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Modal Concepts in the Biological Sciences

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This is dedicated to my parents, who instilled in me a moral compass, granted me the latitude to find my own way, and gave me the support to pursue a discipline like philosophy.
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ABSTRACT

“Modality” refers to the concepts (and surrounding controversies) of “possibility” and “necessity.” Recently, a great deal of attention paid to these concepts in metaphysics. Not surprisingly, this literature has not been adopted in the field of philosophy of biology. In this work, I argue that there is a need to understand how modal concepts function in biology. Biologists already employ modal concepts in a variety of contexts. However, they do not explain how these concepts function or ought to function within the biological domain. From a philosophical perspective, there is a framework for how modal concepts operate in physics. But this framework cannot be adopted by the biological sciences. Since work on modality is relatively new to philosophy of biology, I spend the first three chapters justifying, defining, and restricting the project of creating a modal framework in biology. In the penultimate chapter, I present and criticize the single account of “biological possibility” found in the literature, which is offered by Daniel Dennett. Finally, I provide a positive account of how we should apply modal concepts in the biological sciences.
CHAPTER 1
MOTIVATING, DEFINING, AND RESTRICTING THE PROJECT

Introduction

If we are to explain how things are, we must be able to explain how things might have been, or must be, or couldn’t be (Dennett, 1995, 118).

Could I have been an astronaut or president? Could I have been born in a different time from different parents? Could gold have been green instead of yellow or have a composed of a different atomic structure? Controversies centering around modality (the concepts of possibility and necessity) are at the heart of many deep philosophical disagreements: the necessity of analytic propositions and a priori knowledge (are there any necessities at all?), the ontological status of possibility and necessity (in what sense, if any, are possible things actual?), and the relationship between epistemology and metaphysics (what is the relationship between conceivability and possibility?). These controversies have received much attention recently in philosophy. Little of this work, however, has been translated into the biological literature. There are good reasons for this. Most controversies over modality have no more to do with biology than they do with professional baseball. Yet, as I will argue throughout this project, there is a need to develop a philosophically rigorous foundation for how modal concepts ought to be used in biology.

Restricting the original question to a particular domain, one can ask what is biologically possible? Are unicorns possible? What about flying pigs or centaurs? Do living things need to be composed of carbon or replicate by means of DNA? Are fifty-foot tall humans possible, or two-hundred-meter tall trees? One problem with answering these questions is that the original question itself is vague. In what way are we restricting possibility to the biological domain? Are we concerned with the necessary and sufficient conditions of life? Are we interested in possibility contextualized to a particular environment? Or, are we asking whether something is possible given a particular starting point, say some actual species?

This ambiguity has not prevented biologists and philosophers of biology from employing modal concepts in their explanations. For example, some biologists have made impossibility claims about particular species or higher taxonomic group. Koch et.al. (2004) claim that there is an ultimate height which trees cannot surpass. However, there is a dispute about whether the limiting factor is hydraulic (Niklas and Spatz, 2004) or mechanical (McMahon, 1973). Biologists have also described hypothetical biological spaces, such as the adaptive landscape (Wright, 1932) and morphospaces (Raup, 1963, McGhee, 1999). Finally, theorists like Gould (1989) and Dawkins (1986, 1997) metaphorically employ non-actual organisms to explain particular biological phenomena, but provide no further description of how to describe the set of non-
actual possible organisms. In itself, using modal concepts in explanations is not problematic. Ordinary language is laden with modal operators. For example, if I say that “I can’t go to the movies tonight,” the proposition contains a modal operator (it is not possible that I go to the movies). However, we don’t need a philosophical analysis to understand the conversationally implied content of my claim; namely that I have activities of greater importance than seeing a film.

Unlike the prior example, when modal concepts are used in biological explanations they do require a framework, and at this time I have yet to see a satisfactory account. There are often first-order applications of the terms but there is no second-order discussion of these terms; i.e., they are using these terms without explaining what these terms mean.

Although the completed dissertation is needed to properly clarify and address how and why modal concepts are used in biology, in the introductory chapter I will briefly motivate, define and restrict the project. Next, I will distinguish between the roles that philosophers and biologists will play in settling issues of modality. Finally, I will provide a short chapter-by-chapter account of what will follow. At the end of this introduction, you should have a general idea of the core questions driving this project and how I will address these questions.

Motivating the Project

As the opening quotation claims, in order to know how things are, we have to know how things could have been or could not have been. Making this general point more precise, in order to understand why the biological world looks as it does, we have to understand the different ways things could have gone or could not have gone. A similar point was expressed sixty-five years earlier by one of the architects of the modern synthesis, R. A. Fisher:

No practical biologist interested in sexual reproduction would be led to work out the detailed consequences experienced by organisms having three or more sexes; yet what else should he do if he wishes to understand why sexes are, in fact, always two? (1930, ix).

In order to understand why there are two sexes, we have to first understand why there could not have been more than two. Fisher goes on to discuss population genetic reasons why two sexes are optimum. Within Fisher’s statement is a plea for modal biology. In order to understand why something is the case, we have to ask, “What else could have been?” In order to understand the actual, we have to understand the possible.

Much work in theoretical biology is dedicated to the guiding forces of evolution, such as natural selection, which mold animal forms and ecological relationships. However, a major contributor to evolution, which has historically been neglected, is the role of contingent events. Gould explains the role of contingency in a historical science, such as evolutionary biology:
A historical explanation does not rest on direct deductions from laws of nature, but on an unpredictable sequence of antecedent states, where any major change in any step of the sequence would have altered the final result. This final result is therefore dependent, or contingent, upon everything that came before – the unerasable and determining signature of history (1989, 283).

Emphasizing the historical status of natural selection is a major theme through Gould’s work and never more explicit than in the oft cited metaphor about “rewinding the tape of life” (1989). Here, Gould proposes that if the tape of life were rewound, say to the Precambrian, the biological world would look very different than it does today. Of course, as with any metaphor, there are problems. If one rewinds a tape of Gone with the Wind, one will simply have an encore of the same movie. If the world is deterministic, and the tape of life were rewound, would not the same historical contingencies play out in the same way resulting in an exact replay of the original? Here, I think that Maynard Smith (1992) has the right idea when he wryly suggests that once the tape is rewound, “simply move a horse two feet to the left.” Gould’s claim is not intended to test the theory of a deterministic universe. Although a detailed defense would be necessary, I believe that it is consistent to say that even if the world is deterministic, biology is contingent in a way that the physical world is not. Roughly, this difference relies on the dependence of laws of nature in physics and the absence of strict laws of nature in biology. This difference, and its importance, will be explicated in chapters three and four.

Ultimately, Gould’s metaphor is impossible to confirm or reject (we cannot go back in time) – although there are some very clever attempts to empirically flesh out the role of chance in evolution (Travisano, et. al., 1995; Losos, et. al., 1998).

Contingency, however, is traditionally defined as possible (or, as a non-necessary actual event). I agree with Gould’s claim that the biological world is driven by contingent events. For example, if a asteroid had not struck the earth 65 million years ago, humans would not have evolved. Although it is notoriously difficult to determine the truth value of counterfactuals, my intuition is that the prior claim is true. Assuming that contingency plays a major role in evolution, what are the boundary conditions that constrain evolution? What are the different ways life could have evolved? The standard response to this question, if there is one, might best be represented by the following claim:

\[ \text{NE} \quad \text{Any particular non-existent form of life may owe its absence to one of two reasons. One is negative selection. The other is that the necessary mutations have never appeared (Ridley, 1995, 56).} \]

There is a subtle, but important mistake in NE. I will argue that there are forms that have not occurred, not as a result of negative selection or the lack of the necessary mutation, but because such forms are impossible. Ridley’s claim can be restated as the following:
NE* Any particular non-existent form may owe its absence to one of two things, either the proper mutation never arose (although it could have), or the form did arise, but was selected out.

In NE*, which is equivalent to NE, it becomes obvious that there are particular non-existent forms that are left out of Ridley’s explanation; namely, forms which are impossible. To return to a previous example, two-hundred-meter trees are not impossible because of negative selection (they are unfit) or because the proper mutations never arose. There are no trees of such height because it is impossible for there to be.

I will briefly mention two further examples of the misuse of model terms in biology. In a recent paper, Sterelny (forthcoming) describes various developmental innovations (novelties) as expanding the realm of biological possibility. Developmental (genetic) complexes, such as hox genes, permit phenotypic changes that were previously impossible. What sense of “possibility” is Sterelny using? Typically, “possibility” is a bivalent concept; either something is possible or it is not. As a result, it seems that such biological innovations were possible all along? Secondly, Dennett argues that in biology the interesting way to discuss possibility is in terms of degrees, or probability. Thus, he argues:

> It would be nice, for instance, to have some way of ranking the following in terms of biological possibility: ten-pound tomatoes, aquatic dogs, flying horses, flying trees (120).

I have no idea why such a ranking would be interesting, but Dennett is explicitly arguing that we should think about possibility in terms of degrees. Being bivalent is a necessary property of modal language. If we are talking about likelihood, we are no longer talking about possibility and necessity. Furthermore, by assigning degrees of possibility we would be losing the interesting explanatory power that looking at evolution through the lens of modality may offer.

From the prior discussion, three distinct motivations for this project come to light. First, as the quotation from Dennett to start this chapter states, a science ought to tell us what is possible or impossible. Are flying pigs possible? Are centaurs possible? How do we analyze such claims, from a biological perspective? Flying pigs and centaurs are certainly logically possible; i.e., there is nothing logically contradictory about such organisms. After all, we see these things in cartoons and digitally enhanced movies and can easily imagine such fantastical creatures. The same cannot be said with such things as 3 + 5 = 7 or square circles. In short, how do we (can we) determine what is possible or not in biology?

Second, biologists frequently use modal concepts. In itself, this is not a problem. However, they never explain how they are using these terms. An explanation is needed, because this reader, for one, does not know how they are using these terms. More importantly, however, once the hidden assumptions are fleshed out, it becomes obvious that biologists are using the terms inconsistently.
What one biologist claims is impossible, another will claim is possible. Finally, as evidenced above, many theorists are using modal terms in unacceptable ways, such as claiming that possibility changes or that possibility can admit degrees. This is unacceptable.

A final motivation is that there are deep philosophical problems regarding the use of modal concepts in biology. I am not merely cleaning up the work of sloppy biologists who misuse modal concepts. There are unique problems in applying modal concepts to a historical science as opposed to an ahistorical science, such as physics. Restricting modal language to a particular domain is not unusual. Although controversies remain, physics has well defined rules of usage for modal concepts which can be cashed by looking at the structure of physical explanations. Why did the tree fall in a particular direction? Well, given the laws of nature and the particular environmental circumstances (wind speed, structural integrity of the tree, etc.), it could not have landed elsewhere.

However, the lack of strict laws of nature in biology does not permit the same kind of explanation. As Gould so eloquently wrote, contingency and the role of history play an important role in biology. The importance of history, however, is not shared by physics. Thus, understanding how modal concepts work in biology will ultimately illuminate important differences between the physical and the biological sciences. Furthermore, in order to give full explanations in biology the concepts of possibility and necessity need to be explicated.

**Defining and Restricting the Project**

Simply having a biological entity as a subject in a proposition that contains a modal operator is not sufficient to make that proposition a candidate for understanding modality from a biological perspective. For example, is it possible that I am in London and New York at the same time? Although the subject, Jason, is biological, there is nothing particularly biological about the question. Thus, in order for a question (or proposition) to be assessed within a uniquely biological modal framework, it has to express something that is subject to an empirical biological explanation. Nothing in the prior claim has any biological information of any import. Here, possibility can be assessed at the less restricted levels of physical or conceptual possibility, depending on one’s interests.

In developing a positive framework for assessing modal terms in biological I will follow many of the restrictions that Dennett (1995) makes. (Unfortunately, as I will discuss in chapter four, Dennett’s analysis of biological possibility ends short of the desired goal.) These restrictions, I will argue, are intuitive and also preserve interest for the biologist. Dennett separates his project from the closely related project of exobiology, or astrobiology, which is the discipline that speculates about possible forms of life that could exist elsewhere in the universe. As such, they are talking about what is biologically possible, but they are interested in a broader definition of possibility than Dennett. Differing from exobiology, Dennett contextualizes the search for biological possibility to the contemporary understanding of earthly biology; what is possible given how the biological processes operate locally. As Dennett claims, “we are still beginning in
the middle, making sure that we understand today’s local, earthly circumstances before casting out nets wider” (112). Thus, when evaluating what is biologically possible, I am both trying to understand life as it occurs on Earth as well as our understanding of biology. What are the different ways the “tape of life” could have ended up, and what does our empirical biological knowledge tell us about what could have happened.

Now that we know what the *explananda* are not, what are we talking about in terms of possibility in biology? Generally, the context in which biologists raise modal issues is in reference to (1) biological form, or phenotypes, and (2) biological change, or accessibility of phenotypes from a specific location. However, it is a much more complex question. Are we looking at a phenotype given a particular environment? Are we looking at the phenotype of an individual organism, or more generally of a species? (For example, some phenotypes are not heritable – so it would be possible for an individual to exhibit a phenotype while it could not propagate throughout a population.) The tightrope that I will walk in this dissertation is to develop a sense of possibility that is unique to biology, reflective of how biologists use or ought to use the term, and holds insights for understanding evolutionary processes. This will require developing the concept of biological possibility that has the correct scope – not too broad, such as in astrobiology, and not too narrow, such as the possibility of an organism in a particular environment. These issues will be the dealt with in chapters four through six.

**A Plea for Developing Modal Biology**

Despite the lack of philosophical inquiry into the role of modal concepts in biological explanations, there have been requests for such research. For example, Gould makes the following claim:

> I believe that the question of defining morphospaces and mapping their differential filling through time is so vital to our understanding of life’s history, particularly to the potential contribution of paleontology. Yet relatively little has been done in this area (1991, 422).

Although Gould refers to morphospaces, his sentiment can be expanded to modality in biology more generally. Paleontologists, in particular, are interested in theoretical biospaces because their goal, in part, is to map out macroevolutionary trends. Why is there so much, or so little, biological diversity in the world? Has there been a uniform increase in diversity and disparity over geological time? Importantly, in order to understand the actual course of life on Earth, one must understand the possible ways life could have developed.

To be a bit more specific, McGhee (1999) created a list of ongoing debates in biology that could be influenced by work in theoretical morphology. Theoretical morphospaces are quantitative hypothetical biological spaces, often constructed in order to examine adaptationist or macroevolutionary hypotheses. (I will be explaining morphospaces in-depth in chapter two). Adding to this list,
Maclaurin (2003) ended with the following eight debates relevant to theoretical morphology:

1) Theoretical morphology has already led to a better understanding of growth in living systems.

2) Adaptionist hypothesis can be tested through the use of theoretical morphology.

3) Theoretical morphology can shed light on evolutionary trends in morphospace.

4) Theoretical morphology may shed light on the “great Cambrian disparity” debate.

5) Theoretical morphology might aid in making operational the idea of the adaptive landscape.

6) Theoretical morphology might allow us to better understand the nature of biological diversity and thus aid in the performance of conservation biology.

7) Theoretical morphology may aid in solving a problem posed by biological explanations and teleological language.

8) Theoretical morphology might allow us to sort life into the actual, the non-actual (but possible) and the impossible and, thereby, it might help us better explore the constraints on living systems.

Although the prior list was constructed specifically to refer to theoretical morphospaces and not modality more generally speaking, I will argue that morphospaces cannot be understood without a further exploration of the concepts of possibility and necessity more generally. In fact, I will argue that many morphospaces do not reflect actual biologically possible organisms and need to be revised in order to accommodate recent advances in evolutionary development. Despite this shortcoming, Maclaurin’s list accurately reflects the potential dividends that work in biological modality may yield.

Although he did not do so directly, Darwin himself employed modal concepts in developing his theory. He stated, “the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, should not be considered as subversive to the theory.” Here Darwin is countenancing conceivability as a guide to possibility, although he is doing so in an interesting manner. I might not be able to imagine how an eye could evolve through a series of gradual steps, but the theory of natural selection provides a mechanism that can account for complex morphological features without the need for a concrete story explaining the
gradual process through which eyes evolved. In essence, Darwin was illustrating two different senses of conceivability. He couldn’t conceive of a particular path by which eyes could evolve gradually, but he could conceive of a mechanism that could account for such morphological complexity – namely, natural selection. Descartes, one of the seminal figures in metaphysics and modality, made an analogous claim in his *Meditations on First Philosophy*. He describes a chiliogon, which is a 1,000 sided figure. Although we cannot conceive of a chiliogon, in the sense that the average person cannot visualize a 1,000 sided figure, there is nothing preventing such a thing from occurring. Recently, philosophers such as Yablo and Chalmers have called these two versions of conceivability positive and negative. Positive conceivability is when we can actually image a particular scenario, such as a cube. Negative conceivability is when we cannot image something per se, but there is nothing preventing its existence. Returning to the previous examples, the evolution of the eye and the chiliagon are negatively conceivable.

With one notable exception, Dennett, these pleas have fallen on deaf ears. There are several reasons for this. As already mentioned, much of the philosophical work on modality seems irrelevant. The particular issues that philosophers entertain with respect to modality occur at a coarser grain than biologists are typically interested in. Secondly, the question about biological possibility is ambiguous. As previously mentioned, there is no consistent use of modal concepts in biology. As you will see, the business of understanding biological possibility can get very convoluted. Third, many may think the questions of possibility and necessity have no explanatory role in biology. This is what Dennett’s exploration ultimately concludes. These concerns, and some others that will arise along the way, will be addressed throughout this work. In reference to biological possibility, Dennett states; “the book I was eager to read hasn’t yet been written, apparently, so I’ll have to try to write part of it myself” (107). I reciprocate this sentiment.

