Geology and Natural History of the Various Countries Visited by H.M.S. Beagle Etc.* London: Henry Colburn.

— (1859). *On the Origin of Species by Means of Natural Selection.* London: J. Murray. [1st ed.]

— (1860). Letter to Asa Gray (May 22nd).

— (1868). *The Variation of Animals and Plants under Domestication* (vol II). London: John Murray.

— (1871). *The Descent of Man, and Selection in Relation to Sex.* London: John Murray.

Dietrich, M. and Millstein, R. (2008). "The Role of Causal Processes in the Neutral and Nearly Neutral Theories." *Philosophy of Science* **75**(5): 548-559.

Endler, J. (1986). *Natural Selection in the Wild.* Princeton: Princeton University Press.

Field, H. (1973). "Theory Change and The Indeterminacy of Reference." *Journal of Philosophy* **70**(14): 462-481

Gillespie, J. H. (2004). *Population genetics: a concise guide.* Baltimore, Md: The Johns Hopkins University Press (2nd ed).

— (1987) "Molecular Evolution and the Neutral Allele Theory." *Oxford Surveys in Evolutionary Biology* **4**: 10-37.

Gigerenzer, G., Swijtink, Z., Porter, T., Daston, L., Beatty, J., and Krüger, L (1989). *The Empire of Chance: How Probability Changed Science and Everyday Life.* New York: Cambridge University Press.

Godfrey-Smith, P. (2009). *Darwinian Populations and Natural Selection.* New York: Oxford University Press.

Gould, S.J. (1970). "Dollo on Dollo's law: Irreversibility and the status of evolutionary laws." *Journal of the History of Biology* **3**(2): 189-212.

Heidelberg, L. and Rheinwald, R. (eds.) (1983) *Probability since 1800: Interdisciplinary Studies of Scientific Development* Bielefeld: Universität Bielefeld.

Hodge, M. (1983a). "Law, Cause, Chance, Adaptation and Species in Darwinian Theory in the 1830s, with a Postscript on the 1930s" in Heidelberg and Rheinwald (ed.) (1983a): 287-330.

Kimura, M. (1968). "Evolutionary Rate at the Molecular Level." *Nature* **217** (5129): 624-626

Kimura, M. and Ohta, T. (1971) "Protein Polymorphism as a Phase of Molecular Evolution." *Nature* **229**(5285): 467-469.

Lange, M. (2005a) "Laws and Their Stability." *Synthese* **144**(3): 415-432.

— (2005b) "A Counterfactual Analysis of the Concepts of Logical Truth and Necessity." *Philosophical Studies* **125**(3): 277-303.

— (2006) "How to Account for the Relation Between Chancy Facts and Deterministic Laws." *Mind* **115**(460): 917-946

— (2009). *Laws and lawmakers : science, metaphysics, and the laws of nature.* Oxford ; New York: Oxford University Press.

Matthen, M. and Ariew, A. (2002). "Two Ways of Thinking about Fitness and Natural Selection." *The Journal of Philosophy* **99**(2): 55-83.

— (2009) "Selection and Causation." *Philosophy of Science* **76**(2): 201-224.

McShea, D. and Brandon, R. (2010) *Biology's First Law.* Chicago: University of Chicago Press

Mills, S.K. and Beatty, J.H. (1979) "The Propensity Interpretation of Fitness." *Philosophy of Science* **46**(2): 263-286.

Millstein, R. (2002). "Are Random Drift and Natural Selection Conceptually Distinct?" *Biology and Philosophy* **17**(1): 33-53.

— (2005) "Selection vs. Drift: a Response to Brandon's Reply" *Biology and Philosophy* **20**(1): 171-175

Millstein, R., Skipper, Robert A., and Dietrich, M. (2009) "(Mis)interpreting Mathematical Models: Drift as a Physical Process." *Philosophy and Theory in Biology* **1**:e002.

Ruse, M. (ed.) (2008) *The Oxford Handbook of Philosophy of Biology* New York: Oxford University Press.