**The role of the philosopher and the role of the biologist**

Modal concepts are used in scientific explanations in general and in biological explanations in particular. Attention has been paid to their use in the physical sciences, but has been neglected in the biological sciences. In part, I want to change that. I am not going to argue that biologists have been missing the point, or that biologists need to change their general research agendas. Instead, one of the goals of this project is simply to catalog the variety of ways that biologists are actually using modal concepts in their explanations. Since they are using these concepts in contradictory ways, I will defend a particular usage of these terms. Philosophers of science often find themselves on tenuous ground. If the emphasis of their work is too philosophical, it loses touch with the work of actual scientists and becomes irrelevant. If the emphasis is too empirical, it is no longer
philosophy. It is with this dichotomy in mind that I will attempt to strike a balance between empirical biology and metaphysical concerns with modality. As I have mentioned earlier, this project can avoid many of the traditional and subtle controversies surrounding modality. Likewise, detailed knowledge of relevant empirical work is unnecessary for this project. Ultimately, it is the biologists who are going to establish what is biologically possible. However, it is the responsibility of philosophers to provide the framework for biologists to “fill out”. As I briefly explained, physical possibility is determined by the laws of physics. Philosophers of science determine what kind of necessity laws of nature have, while physicists determine what the particular laws are. Although laws of biology do not play the same role in determining possibility in biology as laws of physics do in determining physical possibility, biologists will still be responsible for supplying the relevant information in order to determine what is possible. To be more specific, my definition of biological possibility will ultimately require evolutionary developmental science in order to inform us what is possible.

When asking what is possible, whether it be metaphysical possibility or more restricted kinds, no one interprets this to mean that we should create a list of possible events. Rather, philosophers are responsible for creating a framework to determine how modal concepts operate. It would be futile and uninteresting to simply create a list of possible events or states of affairs. Likewise, it would be uninteresting and impractical to create a list of possible organisms. Descartes worked a similar project for epistemology. Realizing he held false beliefs and desiring to purge himself of those beliefs, Descartes was not going to evaluate his beliefs one at a time. Rather, he established a foundation which he could evaluate the entirety of his beliefs (or, at least a majority of them) at one time. He developed three skeptical thought experiments intending to show that any knowledge acquired through the senses could not be known for certain. Ultimately, however, Descartes avoided skepticism by arguing for the existence of (1) a good God, and (2) clear and distinct ideas. Although most agree that Cartesian foundationalism is flawed in practice, my project will similarly attempt to provide a framework in order to assess modal claims in biology.

Chapter Summaries

Chapter Two
I make a distinction between shallow and deep motivation for understanding what is biologically possible. By shallow motivation, I am referring to the fact that modal terms are often left undefined by biologists, or that modal terms are often used in a multiplicity of ways. Deep motivation, on the other hand, points to deeper philosophical problems with the use of modal concepts in biology. However, as I will show, even with the problems raised in the chapter on shallow motivation, the solutions are not obvious. Another way to describe the difference between shallow and deep motivation is that shallow
focuses on the empirical use of modal concepts and deep motivation focuses on
the associated philosophical problems. In the second chapter, I will center on the
shallow motivation of the project, leaving a discussion of deep motivation for the
third chapter.

It is not simply that biologists use modal concepts in a variety of ways, but
that the various ways are often in conflict with each other. If the multifarious uses
of modal concepts were the only motivation for the project, then this project
would not be that interesting. However, once the hidden assumptions are
uncovered, it will become clear that modal concepts are expressed in a variety of
conflicting ways. I will explicate the hidden assumptions of various claims and
show how they conflict with one another, or I will show that they are not using
modal concepts in philosophically appropriate ways, such as changing the
bivalent status of modal operators.

The chapter will be divided into three sections, reflecting the three general
categories in which biologists use possibility and necessity in giving explanations.
The first is simply impossibility, possibility or necessity statements. As I have
already mentioned, biologists have claimed that it is impossible for trees to reach
a height above 122-130 meters (McMahon, 1973, Koch, et. al., 2004, Niklas and
Spatz, 2004). Another impossibility claim is made by Haldane (1985), who
argued that it is impossible for there to be fifty-foot tall humans. However, the
impossibility claim about tree height and human height rest on different
assumptions and are in conflict with each other. Furthermore, it may be the case
that neither claim is true!

Second, I will describe various hypothetical spaces. One of the early
attempts (which are still powerful heuristic devices) is Sewall Wright’s (1932)
adaptive landscape. A more recent method describes hypothetical biological
space as morphospace. Morphospaces are quantified hypothetical spaces that
graphically show the different ways organisms could evolve. As you will see,
morphospaces are also constructed using a variety of means, and often neglect
the philosophical subtleties of modal theory. Thus, they ignore the difficult and
potentially interesting challenges that occur when looking at biological space
from a philosophically (or biologically) enlightened perspective. Furthermore,
mainly for practical reasons, morphospaces examine morphological disparity with
respect to only a small number of phenotypic properties. So, when trying to
understand biologically possibility from a general perspective (whether certain
mythical creatures are actually possible) morphospaces cannot provide the
answer. However, even if we ignore the practical challenges morphospaces
present, the theoretical assumptions of morphospaces are such that they do not
provide a reliable guide to actual hypothetical biospace. (Although, “actual
hypothetical” biospace appears to be a contradiction, it is not. This will also be
explained in chapter two.)

Third, modal concepts are commonly used, often implicitly, in thought
experiments and metaphors. For example, Dawkins states:
The actual animals that have ever lived on earth are a tiny subset of the theoretical animals that could exist. These real animals are the products of a very small number of evolutionary trajectories through genetic space...each perched in its own unique place in genetic hyperspace (1986, 73).

He echoes this by saying, “however many ways there are of being alive, it is certain that there are vastly more ways of being dead, or rather not alive.” (ibid, p. 9) Although Dawkins does not describe possible or necessary organisms or how to assess whether a particular non-existent organism is possible, the space that the trajectories meander through is occupied by nonexistent possible organisms. The concept of phylogenetic or species trajectories relies on non-actual possible organisms. Furthermore, a description of the space through which trajectories traverse is lacking. As MaClurin states: “the idea of an evolutionary trajectory is more metaphor than science, unless one accepts that there is at least some truth underlying the implicit spatial morphology” (465). You cannot discuss morphospaces, or other biological spaces, without having a further discussion about meaning of modal concepts in a uniquely biological context.

The use of trajectories, biological space or similar metaphors is not ideosynchratic of Dawkins, but expressed throughout the evolutionary biology literature. Most biologists would claim that the organisms that exist today need not have evolved, and other, non-existent organisms could have evolved. Unfortunately, the story usually ends there. Neither Dawkins nor Gould, in his metaphor of rewinding the tape of life, provide an account of what the hypothetical biological space is composed of, its shape, or how to determine its contents.

Chapter Three

There is a deeper motivation for exploring the question of what is biologically possible. As mentioned earlier, the metaphysical question of what is possible or necessary simpliciter, and the epistemological question of how to determine what is possible or necessary, is contentious in philosophy. However, these questions are less problematic in more restricted domains, such as in physics. Physical possibility is established by the relationship of a state of affairs with physical law. If a particular state of affairs \( P \) is prohibited by laws of nature, then \( P \) is impossible. Physical possibility is not possibility simpliciter, because the laws of nature need not have been the case. For example, it may be physically impossible to travel faster than the speed of light (it is contrary to physical law), but there is nothing conceptually or logically incoherent about an object traveling faster than the speed of light.

Not only do laws of nature establish what is physically possible, but they also are required for the standard account of scientific explanation. The deductive nomological model (DN) of scientific explanation requires laws of nature conjoined with the particular circumstances of an event for a proper explanation. There are standard objections to the DN model, but many think that
the account is not fatally flawed. Furthermore, it is thought that what the DN model gets right is that laws of nature are needed in order to provide explanations. Thus, there are two interrelated issues: (1) explanations are necessary in order to determine physical possibility, and (2) laws are necessary to provide physical explanations.

It is not clear how the methodology used to evaluate modal propositions in physics can be used to evaluate modal propositions in biology. The problem is that it is not clear that biology has laws of nature similar to physical laws. Either biology does not possess laws (Smart, 1963; Beatty, 1995), or, if it does, the laws differ from physical laws in important ways (Sober, 1993; Mitchell, 2003; Lange, 1995; Cooper, 2003; Rosenberg, 2001a, 2001b; Woodward, 2000, 2001). Either way, I will argue, laws of nature cannot be a guide to possibility in biology.

What could fill the role in biology that is occupied by laws of nature in physics? If biology has no laws of nature, how can it provide satisfying explanations? There are several responses to these questions. One is to keep the concepts of laws of nature, possibility, and scientific explanation the same, and biology should strive toward developing concepts in the mold cast by physics. A second approach is to modify traditional concepts to encompass both physics and biology. This approach would be to alter the definition (perhaps weaken) of laws so that they are flexible enough to cover physical as well as biological phenomena. A third approach would be to treat biology as a different kind of science, having different conceptions of laws, possibility and explanation. I will argue that the third approach is best, because there are fundamental differences between physics and biology that are best served by alternative methods as opposed to altering existent ones.

Chapter Four

In this chapter I will evaluate the only philosophical enlightened exploration of what is biologically possible, Dennett’s account in *Darwin’s Dangerous Idea*. Given the popularity of Dennett (at least in philosophical terms), and the response to *Darwin’s Dangerous Idea* by its critics, it is surprising that no one has challenged or championed Dennett’s definition of biological possibility.

Dennett begins by restricting possibility to a uniquely biological domain. Although I disagree with some of the details, the general approach limits the question in an interesting an appropriate way. Next, he describes and dismisses potential candidates for the definition of biological possibility. Finally, Dennett provides his own definition of biological possibility as follows:

\[ X \text{ is biologically possible iff } X \text{ is an instantiation of an accessible genome or a feature of its phenotypic products.} \]

For Dennett, something is possible iff there is a genotype that can code for a specific phenotype. There are problems with this definition. What does it mean to be an “instantiation of an accessible genome”? Is the definition circular, simply replacing the concept of “possibility” with “accessibility”? With some
modifications to this definition, I think that these challenges can be met. However, there is a further criticism, which, as Dennett admits, ultimately dooms this definition as being vacuous and uninteresting. According to Dennett’s definition, how can we empirically verify whether or not something is biologically possible? For example, is a unicorn biologically possible? According to Dennett’s definition, a unicorn is biologically possible iff there is an accessible genotype that codes for a unicorn. But how can we tell if there is an accessible genotype that codes for a unicorn phenotype? Even if we could determine what phenotypes have viable genotypes, it is unclear if this fact would bring any insights into biology.

It seems that if Dennett is correct, modal concepts are not interesting or appropriate concepts for biology. Fortunately, as I will argue in the next chapter, there is an alternative definition which can avoid these problems.

Chapter Five

Dennett leaves us with a definition that can be justified, but is useless. The problem with Dennett’s definition is that if it is correct, it seems that biologists are misusing modal concepts. When they talk about impossible tree height or morphospaces, they are not using modal concepts in a justified way. The challenge, therefore, is to develop a conception of possibility which is unique to biology, that can be philosophically defended and also make sense of how biologists use or should use modal concepts. I attempt to do so using the following definition:

**Restricted Biological Possibility (RBP)**

It is biologically possible for lineage X to acquire phenotype (p) only if (p) is directly accessible from X, and (p) is an instantiation of a viable genotype.

Differing from Dennett’s definition, RBP indexes possibility with reference to a particular species or higher taxa. Thus, RBP is not evaluating biological possibility *sui generis*, as Dennett’s definition does, but is evaluating biological possibility in terms of phenotypic change. After all, when modal concepts are used in the literature they are often in reference to whether existent species can evolve in various ways; e.g. impossible tree heights and shell morphospaces.

While Dennett explained biological possibility in terms of an accessible genotype, the definition that I offer defines possibility in terms of an accessible genotype along with whether a particular lineage can evolve such a phenotype. In other words, instead of defining possibility of a phenotype, I am concerned with the possibility of a phenotype starting from a particular location.

Let’s work through an example to illustrate the difference between Dennett’s definition and RBP: flying pigs. Although this is a trite example, chosen for the purposes of clarity, in the chapter I will discuss examples that are actually used in the literature. According to Dennett’s definition, flying pigs are possible iff there is an accessible genotype that codes for winged pigs. How can we determine if such a genotype exists? Well, this is one of the problems of
Dennett’s definition, it makes evaluating modal claims virtually impossible. How can we determine if there is a genotype that codes for a winged pig? Nonetheless, it seems likely that such a genotype is possible. As Dennett points out, there were creatures as large as pigs that could fly – pterosaurs.

According to RBP, winged pigs are possible if-and-only-if *Sus scrofa* (contemporary pigs), could evolve wings. This brings relevant empirical research to bear on answering this question. It might very well be impossible for contemporary *Sus scrofa* to develop wings, no matter what selective pressures are enacted. For the purposes of discussion, let’s assume the following state of affairs: (1) there is a genotype that can code for the phenotype of winged pig; (2) there are developmental constraints preventing *Sus scrofa* from developing wings, whatever the selective pressure. So, winged pigs seem possible under Dennett’s definition but impossible for RBP. Dennett may respond to this example by rightly claiming that all constraints are merely local, meaning that the developmental constraints that prevent wings from forming on pigs need not have evolved. My response to this, and what my position depends upon, is that species can be defined essentially. I will argue that there are a set of properties that *Sus scrofa* has essentially. To return to the example, I can at once agree with Dennett, that there is a genotype that codes for a winged pig-like creature, but that creature is not a pig but something else. An analogy would be if we went to another planet and found organisms that looked like tigers and could reproduce with Earthly tigers, we should not call them tigers. Why? Because they do not share the same evolutionary history; i.e., they are not a monophyletic group.

The obstacles I need to overcome in order for my definition to work are obvious. 1) I need to explain the relevance of making such a move – tying RBP to existing debates within biology and relate my definition to how biologists use modal concepts. 2) I have to clearly distinguish Dennett’s definition from RBP. 3) I have to have a philosophical justification for species essentialism which is also consistent with systematics and other relevant empirical truths. I will meet all of these challenges in this chapter.
CHAPTER 2
SHALLOW MOTIVATION: MODAL CONCEPTS IN EMPIRICAL BIOLOGY

Introduction

Biologists employ modal concepts to illustrate a variety of biological principles, such as the role that constraints play in evolution, the role of selection and development and macroevolutionary trends that take place over vast sweeps of time. In itself, these varied uses of modal concepts are not necessarily problematic. It might be the case that biologists use these concepts in a colloquial sense – similar to saying that there is no beer in the fridge. Alternatively, it may be the case that once these concepts are fleshed out, they rely on a shared underlying framework, ultimately showing that there is no theoretical difference in the various uses. However, this innocuous interpretation toward the use of modal concepts in biology is mistaken. In this chapter, I will show that the various uses of modal concepts by biologists are confused and conflicting.

In the opening chapter I emphasized that once the framework for model concepts is established by philosophers, it is the biologists that will ultimately be responsible for filling out the framework – to know what is biologically possible will rely on empirical biological data. In the final chapters I will defend a particular conception of how modal concepts should be used in biology. My positive thesis will be consistent with some of the examples in this chapter and critical of others. But before I can put forward my account, I must first explain why an account is needed at all.

This chapter will accomplish two goals. The first is to catalog the different kinds of uses of modal language evident in empirical biology. To this end, I will describe specific examples of (1) impossibility claims, (2) hypothetical biological spaces (morphospaces), and (3) the explicit and implicit use of possibility in biological metaphors. My hope is to understand to what end biologists use modal concepts. Secondly, I will demonstrate that the varied uses of modal concepts either result in conflicting accounts of what is possible, or neglect to provide any account of what is possible. I will show that there are inter-group differences as well as intra-group differences with how biologists use modal claims. For example, there are different kinds of morphospaces which are in conflict with each other (inter-group conflicts) and I will show that some impossibility claims seem to conflict with the account of possibility found in morphospaces (inter-group conflict). Popular metaphors within evolutionary biology rely on hypothetical biological space, but they do not provide an adequate description of that space.

In this chapter, I will be focusing on problems with the applications of modal concepts in empirical biology. A later chapter will describe the unique philosophical challenges in providing a framework for modal concepts in biology. This chapter will be more illustrative than exhaustive. I will describe only a few of
the many different kinds of modal claims that biologists make. Furthermore, there are a host of factors involved in determining biological form, only some of which will be described in this chapter.

**Biological Impossibilities**

**Mechanical and Hydraulic Constraints on Tree Height**

One way biologists use modal concepts is by claiming that a particular biological form is impossible. Trees, it is argued, have an ultimate height of 122 – 130 meters. This limit is reflected by the tallest tree in recorded history at a height of 122.7 meters (Koch, et. al., 2004). The conventional explanation for this, articulated by McMahon (1973), was that ultimate height was a result of engineering/mechanical constraints. McMahon was intrigued by Kleiber’s rule, which demonstrated a strict ratio of metabolic rate and size present in all mammals – the larger the animal, the more heat that the animal must produce. Seeing this scaling relation between size and metabolic rate in animals, he sought to discover if there were similar ratios in the botanical realm. McMahon discovered that there was a ratio of trunk base diameter to height present in trees – the larger diameter the trunk, the taller the tree.

![Figure 2.1](image_url)

**Fig. 2.1** The figure on the left represents Kleiber’s rule, the ratio of metabolic heat production against body weight. On the right, tree height is plotted against base diameter (McMahon, 1973, 179).

In order to demonstrate ultimate height, however, two other factors need to be fixed: ultimate trunk diameter (otherwise taller heights could always be reached by wider trunks) and the tissue properties composing the tree stalk. (Other conditions, such as gravity and not allowing external stabilizers, must also be assumed.) Given these factors, ultimate tree is simply a result of engineering and environmental constraints faced by trees.

Recently, this view has been challenged (Koch, et. al., 2004; Niklas and Spatz, 2004). Rather than the mechanical constraints of trunk diameter and
composition being the limiting factors, it is argued that hydraulic constraints, the ability to efficiently transport water up the stem, are the limiting factors in tree height. Koch et al. explain: “As trees grow taller, increasing leaf water stress due to gravity and path length resistance may ultimately limit leaf expansion and photosynthesis for further height growth, even with ample soil moisture” (851). Gravity, combined with the hydraulic method trees use to transport water, inhibits leaf growth and photosynthesis at extreme heights. As Niklas and Spatz point out, the hydraulic constraint hypothesis more accurately reflect the actual limitations of tree height observed in nature, both at the extreme ends as well as for small and intermediate-sized plants (15661). This is evident in the diagram above, where the solid “buckling” line is set apart from the tallest recorded trees. McMahon explained this discrepancy as a natural safety mechanism - just as engineers often use safety factors in construction. If individual trees approach the ultimate buckling height the safety margin would be low. A defect in stem composition through insect infestation, rotting wood or a stiff breeze would select against trees that approaching the buckling limit. Niklas and Spatz, however, argue that their model of hydraulic constraints more accurately reflects empirical data of tree height, and places the buckling line closer to actual tree height.

Impossibly Tall Trees?
For my purposes, it does not matter which hypothesis, mechanical or hydraulic, is ultimately confirmed. I am, however, interested in whether or not it is correct to say 140 meter tall tree are impossible. I will describe each hypothesis for limiting tree height in turn. For the mechanical hypothesis, the ultimate height of trees depends on stem composition and height/width/mass ratios. Given the material composition of the stem and the respective mechanical properties, an engineer could simply calculate how high trees can grow. However, are these assumptions fair to make? If the selective pressures driving tree height were strong enough, it seems entirely possible that secondary mechanisms might evolve to help support a taller tree than the trunk base diameter normally would allow. Perhaps modified tree limbs or roots would evolve as “legs” to support a taller crown. Another possibility is that if the selective pressure were strong enough, trees might evolve an exaptation to accommodate a taller stem. Although this is not its current function, sap could possibly be selected for providing a stiffening property to the tree stalk. Exaptations are adaptations which were selected to performing a different function from the one it was originally selected for. A classic example of an exaptation is feathers, which originally were selected for thermal regulation, but eventually were selected for their function in flight. Likewise, trees could exapt other structures to accommodate a taller stem.

Another possibility is that trees could have originally evolved differently, with stronger material comprising the stem or an alternative method to bring water to their extremities. The following argument captures my response to the mechanical constraints thesis:
If trees had evolved using a more rigid stem material, they could have grown to taller than existent trees possible can.

Trees could have evolved with a more rigid stem material.

Therefore, trees which are taller than currently existing trees are possible.

Although determining the truth value of counterfactuals is notoriously difficult, the argument appears to be valid and sound.

The hydraulic hypothesis suffers a similar fate. If the limiting factor to tree height is the reduced efficiency of photosynthesis, trees could grow taller if there were other selective forces pushing tree heights. Alternatively, if trees had evolved a different method of fluid dispersion or if they ex-adapt (transform) an existing trait into solving the problem of fluid dispersion, then they would not suffer from the restrictions of their current hydraulic system.

One response to these criticisms might be that the traits, such as the material composition of the stalk and the hydraulic system, have become developmentally fixed over time. At one point in tree evolution (or earlier in plant evolution), there may have been a time where alternative materials or alternative hydraulic systems were possible. But after an initial pathway was chose, these traits became fixed within the population and cannot be altered. Therefore, changing the hydraulic system or stem composition would be too dramatic of a change, and are virtually impossible. In other words, once a species turns down one evolutionary path, it cannot simply change to another, even if it would be selectively advantageous to do so. Even if this were true, it still seems possible that trees (or plants, more generally) could have initially developed differently. If they could have, then taller tree are possible – although they may not be possible to get to from contemporary trees. But there seems no reason to say that because actual trees cannot evolve traits which allow them to grow taller, they could not have originally developed differently. At the very least, Koch et. al., McMahon, and Niklas and Spatz would require very different arguments in order to establish that plants and trees could not have originally evolved differently.

**Attack of the 50 Foot Woman**

Another example of a biological impossibility comes from Haldane (1985), one of the architects of the “hardening” of neo-Darwinism. He argues that it is impossible for humans to be sixty feet tall, or ten times the size of an average human. The reason is that as size increases, body mass increases at a disproportional rate to bone density. Such a giant would have a thousand-fold increase in mass over an average sized human, but his bone diameter would only increase one-hundred times. A sixty-foot-tall human would crumble under his own weight; similar to a beached whale being crushed. As the title of his essay suggests, “On Being the Right Size”, Haldane argues that every species is “built” according to engineering and physical constraints of the organisms.
particular size. Large animals are not simply scaled-up versions of smaller relatives.

An example of the varying physical relationships between organisms and the environment is the extent to which gravity affects organisms of differing sizes. In this unusual quotation, Haldane graphically expressing the challenge that gravity presents for a heterogeneous group of organisms:

To the mouse and any smaller animal it (gravity) presents practically no dangers. You can drop a mouse down a thousand-yard mine shaft; and, on arriving at the bottom, it gets a slight shock and walks away. A rat is killed, a man is broken, a horse splashes (3).

Physical constraints like gravity, which is constant on earth, pose unique problems differently sized organisms. Haldane provides a number of examples from the biological world, such as the differing effect that surface tension has on differently sized animals. When small insects come in contact with the surface of water, they are not strong enough to escape. Humans, however, do not have this problem. This illustrates the interesting fact that not all organisms face identical challenges posed by the environment.

Insects, unlike humans, do not have a system to diffuse oxygen throughout their body. Thus, insects are restrained from becoming more than one-half inch thick. But as Haldane is quick to mention, “If the insects had hit on a plan for driving air through their tissues instead of letting it soak in, they might well have become a large as lobsters, though other considerations would have prevented them from becoming as large as a man” (4).

To return to Haldane’s original example of sixty-foot tall humans, it appears that there are two different things he could mean. First, he could simply mean that sixty-foot tall humans can’t exist if they are simply scaled up versions of six-foot tall humans. This reading of his claim simply implies that organisms have unique design requirements in relation to their size. If this is Haldane’s
intent, then sixty-foot tall humans are possible after all; they would just have a
different form (larger bones) than their normal sized counterparts.

Perhaps Haldane was suggesting that humans could not evolve a robust bone structure necessary to support such an increase in mass. Under this stronger reading, sixty-foot tall humans would be impossible. Such constraints are frequent in evolutionary biology. In this case, it may be a developmental constraint called allometry – the coupling (genetic or developmental) of disparate traits within a species. For example, in the figure below, Ridley notes the allometric relationship between brain size and body size.

![Fig. 2.3 Brain size is plotted against body size in two hypothetical species (597).](image)

According to the stronger reading of Haldane’s claim, perhaps there is an allometric relationship between bone diameter and body size that would not allow the disproportional growth in bone diameter necessary to support such a massive frame. In this case, it would be external as well as internal constraints which combine to restrict human size. The external constraints would be that of gravity and the mechanical restrictions of mass and bone strength/diameter. The internal constraints would be the developmental coupling of bone size and body size. However, even if it is the case that bone diameter is genetically coupled with body mass, it is far from clear that this coupling could not become uncoupled, or that body size and bone diameter could have originally evolved in separate modules. There are numerous examples in the biological world of once connected traits which become separated through selection.

To summarize, it appears that both impossibility claims appear to be false; one-hundred-thirty meter trees as well as sixty-foot tall humans seem possible. It is also important to note that the basis for the impossibility claims differed. For tree height, it was that the internal mechanisms of trees have reached their physical limitations. For human height, Haldane’s stronger claims suggested that there is an unalterable allometric relationship between bone diameter and body size. So it seems, at least for the two examples that were explained, localized constraints are not enough to limit possibility.
Morphospace

Moving beyond impossibility claims, biologists have developed hypothetical biological spaces in order to test adaptationist hypotheses and describe evolutionary patterns through time. Examples of such spaces include Sewall Wright’s adaptive landscape, George Simpson’s phenotypic version of the adaptive landscape and C. H. Waddington’s epigenetic space. Wright’s adaptive landscape, in particular, has been used as an important heuristic in evolutionary theory. The adaptive landscape, as Wright envisioned it, is a hilly landscape, where gene frequencies are graded for their adaptive value.  

Fig. 2.4 An example of an adaptive landscape (evolution.berkeley.edu).

The hills of the landscape reflect a high fitness value and the valleys a low fitness value. Wright was interested in determining if or how populations could move from peak to peak. A population on the landscape will climb to the nearest peak, whether or not that peak represents the highest overall fitness value. The problem is can a population which is stuck on a sub-optimal peak climb to the optimal peak? At first glance it would seem to be impossible, since the population would have to traverse a fitness valley in order to arrive at another peak. Any organisms in the valley would have a lower fitness value than organisms on the peak, thus selective pressures always force populations up a hill, regardless of whether or not a particular hill is the highest on the landscape. Wright used this illustration in order to defend his particular view of evolution - the shifting balance process of ideal evolution. According to this theory, populations can change gene frequency when a sub-population has an advantageous mutation, which later spreads to the entire population. Wright argued that this process allows populations to move from local optima to an overall higher optima.

Although the adaptive landscape may work well as a heuristic, explaining the role of adaptation and local optima, it does not work well as a guide to

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1 There is a discussion about what, exactly, the ungulating plane represents. It may be the multidimensional field of all possible gene combinations graded for their adaptive value or the multidimensional field of joint frequencies of all genes in a population graded for their adaptive value. See Skipper (2004) for a discussion on this topic, where he mediates a debate between Provine (1986) and Ruse (1996) as to the meaning and use of the adaptive landscape.
establishing what organisms are possible - Wright’s model simple assumes what is possible. For example, the adaptive landscape appears as a continuous plane. However, it is less than clear that this reflects the empirical data. Fontana and Buss (1994) argue that the mechanical constraints of protein folding make certain otherwise viable phenotypes inaccessible from any genotype. If true, this would mean that the adaptive landscape is actually filled with holes, instead of continuous. To put it more simply, the adaptive landscape ignores possible genetic and developmental constraints in describing the geography of the landscape.

A more recent form of representing hypothetical biological space is morphospaces. A morphospace is a “n-dimensional geometric hyperspaces produced by systematically varying the parameter values of a geometric model of form” (McGhee, 13). This is accomplished is by picking out a number of variables for a particular trait and creating an n-dimensional morphospace that reflects variation of the parameters. For example, McGhee creates a simple triangle morphospace:

![Fig. 2.5 A morphospace that represents possible triangular form (20).](image)

The triangle morphospace can be represented two-dimensionally since the axes consist of two parameters: apex height and base width. If the illustration were expanded so that the values of the variables were extended to some artificially large number, and the gradations between instances were smooth, we would have a morphospace that captures all possible triangle forms.

Things get more difficult when morphospaces are constructed to represent natural traits, because organisms live in a three dimensional world and traits can often vary in more than two or three dimensions. The triangle morphospace would only work for organisms living in flatland. As the number of parameters increases, the number of dimensions increases proportionally. Topographically,
only three parameters can be visualized in a three-dimensional space. I am not concerned, however, about the ability of morphospaces to *represent* possible phenotypes, but with their ability to *describe* and *assess* possible phenotypes.

A classic example of a theoretical morphospace is David Raup’s construction of shell morphospace (Raup, 1965). Raup creates a three dimensional morphospace for shells which, he claims, encompass the totality of possible shell phenotypes. Dawkins (1996) has an accessible and extensive discussion of Raup’s shell morphospace. According to Raup, shells can vary with respect to three variables \( W \) (expansion rate), \( D \) (distance of generating curve from axis), and \( T \) (translation). Dawkins refers to these variables as flare, verm and spire. Flare is the “expansion rate of the spiral”, or how quickly the spiral unravels. Different values of flare are shown in the following diagram.

![Different values for shell flare](image1)

The second variable, verm, refers to the diameter of the shell tube. Thus, whether the tube of a shell is “snug” or “gappy” depends not only on the flare, but also on the verm. A shell that has a larger verm can still be snug if the diameter of the flare is correspondingly larger.

![A and B have different values for verm, but the same values for flare](image2)

The final parameter is spire, and this refers to the height of the shell. To picture this, you can vary the verm and flare on a single plane. Spire is when a third dimension is added to the plane, creating shells with a conical shape. The
following diagram gives example of actual shells high in values in each of the three parameters.

Fig. 2.8 The shell farthest left represents high flare; the middle shell represents high verm; and the shell on the right has a high spire value (ibid, 206).

Using these parameters Raup created a three-dimensional cube to diagram all possible shell morphologies (see below). The shaded area represents occupied regions of the morphospace, while unshaded represents possible shells that, for one reason or another, do not exist. The figures are computer generated models of the shell phenotypes at any particular point within the cube. As you can imagine, it is impossible to visualize a morphospace that contains more than three parameters.
Fig. 2.9 Raup’s morphospace representing all possible shell phenotypes. The shaded area represents the part of morphospace that is occupied by actual shells. The illustrations are computer generated images of shells in particular regions of the morphospace (1966, 1184).

From any given point within the cube, if you move directly along one of the axis the shell phenotypes will change only with respect to one of the variables. For example, if you pick a point somewhere in the middle of the cube and move directly up or down on the W axis, the shells will only vary with respect to flare while keeping constant with respect to verm and spire. If you pick a point within the cube and move diagonally, shells will vary with respect to two characteristics (or three, if the diagonal not perpendicular to one side).

Dawkins notes some problems with Raup’s model. For one, there are many existent shell forms that are not located within the cube. Verm only describes shells that have circular shapes varies with respect diameter of the tube, but actual shells have oval as well as irregularly shaped shells. Thus, there is no space in the cube of possible shell morphologies where these phenotypes reside. A second problem noted by Dawkins is that the various values can change throughout the growth of organisms. For example, early in development a shell can have a particular verm, but as the organism grows, the verm changes. Again, there is no place in the three dimensional cube that can represent two different values for verm with respect to the same organism. We could say that part of the organism resides in this area of the cube and the later part resides in another region of the cube. A third criticism of Raup is that shells can also vary with respect to the patterns on the surface of the shells. There are a wide variety of patterns that exist on the surface of shells, and these are not represented in Raup’s model.

Although Dawkins’ criticisms certainly apply, they are shallow. When looking at actual shells in nature, should we take into consideration factors such
as weathering and damage? There is no place within the shell morphospace where a chipped or deformed shells would be located. Rather than criticizing Raup’s conclusions, Dawkins criticisms simply reflect the difficulty of constructing morphospaces that represent the actual manner in which shells vary. In response to these criticisms we could think of morphospaces as an idealized space, similar to idealized states in physics. Perhaps there is no place where a complete vacuum exists, yet physics has no problem positing such a place. Likewise, morphospace can be used to explain specific evolutionary phenomena, even with the realization that they are not veridical.

The purpose of the shell morphospace is two-fold: (1) to determine how much of the space is occupied, and (2) to explain why unoccupied space unoccupied. We can determine (1) by overlaying existing shell morphologies onto the shell morphospace, and as Raup’s illustration shows, a relatively small portion of the morphospace is occupied by actual shells. There are two possible explanations why regions of morphospace are unoccupied: an adaptationist explanation and a developmental explanation. According to the adaptationist explanation, empty space represents non-adaptive forms that have been eliminated by natural selection. The developmental explanation suggests that developmental constraints restrict access to certain regions of morphospace; i.e., there are phenotypes that cannot be produced from a particular developmental program (Maynard Smith et. al, 1985; Amundson, 1994; Ridley, 1995). So, (1) either empty space is empty because phenotypes could have formed there, or actually had formed there, but were maladaptive and selected out, or (2) phenotypes are prevented from occupying the empty space because developmental constraints prevent the necessary variations from occurring. These phenotypes could not be selectively disadvantageous, because they could never be formed.

Raup argued for the adaptationist explanation – shells could form in the unoccupied spaces, but are selectively restrained from entering the space. This conclusion has largely been accepted and is empirically supported (Ridley, 1995). Thus, if we artificially selected shells over a vast number of generations, we could fill shell morphospace. To return the discussion about morphospaces to discussion about biological possibility, we can ask whether morphospaces are reliable guides to what is biologically possible? If morphospace occupation is a result of adaptive forces, then morphospaces are reliable guide to the possible. Phenotypes in unoccupied regions of morphospace are possible if the selective forces were different than the actual selective forces. However, when morphospace occupation is restricted by developmental constraints, morphospaces are not a reliable metric for determining what is possible. For example, if the shell morphospace was actually limited by developmental constraints, in what sense are the non-existent forms possible? Unlike the adaptationist explanation, if we artificially selected shells over a vast period of time, the unoccupied regions of morphospace would remain unoccupied.