Rutherford, E. and Soddy, F. (1903) "LX. Radioactive Change." *Philosophical Magazine* (Series 6) **5**(29): 576-591

Rutherford, E., Geiger, H. and Bateman, H. (1910) "LXXVI. The probability variations in the distribution of α-particles." *Philosophical Magazine* (Series 6) **20**(118): 698-707

Sober, E. (1997) "Two Outbreaks of Lawlessness in Recent Philosophy of Biology." *Philosophy of Science* **64**(4): S458-S467.

Shimony, A. (1989). "The non-existence of a principle of natural selection." *Biology and Philosophy* **4**(3): 255-273.

Strevens, M. (2000). "Do Large Probabilities Explain Better?" *Philosophy of Science* **67**(3): 366-390.

Walsh, D. (2007) "The Pomp of Superfluous Causes: The Interpretation of Evolutionary Theory." *Philosophy of Science* **74**(3): 281-303.

Walsh, D., Lewens, T. and Ariew, A. (2002) "The Trials of Life" *Philosophy of Science* **69**: 429-446.

Waters, C. K. (1986). "Natural selection without survival of the fittest." *Biology and Philosophy* **1**(2): 207-225.

NOTES

[1] Or at least it used to be. See, for example, Collin and Miglietta (2008).

[2] See, for example, Darwin (1871): 136

[3] One response, pursued by Elliot Sober, attempts to get around this argument in the following way. Suppose the truth of the distinctively biological generalization "All Ps are Q" is contingent upon the mutation I (or, more broadly, some set of initial conditions) for Q-ness arising at some point in the evolutionary history of Ps. Sober suggests that this gives rise to another generalization, equally biological: I —> (All Ps are Q), "and it is far from clear that *this* generalization is contingent" (Sober 1997: S460). While I share with Sober the strategy of looking beyond the phenomena themselves to look for biological laws, my solution to the problem renders the modal status of the relevant generalizations less ambiguous.

[4] Quoted in Gillespie (1987: 10).

[5] See Gillespie (1987: 27) for an outline of some major problems.

[6] In my characterization of drift, I have attempted to preserve what I think is correct in the "drift-as-outcome" and "drift-as-process" interpretations of drift (see Millstein, Skipper, and Dietrich 2009; Millstein 2002, 2005; Brandon 2005, 2006) without worrying too much about the consequences of adopting a particular interpretation. When discussing drift in the context of explaining evolutionary history, I find it useful to think of drift as a process. When discussing how evolutionary predictions are derived, I find it useful to think of drift as an outcome. My sense is that a similarly principled ambivalence pervades the professional biological literature. In any case, nothing I say with respect to the chances associated with drift seems to me to hang on whether one thinks of it as a process or as an outcome. An excellent discussion of this issue in the context of the neutral theory can be found in Dietrich and Millstein (2008).

[7] However, there are specific cases in which the frequency distributions of the sample are guaranteed to deviate from those of the original population. For example, Brandon and Carson (1996: 322) describe a case in which a population bottleneck reduces the population size from 1,000 in the first generation to 10 in the second generation. If type-A organisms occur with frequency .01 in the original population, it is mathematically impossible for them to occur with this same frequency after the bottleneck (since no class can have just 10% of a member).

[8] This example is inspired by Brandon and Carson (1996: 322).

[9] This underscores Brandon's (2006: 14) point that the most probable explanation for long-term stasis in population composition is stabilizing selection. That is, since 3 out of 4 samples are expected to deviate from the parent distribution, we would expect there to not be long-term stasis in frequency distributions unless those distributions were being maintained by an external force, like selection (see also McShea and Brandon 2010 for a host of biological examples.)

[10] My source for the analogy between fitness and water solubility is Brandon (1990).

[11] Thanks to [correspondent] for helpful discussion on this point.

[12] It is important here to recall that the "rule-breaking" capabilities of "chance" events are the basis upon which the argument against biological laws rests.

[13] Beatty (2008) provides an interesting discussion of the broader upshots of this and related remarks by Darwin.

[14] See, for example, Godfrey-Smith (2009), §3.2.

[15] Matthen and Ariew 2002, 2009; Walsh, Lewens, and Ariew 2002; Walsh (2007). Waters (1986) argues for a similar conclusion.

[16] Field (1973) argues for an even stronger conclusion on grounds which differ from Kuhn's own.