So, when developmental constraints are the limiting factor in morphospace occupation, the morphospace is not a reliable metric for establishing what is possible. Remember, the axes of morphospace are
determined mathematically or geometrically and do not reflect the developmental organization of species. This is not to say that morphospaces do not perform the task that they are designed to perform – but this has to be qualified. Morphospaces can tell us how much of the space is occupied, but they alone cannot establish why a particular part of morphospace is unoccupied. Distinguishing developmental constraints from adaptive explanations requires a variety of information, and is not an exact. Maynard Smith et. al. suggest several strategies for distinguishing between adaptive and developmental explanations (1985).

**Skeletal Morphospace**

A much larger morphospace, which in some sense subsumes Raup’s shell morphospace, is described by Roger Thomas and Wolfgang Reif (1993). The Thomas and Reif space (hereafter TR) is a theoretical design space for all possible skeletons. This space consists of seven dimensions, and each dimension can vary between two and four parameters. However, the TR morphospace is of a different kind than Raup’s shell morphospace. Instead of varying parameters mathematically or geometrically, skeletal space is categorized by different design possibilities. (Hence, McGhee refers to TR’s skeletal space as a design space, instead of a morphospace.) TR carve out the skeletal space by arguing that if skeletons evolve, there are only so many design (engineering/developmental/functional) variations that are possible. They do not say that organisms will inevitably evolve skeletons, but if they do, they will have to evolve along the dimensions described in the skeletal space. A diagram illustrating the various categories is provided in the following figure:

As you can see in the figure below, the dimensions of TR’s space do not vary quantitatively, but qualitatively. Similarly to Raup, TR claim to capture the entirety of skeletal space (Raup claimed his shell morphospace captured the entirety of shell diversity). The skeletal space allows for 1,536 combinatorial possibilities. Since this is a rather unwieldy number of possibilities to use in empirical investigations, TR examine pairs of variables. When the dimensions of skeletal space are grouped into pairs, we are left with 186 possible pairings. Of these, TR claim that four pairings are logically contradictory and four more are functionally “inviable.” From this list, they explored the skeletons of existent organisms (past and present) to determine what extent that the available skeletal space has been occupied. TR conclude that “over half of these potential design paradigms are abundantly represented in the real world, more than two-thirds are at least common, and there are only six apparently viable character combinations for which we have not so far identified examples” (350).
Like Raup's morphospace, TR's skeletal morphospace may highlight an interesting pattern to evolution (most viable design options have been explored), but it is not a good guide to what is possible for at least two reasons. First, unlike Raup's space, TR's skeletal space does not specify any biological forms, but only
biological *kinds*. As a result, many different animals composed of many different forms would be indistinguishably categorized in skeletal space. For example, most mammals would occupy the same categories in the TR model - internal (1.A), rigid (2.C), three or more elements (3.W), rods, plates and solids (4.G.H.K), unit/serial (5.M); built in place (6.X) joined and fused (7.Q.R). Although the skeleton of a horse and a human are quite different, they are "created and assembled" in the same way, thus they would be indistinguishable in the TR skeletal space.

A further difficulty for TR is that, unlike Raup’s shell morphospace, design spaces rely on the human ability to recognize all the possible ways a skeleton could be constructed. For example, if I could conceive of a manufacturing technique or a way to put together skeletons that was not represented in their model, it would be a counterexample to TR’s model (or at least they would have to accommodate the new information). Because their model relies on human ingenuity, there is no conceptual certainty that all of the possible design variants have been exhausted. Perhaps TR’s intuitions about the possibilities of design space were primed by their pre-existing knowledge of organic form, in which case in would not be surprising that most of skeletal space was occupied.

In a certain sense, TR’s skeletal space is not even morphospace, because it is not spacial; it merely lists combinations of skeletal traits. Perhaps one reason for not allowing the character pairs to vary quantitatively is that such a morphospace is impossible to image. Mammals, which are restricted to a few of TR’s categories, vary in innumerable dimensions. What this means is that TR should be less assertive in claiming that there model captures the whole of skeletal space. Even if they have successfully captured the various general ways that skeletal space can vary, it still holds a great deal of variation within each particular set of traits.

**Modality in Biological Metaphors**

Along with impossibility claims and morphospaces, modal concepts are often implicitly or explicitly used in biological metaphors. Moreso than other sciences, metaphors are ubiquitous in biology. Many of these metaphors require talk of non-actual, possible organisms in order to “come off.” It is a project onto itself to examine the role metaphors play in biological explanations. Nonetheless, it appears that biology will not purge itself of metaphors in the near future, so we should take them seriously. Along with explaining the use of non-actual organisms in metaphors, I will explain how these metaphors actually help to shape the discussion of what is biologically possible.

To briefly return to the discussion on morphospaces, the two examples discussed, Raup and TR, were examples of specific morphospace, or what McGhee refers to as “a theoretical morphospace.” They are theoretical, because they are constructed irrespective of actual organic variation – the morphospaces did not rely upon measuring the traits of actual organisms. Once the spaces were constructed, they can be compared to the morphospace in order to determine how much theoretical space is actually occupied. They are “a”
theoretical morphospace, because they are constructed only to represent a very restricted part of a larger morphospace, which McGhee calls “theoretical morphospace.” Theoretical morphospace is the “totality of morphospace of all possible biological forms.” In order to describe the difference between “a theoretical morphospace” and “theoretical morphospace,” MaClurin uses the terminology of “partial theoretical morphospace” and “total theoretical morphospace.” Unlike partial theoretical morphospaces, total theoretical morphospace is used metaphorically. It is more of a referent than a definition – it does not inform us what the structure of total theoretical morphospace is or how to determine its structure, it is simply refers to the space which contains all possible biological forms. Is a centaur located in total theoretical morphospace? There is no procedure to follow to determine whether or not a hypothetical organism exists within such a space. However, if an organism is possible, it resides within total theoretical morphospace.

Other theorists have posited similar metaphors to refer to total theoretical morphospace. Dawkins referred to the “Museum of All Possible Animals:”

Preserved in the museum is every kind of animal form that has ever existed, and every kind that could be imagined. Each animal is housed next door to those that it most resembles. Each dimension in the museum—that is, each direction along which a gallery extends—corresponds to one dimension in which the animals vary (1996, 200).

Dawkins’ metaphor is an attempt to describe what total theoretical morphospace would look like—every trait an organism possesses will have its own dimension in morphospace (or wing in Dawkins’ museum). However, he does not go on to describe what hypothetical animals are permitted in the museum? Again, is there a wing of the museum dedicated to the variation of centaurs?

Dennett emulates Dawkins in a number of ways, one of which is that he also has a metaphor for total theoretical morphospace, which he calls the “Library of Mendel.” Instead of focusing on animal forms, Dennett’s fictitious library contains an exhaustive list of genetic codes. An important distinction between Dawkins and Dennett is that Dennett offers a definition of biological possibility—the only one that I have ever seen. For this reason, I will dedicate a chapter to a discussion of Dennett’s attempt to flesh out a definition for total theoretical morphospace.

Another recent metaphor, or rather thought experiment, which relies on non-actual biological organisms comes from Gould’s monograph, *Wonderful Life*. In order to understand Gould’s thought experiment, I’ll first need to explain some of the themes from Gould’s work in general and specifically from *Wonderful Life*. For the first 3 billion years that life on Earth, only very simple organisms existed. Then, about 530 mya complex animal life appears in the fossil record. However, as the name suggests, it was an explosion of animal life on Earth, lasting 5 to 10 million years. This rise in animal life included the first appearance of such traits as “antennae, limbs, tails, eyes and they include representatives of many modern groups including arthropods, annelids, chordates, and mollusks” (Carroll, 2005).
Fossils from this interesting time were first discovered in 1909 by Charles Walcott in the Burgess Shale, a rock formation in British Columbia. Many of fossils that Walcott found were strange; unlike any kind of existent species. Nonetheless, he thought that the organisms of the Cambrian explosion were just ancestors of organisms that live today. Upon looking at the fossils, Gould argued that many of the Burgess Shale organisms possessed unique morphological structures, unlike any existent animal taxa. Therefore, the fossils are probably not ancestors to any living groups.

There are two main lessons that Gould draws from examining the fossils of the Cambrian explosion. The first is about the nature of evolutionary progress and the second is about developmental regimes of animal form. As time progresses, life seems to exhibit more and more complex forms. This can be attributed to random variation, and the fact that life started from a very simple morphological beginning. Gould, however, has a different view of the progression of life. He claims that during the Cambrian explosion a number of competing body plans (bauplane) originated. For contingent reasons, some of the species survived and some did not. However, once there was an initial selection of a bauplane, variation of species within any single bauplan was limited. To promote this position, Gould makes a distinction between diversity and disparity. Diversity can be represented by the number of different species within any one lineage. For example, beetles exhibit great diversity, with over 500 thousand species. Disparity, on the other hand, is represented by possessing a completely different bauplane. Beetles are a good example of diversity, but not of disparity. To borrow a metaphor from the world of music, different beetle forms represent variation on a theme. Gould argues that once the original bauplane were selected, the possible phenotypes that could have evolved are restricted. Why did some of the species of the Cambrian go on to create the found the main divisions in taxa today, while others simply vanished? Gould claims that while natural selection probably played a role in deciding which species were the victors, the ultimate winners and losers were a result of chance events. To summarize, Gould argued that the major taxa in animal life (and presumably plant life) are confined to particular bauplane, and these bauplane are fixed contingently.

To emphasize the contingent aspects of evolutionary trends, Gould suggested that if we were to “rewind the tape of life,” say, to the Cambrian period, “any replay of the tape would lead evolution down a pathway radically different from the road actually taken” (1989, 51). Of course, when we rewind a tape, say of Gone with the Wind, the same movie will play again. To alleviate the concerns of a Laplacean demon, Maynard Smith suggests that once the tape is rewound, move a horse two feet to the left (1992). Gould’s intent was not to show that determinism wrong, but to counter the “extreme adaptationist” view that natural selection alone shapes evolution. Gould claims that people like Dawkins and Dennett overemphasize the role that natural selection plays in evolution. No one argues that either natural selection or chance events are not present in evolutionary processes; the point of contention is whether selection or
chance takes priority in the evolutionary process - which process does most of the heavy lifting.

Let us take Gould’s thought experiment to the extreme. Imagine that we replayed the tape of life an infinite number of times. What sorts of organisms could or could not develop? If it is true that in an infinite number of trials everything that is possible eventually becomes actual, then an infinite number of rewinds would produce the set of all possible organisms – it would fill Dawkins’ Museum of All Possible Animals and complete total theoretical morphospace. However, since it is a thought experiment, this can never be empirically verified (although there have been several attempts to operationalize the concept of contingency in a number of empirical investigations (Losos, 2001; Travisano, 2002; Beatty, 2006)

There is no doubt that contingent events play a role in evolution – just think of the event that led to the extinction of the dinosaurs. I would even agree with Gould, that contingency plays a major role in evolution. However, does this leave any room to talk about possibility? Does this mean that we should only focus on the contingent events that drive evolution, and ignore the binary notion of possibility and necessity? In their famous paper, “The Spandrels of San Marcos,” Gould and Lewontin state:

In natural history, all possible things happen sometimes; you generally do not support your favoured phenomenon by declaring rivals impossible in theory. Rather, you acknowledge the rival, but circumscribe its domain of action so narrowly that I cannot have any importance in the affairs of nature. Then, you often congratulate yourself for being such an ecumenical chap (1973, 585).

It seems obvious to me that most work in evolutionary biology is dedicated to understanding the contingent events that shape evolution. With that said, I believe that a piece of this puzzle is to define the limitations of evolutionary processes. Rewind the tape of life an infinite amount of times, and there are some boundaries, at least on Earth, that life cannot cross. In discussing the role of developmental constraints in natural selection, Amundson provides the following useful comment:

A comparison with generative linguistics is helpful. There are an infinite number of possible human languages. However, all languages generated by a universal grammar are governed by certain constraints (570).

Likewise with evolution, there are a vast number of ways that life could have gone if the tape were rewound, but there may be some universal laws which govern all lineages. I am not arguing that too much effort has been spent understanding the contingent events in evolution, it is that not enough effort has been spent understanding the non-contingent events.
Conclusion

Biologists employ the concepts of possibility and necessity in a variety of ways: impossibility claims, which rely on constraints; morphospaces, which define hypothetical biological space by mathematical and geometrical abstraction; and metaphors, which invoke but do not define biological possibility. The varied uses of modal concepts often lead to conflicting accounts of what is possible. The reason biologists use hypothetical organisms in explanations is they are required in order to understand the *pattern* and *process* of evolution. The pattern of evolution, how lineages evolve over time, requires an understanding of the space through which lineages traverse. The process of evolution, the mechanisms responsible for shaping lineages, requires morphospace in order to understand whether adaptive or developmental constraints are responsible for guiding or limiting evolution. Despite all of this, very little attention has been paid to provide a universal account of how modal concepts operate in biology. This project is a step in that direction.
CHAPTER 3
DEEP MOTIVATION: PHILOSOPHICAL CONCERNS WITH MODAL CONCEPTS IN BIOLOGY

Introduction

In the last chapter, I examined various uses of modality employed by biologists to sort out empirical issues regarding the process and pattern of evolution. This chapter will look at the philosophical challenges of trying to restrict possibility in a uniquely biological way. In order to develop a restricted sense of possibility to biology, I will show that it is not unusual to provide a pluralistic account of possibility. First off, I will give a précis on the broad notion of possibility and necessity, or possibility simpliciter. This is an attempt to assess what is possible in a deep sense, such as metaphysically possible or logically possible. Much of the work on modality centers on issues regarding possibility at this level, such as whether possible worlds are real or fictions, the connection between conceivability and possibility, and whether one can make sense of modal claims at all. Conveniently, for the purposes of this project many of these issues can be avoided. Distinct from the broad notion of possibility, natural necessity, or physical necessity, is determined nomologically; e.g. through laws of nature. In order to establish a unique modal framework for biology, I will use the natural necessity as a guide. The problem, as you will see, is that it is not clear that biology has true laws of nature. Or, if there are laws within biology, they are weaker than physical laws (they admit exceptions).

A further problem is that laws of nature play an essential role in providing scientific explanations. According to the deductive-nomological (DN) model of explanation, laws of nature, together with any relevant circumstantial facts, combine to provide an explanation. Although there are problems with the DN model of explanation, many philosophers believe one of the DN models virtues is that it identifies that explanations rely on laws. If biology does not have true laws of nature, it may be that explanations in biology are lacking in some respect. Alternatively, if there are explanations in biology, they must be so in virtue of things other than deductive consequence of laws of nature.

Grades of Possibility

Modality is a pluralistic concept. If it was not, this project would be misguided. Kit Fine, for example, describes three varieties of possibility (or necessity); metaphysical, natural and normative (2002). Metaphysical necessity is necessity simpliciter. If something is possible, it must be metaphysically possible. Not even God could violate metaphysical possibility (hence, there is often the rider of God’s limitations in versions of the problem of evil). Natural necessity is nomic necessity – or necessity which follows from laws of nature. Normative necessity, as Fine calls it, are necessity relationships that are defined in regard to Kripkean notion of a posteriori necessity. Normative necessity will ultimately play a large role in my positive account of biological possibility, so I will delay discussion of
this matter until the fifth chapter. For pressing concerns, it is simply enough to
distinguish metaphysical from natural necessity, since this distinction will serve
as the starting point for developing a level of necessity unique to biology.

Metaphysical necessity, however, is not a homogenous category. There are
a variety of distinct categories within the broad notion of necessity, and every
philosopher seems to have their own distinctions and hierarchy. Following Alvin
Plantinga (1974), I will name the most primitive category of modality \textit{broadly
logical necessity}. (Again, since possibility and necessity are inter-definable, it
does not matter whether we define possibility or necessity.) Roughly, a
proposition is broadly logically necessary if its denial is self-contradictory. This
definition may be circular (self-contradictory may be defined as being impossible
to be true), but Plantinga only uses this definition as a general guide. Rather, in
defference to Socrates, he relies on examples to define this category. Here are
some propositions that Plantinga claims are broadly logically necessary:

1) $7 + 5 = 12$
2) If all men are mortal, and Socrates is a man, then Socrates is mortal
3) No one is taller than himself
4) Red is a color
5) If a thing is red, then it is colored
6) No numbers are human beings

Some philosophers identify several distinct categories within Plantinga’s
conception of broadly logical necessity. Potential candidates are logical
necessity, a priori necessity, conceptual necessity, and mathematical necessity.
For example, conceptual necessity might refer to (5), such that it is conceptually
necessary that a red object is colored. Others might argue that this is
metaphysically necessary. While yet others might not want to make a distinction
between conceptual and metaphysical necessity at all. (Those who make the
distinction between conceptual and metaphysical necessity are concerned with
the relationship between conceivability and possibility; i.e. epistemic limitations of
minds and metaphysical limitations of objects, properties, and events.)

While there is still much disagreement about broad logical necessity
(Plantinga) or metaphysical necessity (Fine), these controversies are orthogonal
to the current project. Natural necessity is distinct from broadly logical necessity
because (1) we can conceive of a world where the laws of nature do not hold,
and (2) we discover the laws a posteriori (Carroll, 2006). For example, let us
assume that a law of nature claims that all Fs are Gs. Even though this law is
nomically necessary, it is broadly logically necessary that not all Fs are Gs.
Furthermore, we discover that all Fs are Gs a posteriori. While we can sit in a
lounge chair and determine mathematical necessities, for instance, we cannot do
the same for laws of nature.

A convenient way to view the distinction between broadly logical necessity
and nomic-necessity is from a God’s eye perspective on world making. Once
God made the world, he had to do some more work to establish the physical
laws. To use another example, there are many different maximum speeds of
light that were possible other than the actual speed of light. Thus, it is possible in the broadly logical sense that Superman can travel faster than the speed of light, but it is not nomically possible. On the other hand, God couldn’t have made a world where $7 + 3 = 12$, where a valid argument form leads from true premises to a false conclusion, or where colored objects are not extended.

So, a fairly innocuous definition of physical possibility is:

**Physical Possibility**

$X$ is physically possible iff $X$ is does not violate the laws of physics.

What the physical laws are, and whether or not a particular state of affairs violates physical laws, may be controversial. Can quantum phenomena filter up and affect macro-phenomena? This is a problem for the physicists. As a result, what is physically possible depends on the current state of the field. Is it physically possible, for example, that a particular trajectory of a cannonball be achieved? One would have to fix certain states of affairs such as the angle of barrel extension, wind speed, atmospheric density, gravity ratios, the weight of the cannonball and the amount of explosive being used, before determining whether it would be physically possible. Once the particular circumstances are specified, we would be able to determine the possible trajectories given the set of physical laws.

**Laws and Scientific Explanations: The Deductive-Nomological Model**

One way to understand the relationship between modality and laws of nature is to examine the role that laws play in scientific explanations. The standard account of scientific explanation is the deductive-nomological model (DN), articulated by Carl Hempel. As the name suggests, the DN model has both a deductive component and a nomological component. The propositions in the explanandum (the thing to be explained) have a logical (deductive) relationship with the proposition(s) in the explanans (the explanation). Thus, if the propositions in the explanandum are true, the explanans must be true. The nomological component requires there must be at least one non-trivial law included in the explanandum along with the relevant circumstances of the explanandum. In a classic description of how the DN model explains, Hempel states:

… a DN explanation answers the question “Why did the explanandum-phenomenon occur?” by showing that the phenomenon resulted from certain particular circumstances, specified in $C_1, C_2, \ldots, C_k$, in accordance with the laws $L_1, L_2, \ldots, L_r$. By pointing this out, the argument shows that, given the particular circumstances and the laws in question, the occurrence of the phenomenon was to be expected; and it is in this sense that the explanation enables us to understand why the phenomenon occurred (337, italics in original).

The relationship between modality and explanation is a result of the deductive nature of DN explanations. For example, we can ask “why did the cannonball
land where it did?” If we can provide a DN explanation of that event, it becomes obvious that the cannonball could not have landed anywhere else. Once the relevant laws are fixed along with the particular circumstances, there is nowhere else the cannonball could have landed. To revisit an earlier quote, “if we are to explain how things are, we must be able to explain how things might have been, or must be, or couldn’t be” (Dennett, 1995). DN explanations do just that; once the laws and circumstances are defined, there is only one possible outcome. Of course, looking from the perspective of broad logical necessity the deductive consequence need not have occurred. However, this is not because the logical relationship between the premises fails, but because the particular law(s) of nature used in the explanans could be false.

There are well-known counterexamples to the DN model of scientific explanation. These counterexamples include cases of the asymmetry of explanation and cases where vacuous laws are used. However, many see these counterexamples as identifying that the DN model needs to be augmented in some way, not abandoned. In this light, the DN model may be necessary for an explanation, but simply not sufficient for one. Similarly, many feel that the virtue of DN explanations is that they identify that laws of nature are required explanations.

**What is a Law of Nature?**

Now that we have established that laws are required to determine physical possibility, we need to articulate what a law of nature is, in order to determine whether biological generalizations fit this mold. A reasonable method for determining what is biologically possible would be to follow the model used for physical possibility. Accordingly, what is biologically possible is whatever is permitted under the laws of biology.

**Bionomic Possibility**  

X is biologically possible iff X does not violate the laws of biology.

Here is the rub. Unlike physics, it is highly contentious whether or not there are natural laws in biology. Even though there are disputes about what a law of nature is in general, philosophers have traditionally looked to physics, not biology, for paradigmatic examples of laws. The quest, therefore, has been to capture the essential characteristics of laws, not to dispute their existence. Although debates about the ontological nature of laws are ongoing, there are some properties that most philosophers agree that laws should have. According to the “received view”, laws of nature must:

1) be universal, not individualistic (holds universally and not merely locally)
2) support counterfactuals
3) be empirical, not analytic
4) be used in scientific explanations.
First, I will examine each of these claims separately. Many of these properties are actually related to each other; e.g., the use of laws in scientific explanations is partly due to the support they provide for counterfactuals. Next, I will examine why some have argued that biology generalizations are not laws of nature. Finally, I will explicate some attempts to grant biological generalizations nomic status despite the fact these generalizations do not possess all of the required properties. It seems that there are a few conceptual paths to take when comparing physical laws to biological laws. We might find that biological generalizations are exactly like physical generalizations. No one takes this view. All of the theorists that I have read admit to differences between physical and biological generalizations. The interesting bit is what the differences are between physical and biological laws, and how these differences affect explanations in biology.

The first condition of the received view claims that laws of nature are supposed to be universal; they should not reference particular times, places or objects. The motivation behind this requirement is to eliminate claims that are true, but do not hold universally. Propositions like, “I had an even number of coins in my pocket on VE day”, are prohibited from being a law of nature. Even assuming that the proposition is true, it would not be a law of nature because it references particular times and locations, namely VE day and to the contents of a particular pocket. If universality was not a requirement, it seems that many individual events could be considered laws of nature and laws would become meaningless by their vast numbers.

The requirement that laws of nature support counterfactuals is closely related to the universality requirement. The requirement is intended to distinguish accidental generalizations from those that have actual nomic force. For example, take the following two claims:

(A) all gold spheres are less than a mile in diameter
(B) all uranium spheres are less than a mile in diameter

Although both (A) and (B) appear to be universally true, (A) is only accidentally true, while (B) is true in all possible worlds where the laws of nature are isomorphic to ours (because of the unstable nature of uranium). There are possible worlds that share all of the physical laws of our world, which contain a gold sphere more than a mile in diameter. Distinguishing accidental generalizations from nomicly necessary ones has been a thorn for the Humean account of laws of nature. According to Hume’s regularity theory, laws are merely constant conjunctions of causal events. Under this view both (A) and (B) are laws of nature, because the world does not contain instantiations of either claim.

Another way to distinguish (A) from (B) is that (B) supports counterfactuals whereas (A) does not. The counterfactual supporting requirement separates nomically necessary claims from those that are merely contingently true.
The final property of the received view of laws of nature in the requirement that laws be empirical and not analytic, (purely) mathematical, or conceptual. After all, it would seem odd to say that “triangles have three sides” is a law of nature. Thus, laws of nature are not necessary in the broadly logic sense described above, but nomicly necessary. A world that is physically isomorphic to our world with respect to laws of nature does not contain any uranium spheres that are one mile in diameter, but there possible worlds that are not nomicly identical to ours that contain uranium spheres of the required size. Large uranium spheres are possible, but just not nomicly possible - while gold sphere are possible in both senses.

Biological Generalizations: Laws or Something Less?

For good reason, philosophers of biology and philosophers of science have spent a great deal of effort trying to understand whether the causal generalizations found in biology are lawful and how explanation works in biology. In what follows, I will describe several accounts of whether there are laws of biology. Afterwards, I will relate the discussion of biological “laws” to biological explanations. After all, the quest for establishing laws of biology is ultimately to ground biological explanations.

Table 3.1. A smorgasbord of positions on biological laws.

| No Biological Laws (Smart, 1963; Beatty, 1995; Brandon, 1997) | The generalizations in biology do not possess all of the attributes of traditional laws of nature. Beatty claims that biological generalizations either are: (1) mathematical, conceptual, or physical in nature; or, (2) are not universal or have exceptions. |
| Biological Laws are Mathematical, Conceptual, or Physical Laws (Sober, 1997; Rosenberg, 2001) | Biology has analytic generalizations, but they are unique biological laws, because they explain biological phenomena. Examples: fundamental laws of population genetics and the conceptual necessity of natural selection. |
| Ceteris Paribus Laws (Lange, 1997; Sober 1997) | Biology has non-strict ceteris paribus laws, where a generalization will hold given certain antecedent conditions. This is a way to accommodate the exceptions of biological generalizations. |
| Non-strict Laws (Mitchell 2002, Lange 1995, Cooper 2003) | Laws admit of exceptions, but they are still considered laws because of the role that they play in biological explanations. Laws are not binary, but come in degrees (some laws hold over more cases than others). What is a law depends on the discipline. |
There are No Laws of Biology?

Historically, philosophers of science have looked to physics to for paradigmatic examples of natural laws. Any generalizations that did not meet the stringent requirements of physical laws, such as the law of supply and demand in economics, were not considered laws. The reason that the biological generalizations were not law-like is because they failed the universality requirement and they did not support counterfactuals. Biological generalizations either have exceptions, or are merely contingently true. This position is defended by Smart (1963), Brandon (1997), Woodward (2002) and Beatty (1995). Of these, I will examine Beatty’s (1995) account, because it is perhaps the clearest articulation of the why biological generalizations differ from physical ones. Beatty argues for the evolutionary contingency thesis (ECT). The ECT states that all biological generalizations are:

- a) just mathematical, physical, or chemical generalizations (or deductive consequences of mathematical, physical or chemical generalizations plus initial conditions), or

- b) distinctively biological, in which case they describe contingent outcomes of evolution.

I shall deal with the latter claim first. Beatty notes that any generalization that is distinctively biological can only be contingently true. There are two general reasons for this. One is that generalizations are not universal – there are exceptions, either actual or possible; another is that even if there are universal generalizations (frozen accidents), they are fixed via contingent events in evolutionary history.

For example, imagine a law that states “the $S$ is a $T$”, where $S$ is a species and $T$ is a particular trait common to that species. Due to the nature of evolution, there are principled reasons why this generalization will not hold universally. First, a necessary component of natural selection is variation. So, generalizations that posit species as a subject are not going to hold (at least counterfactually), because of the (actual and possible) variation that species exhibit. Evolution provides a moving target that alludes being captured by generalizations. For example, Rosenberg (2001b) discusses the generalization that “all zebras have stripes.” The explanation of this fact is that the visual illusion created by vertical stripes confuse lions - they have a difficult time distinguishing zebras from the background savanna grasses as well as identifying particular zebras amongst a herd of running zebras. However, as Rosenberg notes, this “arms race” between predator and prey will result in lions evolving different visual mechanisms which can distinguish zebras easier, followed by evolutionary changes within zebra lineages. Thus, any generalization that captures a trait of a species will only hold temporarily.
A second reason why universal claims do not hold is because natural selection cannot discriminate between functionally equivalent, but morphological disparate, traits. Rosenberg argues that there are no laws in biology (unless you manipulate the meaning of “law”), because natural selection is blind to functionally isomorphic traits (Fodor 1981; Rosenberg 2001b). If two traits are functionally identically but structurally different, natural selection is indifferent to which is ultimately selected.

Even if traits do hold to near universality, they still appear to be contingent. There are phenotypic traits that are found almost ubiquitous throughout the biological world. For example, Beatty takes the metabolic process of the Krebs cycle, which is a prominent biological process found in almost all aerobic organisms. He claims that this process is genetically based, and thus “the prevalence of the Krebs cycle among aerobic organisms …is a matter of evolutionary history” (1995, 49). Life need not have evolved with the same genetic code, consisting of four nucleic acids A, C, T and G. A second example, discussed by Mitchell (2002), is Mendel’s law of segregation. This law states “in all sexually reproducing organisms, during gamete formation each member of an allelic pair separates from the other member to form the genetic constitution of an individual gamete (331). However, there have been exceptions to this rule. First, this only occurs in sexually reproducing organisms, so this doesn’t hold universally. Second, even among sexually reproducing species, some organisms experience meiotic drive, which skews segregation. Thus, any generalization found in biology, even if it does hold universally, is a product of contingent historical events.

To return to the first part of the ECT, Beatty claims that biological generalizations are mathematical or deductive consequences of specified antecedent conditions. If generalizations have this quality, then they are not laws of nature because they are not empirical, but analytic. Examples of non-empirical generalizations in biology are the theory of natural selection itself (Dawkins, 1983; Rosenberg, 2001b) and Fisher’s (1930) theorem of natural selection, which claims that the rate of increase in fitness of a population at a time equals the additive genetic variance in fitness at that time (Sober 1997, 459). Both of these examples will be explained in detail further along in this section.

Ceteris Paribus Laws and Analytic Laws

One response to the contingency of biological phenomena is to construct ceteris paribus laws. Ceteris paribus laws build in antecedent conditions into the formulation of a law. To borrow an example from the last section, we found that Mendel’s law of segregation admits of exceptions in the cases of meiotic drive and asexual reproduction. In order to transform Mendel’s law into the form of a ceteris paribus law, we could build in antecedent conditions which would make the law true. So, given sexual reproduction and no meiotic drive, a 50:50 segregation of alleles will follow.
A more formal account of ceteris paribus laws is given by Sober (1997).

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\begin{array}{c}
I \\
t_0
\end{array} \quad \rightarrow \quad \begin{array}{c}
(P \rightarrow Q) \\
t_1 \\
t_2
\end{array}
\]

If (I) holds, then it is necessary that the relationship \((P \rightarrow Q)\) holds. Sober agrees that (I) is a contingent event, but it is necessary that if (I) occurs, \((P \rightarrow Q)\) must hold. Sober gives the following alternative characterization of Beatty’s ECT (b):

\[(L) \quad \text{If I obtains at one point, then the generalization (if p then q) will hold thereafter.}\]

Sober builds in antecedent conditions in law statements, making the conditional contained in the consequent necessarily follow from a true antecedent. What is (I)? It could be an infinite number of disjunctions. So although there are a contingent elements antecedent to the conditional \((p \rightarrow q)\), there is an analytically necessary relationship between I and \((p \rightarrow q)\).

The general problem with ceteris paribus laws is that they appear vacuous. If a violation of the law is discovered, then the antecedent conditions simply need to be adjusted to accommodate the new violation. Any violations of the law could simply be absorbed into the antecedent conditions. For example, if another mechanism was found that violated Mendel’s law of segregation, the antecedent conditions would simply be modified to account for this new mechanism. Furthermore, with the contingent nature of species, any regularities are relatively short lived. In criticizing ceteris paribus laws, Rosenberg states glibly that “ceteris is never paribus.”

Sober also defends the position that analytic or mathematical laws can function as true laws of nature. Sober claims that so-called process laws (generalizations which are mathematical, logical or analytic) should be treated as laws of nature. According to Sober, a process law is “a counterfactual-supporting, qualitative generalization, which describes how systems of a specified type develop through time” (459). An example of a process law in biology is Fisher’s fundamental theorem of natural selection, which says that the rate of increase in fitness in a population at a time equals the additive genetic variance in fitness at that time. This is a mathematical necessity, but Sober argues it should be a law of nature, because “Fisher’s theorem governs the trajectories of populations just as Newton’s laws govern the trajectories of particles” (459).

The standard response to permitting mathematical generalizations as laws of nature is that they are not empirical. However, as Sober notes, this fact alone should not rule out mathematical generalizations. My criticism is that even if there are mathematical generalizations in biology that are hold universally and are a priori, such as mathematical generalizations in population biology, these generalizations have a very limited scope and can only explain a relatively small range of phenomena (if they are truly explanatory at all).
Degrees of Lawhood

Instead of turning to ceteris paribus laws or a priori laws, another common response to broaden the laws of nature to include generalizations which admit of exceptions (Lange, 1995; Mitchell, 1997; Cooper, 2003). Although these accounts differ in their details, they all agree that because of the role that non-universal generalizations play in biological explanations, the definition of “law” should be altered to accommodate contingent biological generalizations.

As representative of this group, I will examine Lange’s (1995) account. Lange claims that there are laws pertaining to generalizations about particular species. For example, the claim that “robin’s eggs are bluish-green” is a law of biology, even if it is contingently true. Here, contingent could mean two things: either that it holds universally, but the reason is that it was “frozen” into the robin’s genotype by a contingent event it evolutionary history; or, it could mean that it just happens that robin’s eggs are bluish-green - given appropriate selective pressure and the proper variability, robin’s could develop different colored eggs. Either way, Lange argues, it is an example of a law of biology that makes reference to a particular species.

In order to defend this claim, Lange makes two moves. The first is that he argues that laws of nature can reference particular times, places, and entities. This is in direct conflict with the first condition of the received view of laws, which claims that laws must be universal (qualitative in nature). As an example, however, Lange discusses Dirac’s famous “law” that the gravitational constant bears a proportional relationship to the big bang. Whether or not this is a law of physics, its candidacy to “lawhood” was not impeded by the fact that it made reference to a particular time. Lange also discusses Tooley’s thought experiment about a theoretical garden governed by the law “all fruit are apples.” Tooley suggests that if there is a possible world where there is a garden where all fruit are apples, and if one attempts to bring in another kind of fruit to the garden, it turns into an apple. Bizarre as it may be, Tooley claims that “all fruit in this garden are apples” would be a law statement in that world, despite its explicit reference to a particular garden. Laws about species are laws about particulars, because species refer to particular times and places. Any law that makes reference to robins, is not referencing any organism that has a particular genetic code or phenotypic characteristics similar to robins. For example, if there were robin-like organisms on Alpha Centuri, they would not be robins, because in order to be a robin they must have a particular history, and the “robins” on Alpha Century do not have the appropriate history. Thus, laws that refer to species are particular laws.

The second move that Lange makes is to argue that claims such as “all S are T” are laws despite their contingent nature. Lange claims that such generalizations are “default assumptions”: “if you believe (with justification) that some thing is an S, then you are entitled to believe it T in the absence of information suggesting that it is not” (440). For example, Lange uses the generalization that “crows are black.” Even if this claim holds universally, it is contingent since if a suitable population of crows lived primarily in a cold climate they may have developed white strains, given the existence of the right kind of
mutations, etc. However, such hypothetical scenarios are beyond the scope of “all crows are black”, because such scenarios are just that, contrary to fact. So Lange claims that we can consistently hold that “all crows are black” is a law statement while also believing that there could have been white crows.

This account relies on two factors: how readily available information is to the contrary, and how tolerant of error we can afford to be. Lange explains this in the following:

So, for example, we are more willing to say ‘The lion is tawny’, while knowing that white lions occur occasionally, than to say ‘The Witch’s Hat mushroom is nonpoisonous’, while knowing that Witch’s Hats occur occasionally, because our tolerance for eating poisonous mushrooms is lower than our tolerance for making inaccurate predictions of a lion’s color (440).

So, Lange concluded that there can be laws pertaining to species, even though they admit of exceptions. His reason for this is a familiar one – laws are needed for explanations. If generalizations about species are genuinely explanatory, then we should call those generalizations “laws”, even if they do not conform to the standard definition of law. He states, “whether a claim is regarded by scientists as stating a natural law should be judged by whether that claim functions in scientific practice as a law statement” (442). Furthermore, he argues that what counts as a law will “vary according to the scientific discipline” (444).

As you can see, there are a variety of positions regarding the ontological status of laws in biology. Not surprisingly, the disagreements between the philosophers are not about empirical matters, but about the conceptual nature of laws and their role in explanations. In his work on biological explanation, Woodward (2000) calls the notion that laws are a necessary component of explanations the ‘nomothetic thesis’. Woodward goes on to note, I believe correctly, that “the substantive issue that lurks behind the terminological disputes is what are the characteristics that a generalization must posses if it is to figure in explanations (not what it takes for a generalization to be a law)” (197). The debate about the presence of laws in biology should not be a semantic debate about where to apply the term “law”, but a conceptual debate about how explanations in biology function.

Laws, Explanations, and Possibility

In order to examine whether biological explanations can provide a basis for determining modal claims, I will examine Rosenberg’s (2001b) and Woodward’s (2002) accounts of biological explanation. Rosenberg defends the position that, once it is carefully articulated, the traditional Hempelian DN model of scientific explanation can function in biological explanations. Woodward, on the other hand, argues for a modified account of explanation that does not rely
on strict laws, such as those found in the physical sciences. Neither position, however, will be equipped to tell us what is biologically possible.

**Rosenberg on Biological Explanation**

Rosenberg argues that the key to understanding the role of explanation in biology is to understand that biology, unlike physics, is a historical science. Evolutionary biology “can only provide an account of processes within time periods of varying lengths, and not across several time periods”. The question then becomes how does the DN model of explanation accommodate historical events? How can the DN model, say, explain why Caesar crossed the Rubicon? As Rosenberg notes, Hempel had already addressed this problem. Hempel claimed that historical explanations have the following characteristics: 1) they do rely on laws, but these laws refer to rational action; and, 2) these explanations are often “explanation sketches”. Explanation sketches are simply incomplete explanations, which “either presuppose information available to interlocuters or give promissory notes to deliver further details hereafter that will complete the explanation” (2001b). Only once all of the relevant laws and circumstances are put into an explanation does the explanation become complete.

Thus, historical explanations, like physical ones, rely on laws. However Rosenberg, like Beatty, believes that the generalizations used in biology are not laws, because they admit of exceptions, or are a contingent result of evolution, biological laws are not universal. (Actually, Rosenberg (2001b) argues that because evolution cannot discriminate between functional equivalents, biological laws will always fail). Instead of arguing that biological generalizations are laws, Rosenberg argues that biology has just one law of nature – that of natural selection itself. Rosenberg lists a fairly uncontroversial picture of the essential characteristics of natural selection:

1) Biological systems not on the verge of extinction or fixity reproduce with heritable variations.

2) If heritable variation obtains among biological systems, then there will be fitness differences among the biological systems.

3) In the long run, the more fit variants will leave a higher proportion of descendants than the less fit variants.

From these premises, it follows that:

4) Until fixity or extinction is attained, there will be descent with modification – evolution.

Thus, given variation, heredity and selection (differential fitness in a world of limited resources), descent with modification will occur. How is natural selection a law? Rosenberg argues that
…evolutionary theory describes a mechanism – blind variation and natural selection – that can operate everywhere and always throughout the universe. Evolution obtains whenever tokens of matter have become complex enough to foster their own replication so that selection for effects can take hold (755).

He is certainly not alone in claiming that evolutionary process is universal, applying anywhere life (or complex systems) occur. Dawkins famously argued for the same thesis, calling it “universal darwinism” which encouraged the application of evolutionary theory to other fields such as cultural evolution and meme theory (Dawkins, 1983; Dennett, 1995; Blackmore, 2000), the evolution of science (Hull, 1990), the evolution of economic organizations (Hodgeson, 2006), etc. I see serious problems with claiming that natural selection is a laws, and I will address them momentarily.

Assuming that Rosenberg has correctly identified the “one true law” of biology, how do biological explanations work? Following Hempel, Rosenberg argues that biological explanations are simply explanation sketches. Rosenberg believes that biological explanations are possible given only the law of natural selection, and the proper circumstantial evidence. Rosenberg states:

In order to complete an ‘ultimate’ or adaptational explanation of any particular ‘The S is T’ statement, it would be necessary to show why Ss having T, rather than an R or a W etc., came to be the actual solution to the design problem set by S’s environment. This would require an identification of the in-principle alternative solutions to the problem T solves, an account of which of them were available to S, details which show why T solved the problem better than the other available solutions, and an account of the subsequent environment of S which shows why T is maintained even after local environmental conditions (and their adaptational problems) have changed. Since such auxiliary information is neither available nor otherwise worth securing, adaptational explanations would perforce be explanation-sketches, with assumptions not open to direct and obvious test. But at least their explanans and explanada would be linked (in ‘objective dependencies’) to their explanans by nomological generalizations in the way required for scientific explanations, were we to accept the components of the theory of natural selection as laws. Though biology cannot fill in the details, it can be confident that nomological generalizations involved are known and have been since 1959 (756).

Although Rosenberg initially argues that biology should be treated differently than the physical sciences because of the influence of history in biology, his solution ultimately treats the two explanations the same – they both rely on laws and explanation sketches. The only difference, perhaps, is that biological explanations will more often take the form of explanation sketches because of the complex historical elements - environmental problems that organisms face, the variations that selection has to choose from. Furthermore, these explanation
sketches would likely remain sketches, because the information required to flesh them out is erased by history.

The use of explanation sketches and our inability to provide ‘ultimate’ explanations is not reason for alarm. However, I think that Rosenberg’s account fails for three reasons: (1) the ‘universal’ mechanism of natural selection does not function like a law, (2) even if it did function like a law, it cannot provide deductively valid explanations, and (3) it is not an elegant or pragmatic framework for explanation in biology.

**Is Natural Selection a Tautology or a Contingent Truth?**

It seems that there is a dilemma when considering whether natural selection as a law of nature: either it is a conceptual necessity, or it is not. If natural selection is a conceptual necessity, then it does not appear to be law of nature. Laws of nature are required to be empirical, and conceptual necessities are not empirical. The idea of natural selection as a conceptual necessity is often referred to as the “tautology problem” in the philosophy of biology. The problem runs as follows: among a variety of individuals, nature ‘selects’ the most fit individuals (through survival and reproduction). But fitness is going to be defined through reproduction. Roughly put, the tautology is that natural selection is “survival of the fittest”, where the fittest are defined as the ones that “survive”. Many theorists have identified this apparent vacuity with evolutionary theory. Popper, most notably, thought that natural selection could not be falsified – he thus argued that natural selection was a “metaphysical research project”. If natural selection is a conceptual truth, then Rosenberg needs to argue how a conceptual truth can function as a law in explanations. (After all, he criticizes Sober’s treatment of mathematical necessities as laws of nature. Rosenberg likens mathematical laws of biology to the rules that govern moves in chess. However, the rules in chess don’t explain why one player makes a particular move, they just limit the kinds of moves that one can make.)

Others have defined fitness in a way that is not circular. The “propensity interpretation” of fitness looks at the reproductive success of more than one generation (Beatty and Finsen, 1989; Gillespie, 1977). Thus, an organism that has a lower number of higher quality offspring would be more fit that an organism that has a higher number of lower quality offspring. Once fitness is spread over generations, it “has the virtue of making the slogan ‘the fittest survive’ into a contingent truth and the vice that it turns the theory into a falsehood” (Rosenberg, 2001b). However, I’m not convinced that the move made by the propensity interpretation of fitness eliminates the circularity – it simply relocates it, spreading it over several generations. Given the propensity interpretation of fitness, Rosenberg still believes that natural selection is a universal. How can he think that unless it is conceptually necessary?

**Can Natural Selection Explain?**

Even if Rosenberg is correct in arguing that natural selection is a law in the traditional sense, it still doesn’t appear that it alone can explain. For example, let’s revisit Gould’s thought experiment about rewinding the tape of life.
Gould argued that given identical starting positions, each running of the tape would produce dramatically different organisms. Natural selection alone can’t explain why the biological world is the way it is. Rosenberg argument is motivated by the desire to avoid using the contingent generalizations of biology in explanations. However, his explanatory framework does not capture these contingent events.

Sterelny also offers a criticism of this picture of evolutionary theory. As I mentioned, the ‘universal’ notion of selection has given rise to applications of this theory to explain social evolution, evolution of science, economic change etc. Sterelny notes that although that the general principles of variation/selection/reproduction hold for these phenomena, it is the details of biological systems which provide the insight. One can look at the historic impact of evolutionary theory as evidence of this; Darwinian theory is one of the most influential scientific thesis in history. However, this has not translated into successful adoptions of the Darwinian framework to explain social, scientific, or economic change. Sterelny argues that the reason why Darwinism is so successful in explaining biological phenomena and so unsuccessful in characterizing non-biological phenomena is due to the peculiarities of biological phenomena.

Woodward on Biological Explanation

A second, and perhaps more popular, strategy for grounding biological explanation is through the use of non-strict laws, or laws that admit of exceptions. How can laws which admit of exceptions be used in explanations? It is argued that non-strict biological laws can support a certain range of counterfactual conditions. I will take Woodward’s (2001) treatment as an example. Woodward, unlike Mitchell, Lange, Sober or Cooper, is not interested in the terminological debate about whether to call biological generalizations laws. Instead, he focuses on how biological generalizations must function in order to provide explanations. Woodward argues that generalizations need to possess invariance in order to be explanatory. He defines “invariance” as:

...a kind of robustness or stability property: a generalization is invariant if and only if it would continue to hold under some range of physical changes involving interventions. Heuristically, the notion of an intervention represents an attempt to capture, in non-anthropocentric language that makes no reference to notions like human agency, the conditions that would need to be met in an ideal experimental manipulation of the value of some variable X performed for the purposes of determining whether X causes a second variable Y (4).

Others have defended similar views of biological explanation, each having their own particular brand of the “robustness” condition: resiliency (Skyrms, 1980), stability (Mitchell, 2000), nomic-force (Cooper, 2003), and default assumptions (Lange 1995). Although they differ in details, all of these accounts claim that explanation can occur in biology despite the absence of exceptionless laws.
What matters for these accounts is that the explanans and the explanans are in the proper causal relationship with each other and hold over “enough” counterfactual conditions. I will not explicate the subtle differences between “invariance” and its competitors, because the details will not matter for my purposes.

What kind of relationship must there be for explanations to be invariant? Woodward claims:

> Invariance must be stable or invariant in the right way in the population P. The counterfactuals that matter for successful explanation have to do with what would happened under interventions that change the values of the explanans variables for the very system whose behavior we are trying to explain (what we might call “same object counterfactuals”), rather than with counterfactuals that describe the behavior of other systems (2001, 2).

I think there is an essential component of the traditional DN model that is missing in these versions of biological explanation which rely on invariance or some other surrogate notion – they don’t tell us what is possible, necessary, or impossible. Another way of stating this is that the “limited” way in which biological generalizations support counterfactuals destroys the deductive relationship of the traditional DN model between the explanandum and the explanans. If, as Woodward claims, a generalization may be invariant and hence explanatory even if it has exceptions, then the law admits counterexamples. It follows that a biological explanation could explain why “the S is a T”, while admitting that some Ss are not Ts.

There are two lessons that can be drawn from this: one happy and one sad. The happy conclusion is that, perhaps, this is the only kind of explanation that we can achieve in biology – explanations in biology are simply going to be weaker than physical explanations. The contingent nature of evolution precludes a deductive relationship between the explanandum and the explanans. Biological explanations are going to be explanatory in spite of being able to support a limited number of counterfactuals. The sad picture is that this deficiency indicates that this model of explanation is defective. The fact that these explanations only support a restricted number of counterfactuals means that these explanations are incomplete. There may be true explanations in the biological science, but Woodward’s model of the invariance relationship is insufficient to capture it. The question, according to the sad picture, is how can explanations explain if things could have been otherwise?

Regardless, from either the happy or the sad perspective we will not be able to determine what is possible. The difference between the two perspectives is that one claims that this acceptable, while the other finds something missing because of the lack of counterfactual completeness. Physical explanations in the traditional DN model have counterfactual completeness. The upshot is that even if current strategies to defend explanation in biology are successful, the project of determining what is biologically possible is left unanswered.
Conclusion

In the last chapter I examined several disparate uses of modality in empirical biology. Biologists use possibility claims and possible biological space in a non-trivial, non-colloquial matter. However, after examining several examples which make use of modal language we were left wanting for a theory of biological possibility. That was the shallow motivation – biologists use modal language to explain the pattern and process of evolution (which is the central question in evolutionary biology and, perhaps, biology from a broader perspective). This chapter examined the deeper motivation for developing a framework for the use of modal concepts in biology. Once we make the distinction between logical and natural necessity (or between broadly logical necessity and nomic-necessity), we can try to adapt the model used in physics for use in biology. However, I argued that there are deep philosophical reasons why this strategy will ultimately fail. Possibility and necessity in physics relies on strict laws of nature. When placed in the right arrangement in the DN model, laws, along with the relevant circumstances, explain why an event occurred and why no other event could have. However, laws of biology, whether or not there are any, do not function like physical laws. Furthermore, even if explanations are possible in biology despite the absence of strict laws, these explanations permit exceptions or hold only over a restricted set of counterfactuals. So, even if a treatment of laws of nature and explanation in biology are successful, they will not tell us what is possible, necessary, or impossible in biology. Now that I have established the empirical and philosophical motivation for this project, the next two chapters will be an attempt to provide an account of how to deal with modality in biology. Next chapter will explicate Dennett’s attempt at defining biological possibility. In the penultimate chapter, I will develop a novel framework for modal concepts in biology.
CHAPTER 4

DENNETT’S CONCEPTION OF BIOLOGICAL POSSIBILITY

Introduction

The contrast between the actual and the possible is fundamental to all explanation in biology. (Dennett, 1995, 103)

From the content of the last two chapters, you should now be in a state of aporia. First, biologists are using modal concepts without explaining how these concepts function. Second, the standard framework to delimit possibility in a science – via laws of nature in DN explanations – cannot be adapted to fit biology, since biology does not possess strict laws of nature. The laws of biology, if there are any, have exceptions, are contingently true, or are mathematical (or physical) generalizations. It seems that we need to understand how modality functions in biology, both from the perspective of the empirical biologist and from the perspective of the philosopher of science. Where do we go from here? As I mentioned in the introductory chapter, Daniel Dennett (1995) is the only philosopher (to my knowledge) who offers a definition of biological possibility. A virtue of his approach is that he defines and restricts the project in a way that makes it interesting and viable. If the problem of biological possibility is going to be solved, I believe the solution will follow the general guidelines outlined by Dennett. However, as Dennett admits, this definition (unlike his set-up of the problem) does not prove to be very interesting. Instead of sticking with the bivalent (all or nothing) conception of possibility, Dennett suggests that we talk about possibility in terms of probability.

If Dennett is correct, and his definition of biological possibility is the only one that is grounded metaphysically, then I agree that the bivalent conception of possibility is not useful for biology. Fortunately, as I will argue for in the next chapter, I think that there is an alternative, perhaps complimentary definition of biological possibility that is interesting as well as grounded philosophically that avoids the problems of Dennett’s definition. In this chapter, I will discuss how Dennett arrives at his definition of biological possibility and why it ultimately fails.

Setting the Table

Dennett makes some initial restrictions to the project, which I feel are intuitive and also preserve interest for the biologist. Dennett separates his project from the closely related project of exobiology, or astrobiology, which is the discipline that speculates about possible forms of life that could exist elsewhere in the universe. Astrobiologists are interested in biologically possibility, but from a very broad perspective. There search for what is biologically possible includes other-worldly life that may have arisen elsewhere in the universe. Differing from astrobiology, Dennett’s search for biological possibility is restricted to our
contemporary understanding of Earthly biology; what is possible on Earth, given how the biological processes operate locally. As Dennett claims, “we are still beginning in the middle, making sure that we understand today’s local, Earthly circumstances before casting out nets wider” (112). Thus, when we are evaluating what is biologically possible, we are trying to understand life on Earth, and not life in a broader context.

This restriction is reasonable, since a problem for astrobiology is that the sample size for making any inductive generalizations about what other-worldly life would be like is one - Earth. We only have knowledge about Earthly life and any theorizing about radically different kinds of life is highly speculative. This criticism was first raised by David Hume in his attack of the argument from design. Well before Darwin (and Paley, for that matter), Hume claimed that we cannot infer a designer from the apparently designed organisms in the natural world, because we do not know what other worlds look like; worlds that have been designed by a designer and worlds that have just come into being. Likewise, it is difficult to speculate about how different life could be on other planets, or even if life occurs elsewhere in the universe. Dennett’s strategy seems to be more fruitful – we must first understand how possibility claims function with Earthly biology before applying them elsewhere. This is intuitive to biologists, since our understanding of biology is restricted to how life functions on Earth – our understanding of biological possibility should reflect this restriction.

In order to discuss what is biologically possible, we must first narrow the realm of possibilia. Dennett uses a Russian Doll model of modality, where different varieties of possibility are nested: logical, physical, biological, historical and actual.

Fig. 4.1 Dennett’s Modal Stratification (107).

This strategy is similar in spirit to the modal stratification described in the last chapter, but the content is slightly different. Logical possibility is not as
homogenous as Dennett’s diagram suggests. Those who wish to make fine-grained distinctions subdivide this category into metaphysical, conceptual, and mathematical possibility. Recall that I endorsed Plantiga’s nomenclature of *broad logical necessity*, which is a more pluralistic account of possibility than Dennett’s logical possibility. This debate, however, is orthogonal to the project at hand. Physical possibility, on the other hand, is a clearly defined category that, again, relies on laws of nature to distinguish the possible from the impossible. Dennett exemplifies the distinction between logical and physical possibility by saying that it is logically possible for superman to fly faster than the speed of light, but it is not physically possible to do so.

Biological possibility is a subset of physical possibility, which, in turn, is a subset of logical possibility. Thus, anything that is biologically possible must be physically possible – a claim that no credible biologist would dispute. The next category in Dennett’s stratification is historical possibility, which describes possibility by temporally indexed events, such as the possibility of me winning a spelling bee. Since I have long passed the age of entering spelling bees, and I have not already won such an event, it seems that this possibility has become closed to me. Historical possibility may ultimately play a role in understanding biological possibility, since evolutionary biology is a historical science. But for now, I shall move on to Dennett’s final category, the actual. The set of everything actual is, not surprisingly, composed of all and only the things that are actual. Some philosophers, such as Ayer (1968), argue that the only possible things are the actual things. However, actualism, as it was called, is a philosophically barren doctrine and has largely been abandoned.

**Biological Possibility: Preliminary Attempts**

Before settling on his unique definition of “biological possibility”, Dennett explores some initial candidates. He claims that “there might be two kinds of grades of biological impossibility: violation of a biological law of nature (if there are any) and mere “biohistorical” consignment to oblivion” (106). I will call these tow forms “bionomic possibility” and “biohistorical possibility”. Similar to the strategy developed in the last chapter, a natural “first try” at developing a framework for biological possibility is to borrow the framework that is developed for physical possibility. Again, physical possibility depends on laws of nature. A more formal definition for nomological possibility is as follows:

\[ P \text{ is nomologically possible for a relevant body of nomos just in case } P \text{ is consistent with the body of truths expressed by those laws (Gendler and Hawthorne, 4).} \]

From this definition, physical possibility is defined as:

\[ P \text{ is physically possible just in case } P \text{ is consistent with the body of truths expressed by physical laws.} \]
Moving from physical to biological possibility, the same strategy will yield the following definition:

**Bionomic Possibility:**

P is biologically possible just in case P is consistent with the body of truths expressed by the laws of biology.

What follows from this definition is that something is biologically possible only if it doesn't violate the laws of biology. However, as I argued in excruciating detail in the last chapter, the laws of biology, if there are any, are not equipped to support counterfactuals in the way that physical laws are. Following Beatty's “evolutionary contingency thesis,” biological generalizations are either (a) mathematical, physical, or chemical generalizations, or (b) contingently fixed by history or they admit of exceptions. Either way, the “laws” of biology are not guides to the possible in the ways that physical laws are. Dennett likens biological “laws” to the QWERTY phenomena - the standard arrangement of the top row of keys on a standard keyboard. Although the QWERTY keyboard is not the optimal arrangement of keys on a keyboard, it has become too engrained in our culture to change. There is nothing legal, physical or otherwise that prevents someone from producing a better keyboard, but it is almost “as if” there were law-like constraints preventing such a change. Dennett gives a generalized argument why laws cannot give us possibility than was given in the last chapter. He argues that “the imperious restrictions we encounter… may look like universal laws of nature from our myopic perspective, but from a different perspective they may appear to count as merely local conditions, with historical explanations” (123). Thus, the “bionomic possibility” definition fails because there are not the right kinds of generalizations in biology.

Had the world been slightly different than the actual world, and an alternative keyboard was developed to the same levels of efficiency, the QWERTY phenomena would now be called something else, perhaps the less satisfying WQYUZP phenomena. Thus, the origination of the QWERTY keyboard was a contingent historical event, but it has become engrained in our society. Species seem to follow this same pattern. For example, it might be the case that mammals are “locked” into their quadroped body, unable to evolve additional appendages. However, there was probably a time in their evolution (or, perhaps even before the mammal lineage split off) where evolving an additional set of limbs was a real possibility. This seems to lend support to the biohistorical interpretation of possibility. Dennett receives further inspiration for this view from George Williams, a well-respected evolutionary biologist, who claims:

I once insisted that ‘...the laws of physical science plus natural selection can furnish a complete explanation for any biological phenomena' (Williams, 1966, pp. 6-7). I wish now I had taken a less extreme view and merely identified natural selection as the only theory that a biologist needs in addition to these of the physical scientist. Both the biologist and the
physical scientist need to reckon with historical legacies to explain any real world phenomenon (1985, p. 20) (from Dennett, 123).

It seems that the problem with the tradition role of laws and explanation is that it is not suitable for a historical discipline like evolutionary biology. Perhaps we can develop a definition of biological possibility that incorporates the historical element of evolutionary biology. Thus, a rough approximation of “biohistorical possibility” may be:

**Biohistoric possibility:**

X is biological possible, unless X is historically consigned to oblivion.

Although “consigned to oblivion” is a vague notion, the spirit of the claim is obvious. Sometimes called “happy accidents,” certain traits acquired by ancestors became ingrained, such that they cannot now be altered. Dennett explains biohistorical possibility with the following example:

There might have been a time, in the very distant past, where when the possibility of six-limbed mammals on Earth had not yet been foreclosed, but it might also be true that once our four-finned fishy ancestors got selected for moving onto the land, the basic four-limbed architecture was so deeply anchored in our developmental routines that alteration at this time is no longer possible (106).

The development of evolutionary “novelties” such as skeletons, photosynthesis, eyes, the spinal cord, brains, the quadroped body design, etc. allow access to regions of morphospace that were previously inaccessible. However, once these initial design patterns are ingrained within a lineage, it may be difficult or impossible to evolve a new body plan, even if an alternative body plan is optimal. Fisher’s adaptive landscape can illustrate this point nicely. Even if there are higher peaks on the adaptive landscape, species may not be able to reach that peak because they would have to cross a fitness valley to get there. Importantly, the reason why a species becomes trapped at a sub-optimal peak is because of (contingent) historical events.

Novelties, which are events in evolutionary history which allow a diversification of body plans, have the dual function of opening up new regions of morphospace and closing other regions off. Here, an analogy can be made between the phylogeny of a species and the construction of a house. Once certain decisions are made about the design and construction of a house, certain options become available while other are closed off. If the bathroom has limited space, for example, you will be limited in the kinds of designs that fit within that space. Likewise, since bats have evolved bat-like wings, they are probably restricted from evolving the more efficient bird-like wings.

Sterelny (forthcoming) discusses the advent of evolutionary novelties as responsible for “increasing the space of evolutionary possibility.” What is responsible for this increase in possibility? Sterelny argues that:
1) they are revolutions of biological inheritance systems, involving the expansion of the transmission of heritable information across the generations, and

2) they are revolutions in selection for they involve the assembly of a new, higher level agent out of previously independent agents.

Sterelny discusses increasing space of evolutionary possibility in the context of the minimalist conception of macroevolution – which is that microevolutionary processes are sufficient to explain macroevolutionary changes. Novelties, which are revolutionary changes of a sort, are a challenge to the minimalist picture.

There seems to be a problem with the biohistorical conception of possibility and the idea that biological novelties are “possibility-expanding”. From a broad perspective, it seems that phenotypes that are “biohistorically” consigned to oblivion are possible. To return to Dennett’s example, from a broad perspective it seems that six-limbed mammals were possible all along. Six-limbed mammals may be impossible to evolve from current mammal lineages - given the laws of biology – but six-limbed mammals inhabit not so distant possible worlds. The reason that mammals have four instead of six or eight legs is due to contingent historical events in the mammalian lineage. Had those events turned out otherwise, mammals could have had a different number of appendages. To return to Sterelny’s example of novelties that “expand biological space”, it seems that such phenotypes are possible before the novelties evolve. Sterelny gives the following example of expanding biological possibility: “until genes were organized into chromosomes, and the fidelity of gene replication improved, prokaryotic cells were not in the space of evolutionary possibility” (forthcoming). But it seems that prokaryotic cells were possible before the advent of chromosomes, etc. What Sterelny’s example captures is that certain developmental/selecionist/ecological advances are required in order to reach certain areas of morphospace. In other words, in order for evolution to achieve, say, a tiger, a vast number of novelties need to come about. But if we could stand at the beginning of life and ask whether tigers are possible, it seems that the answer must be yes, since tigers actually did evolve. Furthermore, if we could stand at the beginning of life on Earth and ask whether six-legged tigers are possible, it seems that the answer would probably be yes.

The biohistorical interpretation of possibility, as well as Sterelny’s “possibility-expanding” conception, belies the bivalent nature of possibility. To illustrate this point, I can ask whether it is physically possible for me to be in Australia five seconds from the now. It seems to be impossible, give that I am in North America and there are no technological devices that can transport me down under in the requisite time. However, this doesn’t seem to violate physical possibility, because no physical laws would be broken had I been in Australia to begin with. Likewise in biology, although lineages have developed in ways that reveal and restrict areas of morphospace, it seems that this says nothing about what is or is not possible. Biohistorical possibility doesn’t answer the question posed by Gould, that if the tape of life is rewound, what are the different ways life
could have turned out? Biohistorical possibility only claims that given the contingent nature of evolution, once developmental “choices” are made, the downstream variation and selection of lineages is restricted.

**Dennett’s Broad Conception of Biological Possibility**

Although the bionomic and biohistorical conceptions of possibility fail, they both contain elements that may be useful for establishing a framework for biological possibility. Following the model for physical possibility, bionomic possibility preserves bivalency: either X conforms to or conflicts with the laws of nature, giving a clear demarcation (if only in theory) between the possible and impossible. The biohistoric conception emphasizes the historical nature of evolutionary biology. Perhaps modal concepts in the biological science will simply have to be treated differently than they are in the physical sciences. In seeing the failures of both conceptions, Dennett must separate the wheat from the chaff in order to construct his own definition of biological possibility.

In order to make headway on this project, Dennett makes another intuitive, but somewhat arbitrary restriction. As I mentioned earlier, Dennett quest for biological possibility is restricted to Earthly life, but what exactly does this mean? What traits do all Earthly biota share? While he is aware of exceptions, Dennett assumes that all life is composed of DNA. Although it is true that not all living things are composed of DNA (viruses are composed of RNA), and that it may be a historically contingent fact that nearly all life on Earth has DNA versus some other replicator, Dennett has to have a starting point with which to begin, and DNA seems like the best candidate. From this modest beginning, he creates an imaginary catalog of all possible organisms, which he calls the Library of Mendel. 

Dennett drew inspiration for this fictional library from a short story by Jorge Luis Borges (1962), who imagined a library which contained all of the books that have been written or could possibly be written. Borges called this the “Library of Babel”. The books contained in the library were constructed of 500 pages, contained a limited number of lines per page and a limited number of characters per line. For books longer than the 500 page limit, additional books can be combined to form a multi-volume work. Borges conceived the Library of Babel as containing a numerically exhaustive set of all possible books. Thus, for example, there would be a “vast” number of books that very closely resemble Moby Dick, but only vary by one misplaced word. Of course, there are some restrictions to the Library of Babel, such as the exclusive use of the Latin alphabet, but this “arbitrary” restriction is similar to Dennett’s restriction that all life contains the DNA alphabet.

Following this strategy, Dennett imagines the Library of Mendel to house the numerically exhaustive list of all possible genetic combinations. He does this by imagining all possible protein combinations (A, C, T, and G) on an average length genome. Given that there are about $3 \times 10^9$ nucleotides in the human genome, it would take 3,000 of the 500 page volumes to give a complete genetic “book” for any individual human (p. 111). Of course, a vast majority of the “boxed sets” of 3,000 books code for lifeless lumps of matter, but there are 3,000 volume
boxed sets for every organism that exists, ever existed, and could ever exist. Every possible permutation of proteins on the DNA strand would be represented in the Library of Mendel.

Before offering his definition of biological possibility, Dennett addresses several complications that arise when imagining the Library of Mendel. First, simply because a DNA strand exists, it does not follow that you can construct an organism from that strand. Genomes need “genetic readers” in order to be transformed into phenotypes. This was one of the criticisms levied against the fanciful technology represented in the film, *Jurassic Park*. In the film, dinosaurs were created from ancient strings of dinosaur DNA that were found embedded in amber. The problem with the technology is that even if we could get dinosaur DNA, we do not have the “genetic reader” required to turn the DNA into a full-fledged dinosaur. What is a DNA reader? In humans, the egg can read and construct bodies from the instructions encoded in DNA. Without these readers, hypothetical genomes could not code for hypothetical organisms. This objection, however, is one of practical concern and not relevant to our exploration of possible biological space.

A second concern is that we need to specify an environment before we can assess whether a particular non-actual organism is viable. One of the restricting factors in the evolution of complex life is the limitations and opportunities environments present to species. To take an extreme example, terrestrial mammals would not be possible before other forms of life occupied the land – there would be nothing to consume. The point Dennett is making is that we cannot assess the possibility of hypothetical organisms in a vacuum – we must always assess their possibility in the context of an environment. However, the question then becomes which environment should we specify when we are asking whether a particular organism is viable? What are the possible ecosystems that could have evolved on Earth? This question is a very important, but complicated one – and one which Dennett does not answer. For the time being, I will eschew this question as well.

A third concern Dennett raises is the complex relationship between genes and their products. Although we may be able to describe organisms like a centaur, dragon, or unicorn, it does not mean that there are (possible) genetic “recipes” for such creatures. Even in the Library of Mendel there may not be a dragon genome. As Dennett states:

The fact that we can consistently describe a finished product – say a giraffe with green stripes instead of brown blotches – does not guarantee that there is a DNA recipe for making it. It may just be that, because of the peculiar requirements of development, there simply is no starting point in DNA that has such a giraffe as its destination (117).

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2 Dennett must develop new words to describe the large number of possible genetic combinations and to describe the small numbers of finding viable genomes amongst the vast majority of genetic gibberish. Dennett coins the term “Vast”, which stands for “very-much-more-than-astronomically” to describe the largeness of the numbers involved in this thought experiment.
The complex relationship between genotypes and phenotypes prohibits, at this time, a clear understanding of what is possible. Some variations may not be possible from a particular starting point, say in actual mammals, but it may be possible given a different genetic recipe. Perhaps it would be genetically impossible for the human genome to be altered to produce bird-like wings. However, given a genetic recipe that differs from the actual humane genome in important ways, a winged human-like phenotype may be possible. Here, Dennett raises the possibility that there may be phenotypes that simply have no possible genotype that codes for them. However, Dennett warns that we shouldn’t take the likelihood to seriously. A theme running through Dennett’s book is Orgel’s Second Rule, which states that “evolution is smarter than you are!” “Proving that there is no straightforward way for biology to accomplish some trick is never a proof of impossibility” (117).

With these issues and the Library of Mendel in the background, Dennett is ready to offer his definition of biological possibility. For reasons to be explained later, I’ll call his definition broad biological possibility.

**Broad Biological Possibility**

X is biologically possible iff X is an instantiation of an accessible genome or a feature of its phenotypic products (118).

This definition seems to capture the best elements of both the bionomic and biohistorical elements. The only universal, law-like feature common to (almost) all living things is that they are constructed from a similar DNA recipe. Thus, the definition preserves bivalence by claiming that if there is genome that codes for a possible organism, then it is possible; if there is no code, then the organism is not possible. Broad biological possibility also appears to capture the historical element of evolutionary biology the “accessibility” requirement of the definition. What does Dennett mean by “accessibility”? What genomes are accessible and from where? As I mentioned earlier, there may not be a way for actual tigers to evolve an extra pair of legs – the requisite genetic change may be too large. Nonetheless, the six-legged tiger genome is probably accessible from a starting point somewhere in the distant past. In other words, bacteria can transform into brontosaurus, given enough time. This is clearly possible, because it is actually happened! Dennett then claims that all (viable) genotypes are actually accessible, since all life is connected. Dennett states that:

> No man is an island, John Done proclaimed, and Charles Darwin adds that neither is any clam or tulip – every possible living thing is connected by isthmuses of descent to all living things (121).

This claim seems to implicitly rely on the assumption of what I’ll call the universal accessibility of biological form.
Universal Accessibility (UA)

Any viable genotype is accessible through evolution, given infinite amounts of time, genetic variation, and environmental variation.

UA differ from a concern that was raised earlier, which was the fact we can consistently describe an organism, it doesn’t follow that there is a genome that codes for such an organism. Such an organism is impossible because there is no genome that codes for that organism, not that the particular genome is inaccessible.

UA can actually be distinguished into two separate forms, weak and strong. It turns out that each form has its own associated puzzle.

Weak Universal Accessibility (Weak UA)

From the beginning of life, any viable genotype is accessible given infinite amounts of time, genetic variation and environmental variation.

According to weak UA, every viable genome in the “Vast-ness” of morphospace is assessable from the beginning states of life. Remembering the rewinding the tape thought experiment, if the tape of life were rewound to the beginning, every possible genome is accessible. By designating the beginning of life as the starting point to determine accessibility, weak UA rules out developmental and historical constraints that lineages acquire as they become more complex and are “forced” to make developmental decisions.

A second interpretation of UA is as follows:

Strong Universal Accessibility (Strong UA)

Any genotype is accessible from any other genotype, given infinite amounts of time, genetic variation, and environmental variation.

Strong UA goes further than Weak UA by claiming that any possible genome is accessible from any other genome, regardless of developmental constraints that a particular lineage may acquire during its travels through morphospace. Certainly the likelihood that a horse could evolve into a horsefly is “Vastly” improbably, it is nonetheless probably. Strong UA becomes less surprising when you consider that any particular existent organism, such as an elephant, is a “Vastly” improbable endpoint on a 1.5 billion year evolutionary path.

It is not clear which version of UA, strong or weak, Dennett endorses. To return to a previously mentioned quote, Dennett expressed “every possible living thing is connected by isthmuses of descent to all living things.” This is certainly true, if all living things have a common ancestor. What is not clear, however, is if Dennett believes that complex organisms with developmental constraints have the ability to transcend these constraints in the long run.

Either version of UA, however, has potential counterexamples. Strong UA claims that any viable genome in the Library of Mendel can be reached from any other viable genome. If it is the case that complex organisms cannot violate developmental constraints, Strong UA would be false. Perhaps some traits, such
as the dorsal location of the nervous system, are so entrenched in the bodily design that they cannot be eliminated. This, however, is a bold statement. Dollo’s law, which claims that organism can never return to the exact form from whence they came, seems to be in opposition to Strong UA. Dollo argued that:

An organism never returns exactly to a former state, even if it finds itself placed in conditions of existence identical to those in which it has previously lived. But by virtue of the indestructibility of the past... it always keeps some trace of the intermediate stage through which it has passed (as quoted in Macintyre, 359).

But once again, Dollo’s law is not a law in the strict sense. Instead, Dollo’s law that species cannot reserve along their evolutionary trajectory is a probabilistic statement. There is nothing “unlawful” about reversing evolutionary trends. It is, however, highly improbable that such a trend actually occur. Environmental pressures, mutations, and selective pressures would have to be exactly right for such a trend to occur, and the likelihood of this is exceedingly slim. Thus, it seems that there is nothing unlawful about Strong UA.

A challenge to Weak UA (which, of course, would also challenge Strong UA) would be if there are possible genotypes that could not be reached from any evolutionary starting point. I will call such fictional creatures deviant organisms, because they stand in isolation from normal evolutionary processes.

**Deviant Organisms**

Organisms (or traits) that are an instantiation of a viable genome, but the genome cannot be reached from any evolutionary trajectory.

The possibility of deviant organisms isn’t as far fetched as one might originally think. Intelligent design theorists not only think that deviant organisms are possible, but actual! Reviving the creationist movement, intelligent design theorists claim that cellular machinery (the organelles that compose individual cells) are too complex to be formed via the gradualist conception of evolution.

Intelligent design theorists have not found a welcome home in the biological sciences, and I do not intend to support their efforts here. The interesting question, however, is how can we tell if a particular phenotype is too complex to be formed though Darwinian processes? Not surprisingly, ID theorists are often charged with having their biological views clouded by their religious leanings. I argue that looking at the possibility of deviant organisms could be a naturalistic way to examine the merit of ID. If we can produce a sound argument about why a viable genotype could not be reached from any starting point, then it seems that intelligent design is possible. However, even if deviant organisms are possible, there is still an argumentative leap to say that there are actual examples of deviant organisms.

The interesting question is what kind of argument, if any, could support the thesis that deviant organisms are possible? The question could not be answered
through empirical investigations. What kind of empirical evidence would suggest that a genome is inaccessible? A further concern is that any argument maintaining the possibility of a deviant organism, is more a reflection of the lack of creativity of the author, and less a reflection of the biological world. For example, I am ignorant about the origination of many of the traits found in the biological world. It is mysterious to me how eyes, brains, circulatory systems, and the fantastic reproductive “tricks” of some orchids evolved. Importantly, however, these traits are not mysterious to biologists. Although some details pertaining to the origination of such traits may remain reticent, the general framework on how they evolved is not in question. Thus, any deviant organism that may be hypothesized is just waiting for a bright biologist to devise an origination story about how such an organism could evolve. No need to worry about giving a “just so story”, because any story will do.

An argument positing deviant organisms must be a conceptual one, which gives principled reasons why a viable genotype cannot possibly be accessed from any starting point. I don’t know of any argument that would support the possibility of deviant organisms, but I don’t rule out that one can be given.

The Limitations of Broad Biological Possibility

Regardless of which version of UA Dennett supports, or whether counterexamples to either form of UA exist, a serious weakness of the definition of broad biological possibility has been exposed. Namely, it does not succeed in restricting possibility in a historical way. Because Dennett argues that any viable genotype is accessible, there is no way to delimit possibility in any interesting way. Biological possibility is merely reduced to being linked to a viable genome. It is in this sense that Dennett’s definition is a bit circular; biologically possible is simply defined as genetically viable. This is why, upon reaching his definition, Dennett finds it to be ultimately an uninteresting concept for biology. Following Wittgenstein, he throws the ladder away once he has climbed it. Another failing of this definition is that it is useless to biologists. There are no mechanisms to test whether a particular phenotype has a genotype that codes for it. If there is a viable genotype that codes for a centaur, then it is possible, since all viable genotypes are accessible. However, there is no way to determine whether such a genotype exists. Most importantly, broad biological possibility doesn’t add any explanatory light on existent debates in evolutionary theory.

Realizing these problems, Dennett abandons the quest for biological possibility, claiming that, once found, such a definition is useless:

Perhaps after all we don’t need the concept of biological possibility (with its required all-or-nothing application) for any serious investigative purpose. Perhaps degree of accessibility in the Library of Mendel is all we need, and is in fact a getter concept than the all-or-nothing version could be. It would be nice, for instance, to have some way of ranking the
following in terms of biological possibility: ten-pound tomatoes, aquatic
dogs, flying horses, flying trees (120).

I do not know why determining the relative likelihood of flying horses and flying
trees is interesting, but I do agree that if this is the only definition of biological
possibility that is justified, then it simply is not an important concept in biology.
Perhaps, because of the historical nature of biology, modal concepts cannot be
used in the same way in biology as they are in physics. But this is ultimately
unsatisfying, since many biologists seem to rely on modal claims and
hypothetical biological space (as discussed in chapter two).

Near the end of his chapter on the possible and the actual in biology,
Dennett leaves a curious insight about how one might proceed. He claims that,
“a restricted concept of biological possibility is the sort we want; the ideal of a
universal concept of biological possibility will be misguided” (123). Dennett could
not find a way to philosophically ground a restricted concept of biological
possibility. Consequently he argued for the use of probability instead of
possibility in biology.

Following the work some philosophers working on modality, I believe there
is a way to salvage a restricted conception of biological possibility – a way which
makes sense of how biologists are actually using these concepts.
CHAPTER 5
RESTRICTING BIOLOGICAL POSSIBILITY

Introduction

My project, to this point, has been largely expository and critical. I have explained how empirical biologists employ modal concepts and I have argued that modal concepts are required for complete explanations of why the biological world appears as it does. Despite the use of and usefulness of modal concepts, there are no straightforward methods to restrict modality to a uniquely biological realm (but there is motivation for presenting a stratified view of modality). In what follows, I will present the positive contribution of this project; namely, I will offer a unique definition of “biological possibility.”

I do not arrive at a definition of “biological possibility” ex nihilo. My definition will ultimately relate to, and justify, how some biologists are using modal concepts, while suggesting others may be applying these concepts inappropriately. Ultimately, as I argued in the introductory chapter, biologists are going to tell us what is biologically possible. The role of the philosopher is to construct the appropriate metaphysical framework for biologists to flesh out. In this role, I believe that philosophers have already developed the conceptual tools for establishing “biological possibility.” The difficult task is to arrange these tools in the appropriate ways. A danger in this strategy is that one may “cheery-pick” theories, not on their individual merit, but because they fit the overall puzzle. Obviously, I hope that I have avoided this temptation.

In previous chapters I have attempted to treat the empirical and philosophical issues separately. It is time to thread the two into a single, cogent argument. First, I will provide a definition of “biological possibility.” Secondly, I will develop the conceptual components required by my definition. This will include discussions of taxonomy, species concepts, and resurrecting biological essentialism; all of which are controversial. Next, I will explain how my definition is relevant to ongoing debates in biology. Finally, I will map the particular examples that biologists used about possibility (the impossibility claims, morphospaces, and metaphors) onto the definition, thereby endorsing particular methods of applying modal concepts in biology.

Restricting Biological Possibility

Finding a good definition is an extremely difficult task. One of the themes in the Socratic dialogues is the difficulty of defining terms such as “justice,” “beauty,” “friendship,” “virtue,” and “courage.” At the end of most of the dialogues, Socrates’ interlocutors are left in a state of confusion, or aporia, unable to develop a coherent and complete definition. Recent work in the philosophy of language has pronounced the difficulty in finding precise definitions (alternatively, in the case of Wittgenstein, embraced the vagueness of definitions). Although I do not pretend to conceptually analyze what constitutes a good definition (this is not a project in the philosophy of language), I will list some general principles that a satisfactory definition of “biological possibility” must
achieve. In a sense I am not attempting a “definition” but creating a framework; i.e., a methodology for understanding modality in biology. The following suggestions are unique to the task at hand and not intended to be generalizable to ordinary definitions. The framework for biological possibility should:

1) reflect how (some) biologists use modal operators. As described in chapter two, not all biologists use modal concepts consistently. However, a good definition will endorse some usages and criticize others. Note, however, to say that some biologists are using modal concepts incorrectly is not to say that they are in error. They may employ these concepts to fulfill alternative conceptual needs.

2) provide a procedure, or framework, to determine what is biological possible. In short, the definition must be empirically tractable. Although, it may turn out to be practically impossible to empirically verify whether something is possible, it should be theoretically possible.

3) be metaphysically sound. The bivalent nature of possibility should not be altered. This is consistent with saying that certain possibilities are more “likely” than others – but there must be a relatively clear demarcation between the possible and impossible.

4) be interesting. If it turns out, as Dennett concluded, that determining what is biologically possible is ultimately uninteresting, then it is not a worthy project to pursue; i.e., we should not simply create a realm of biological possibility simply because we can.

Dennett’s definition failed on all of these counts. His definition doesn’t reflect the actual use of modal operators by biologists. Dennett did not survey the literature to determine how biologists are using modal language. For Dennett, it is a vacuous procedure to determine whether something is possible; we simply have to try to construct a genome to see if any particular phenotype is possible. Ultimately, Dennett argues that in biology we should transform talk of “possibility” into “probability.” This would trivialize the standard bivalent account of modality. Finally, as Dennett admits, this definition is not interesting (hence his desire to shift from modal language to stochastic language).

Dennett, to his credit, acknowledges these shortcomings. In what appears to be almost a throw-away sentence Dennett advances an avenue for further research:

The imperious restrictions we encounter in the Library of Mendel may look like universal laws of nature from our myopic perspective, but from a different perspective they may appear to count as merely local conditions, with historical explanations. If so then a restricted concept of biological possibility is the sort we want; the ideal of a universal concept of biological possibility will be misguided (123).
It seems that if we are going to make progress on establishing “biological possibility” we need to restrict our pursuit in the right sort of way. Unfortunately, Dennett does not elaborate on what this “restricted” concept of biological possibility may resemble. The challenge appears to be how we can make contingent, historical generalizations count toward explanations of what is possible. Here are some possible candidates for restricting biological possibility. Some of which we have already considered, but they are included here on pains of completeness.

**Astrobiological Possibility**

This is the most inclusive sense of biological possibility. If something is not possible in this sense, then it simply is beyond the scope of the living. This sense is much more inclusive than Dennett’s definition, because anything that is possible on earth is (obviously) possible in the universe. The problem, however, is that biologists and philosophers do not have inductive grounds with which to make inferences about how life may emerge elsewhere in the universe. What are the different forms alien life may acquire? Furthermore, biologists are, for the most part, not interested in the associated questions about life on other worlds. (Or, if they are, they are using life on earth to make assumptions about life elsewhere. While this approach may develop some useful strategies for searching for extraterrestrial life, one should not consider it complete.) Biologists are interested in how life on earth emerged and evolved. Thus, when biologists are employing modal concepts they are restricting their discussions to this world.

**Biomechanical Possibility**

To speak loosely, there are only so many ways for organisms to make a living in this world. There are only so many manners of locomotion organisms can possess. Furthermore, there are only so many ways to construct a particular phenotype. For example, Rudolf Raff (citing the work of Mittenthal), states that the tubular gut is probably the most efficient form of digestive organ, and may have arisen several times independently” (1999, 314). Organisms have an orifice in order to intake food, a gut to extract nutrients, and an exit to expel waste. Furthermore, Raff argues, there are only so many ways that a tube could be engineered:

by invagination and pinching out of a solid sheet, by ingrowth from an end, like a finger being pushed into a rubber sheet, or by cavitation from a solid matrix. All of these are used in animal development (314).

A similar but more complex example is the skeletal space fleshed out by Thomas and Rief (discussed in chapter two). The skeletal space is a grid of all the possible manners in which skeletons could be constructed and assembled. One problem with the diagnosis of biomechanical possibilities of the tubular gut and with skeletal space is that it is dependant upon human cognitive capacities. If I could imagine another way in which to “manufacture” a tube, then Raff’s
explanation would be incomplete. In fact, there are other manufacturing
techniques that can produce a tube. fiberglass cylinders are often manufactured
by a process called filament winding. This process takes strands of fiberglass
and systematically wraps a rotating cylindrical mould until one reaches the proper
thickness. Once finished, the mould is released from the shell producing a
perfect cylinder. now I am not claiming that we are likely to find skeletal
construction via filament winding in the natural world. i mention this only to
illustrate that it may be cognitive limitations on the part of theorizers that limit the
construction methods and assemblages that may exist. Thomas and Rief, both
expert paleontologists, were no doubt influenced by their vast, preexisting
knowledge of skeletal designs already found in nature when carving out
theoretical design morphospace of skeletons. They didn’t invent their skeletal
space “sitting in an armchair” and then went in the world to find corresponding
instances.

Therefore, the problem with restricting biological possibility to
biomechanical principles is that they are subject to the cognitive limitations of the
theorists. In trying to determine design limitations, human creativity is often the
limiting factor. In fact, the causal arrow has often run in the other direction. We
have learned countless engineering “tricks” from the natural world; the
hypodermic needle being a clear example. If we had not already witnessed the
design characteristics of some actual organisms, would we think they were
possible?

**Ecological Possibility**

There are two scenarios to restrict possibility to ecological factors. First,
there are likely only a finite number of possible ecosystems. For example, a
world in which only microorganisms and mammals existed would be a
biologically impossible world, since mammals rely on a number of other life forms
for existence. Another way to describe this is through niches. There are only so
many niches that are possible, and, eventually, natural selection will produce
species that exploit these niches. This process is evident when you compare
Placentalia mammal and Marsupialia mammal niche exploitation. Both lineages
contain members that are remarkably similar and occupy the same niche, despite
having separate evolutionary trajectories. Ungulates, for example, take the role
of prey in many ecosystems while kangaroos occupy this role in the great
marsupial experiment called Australia.

The problem restricting biological possibility in this way is that, again, we
have no idea of the ecological assemblages that are possible on Earth. Like the
criticism of biomechanical possibility, there are no principles ways in which we
can be certain that we have exhausted all of the possible ecosystems.

A second way that something may be ecologically impossible is that a
particular organism or species may not be able to survive in particular
environments. For example, if we were to introduce species S into environment
E, it might be the case that another species R already occupies the ecological
niche that S would normally occupy. In such a case, S may not be sustainable
within environment E, although S may be sustainable in other environments.
Although this restriction is potentially interesting and relevant to conservationists, it doesn't delimit possibility in the right sort of way. I am interested in what is possible given any kind of environment.

**Selective Possibility**

Natural selection is the central force driving evolution. Restricting biological possibility to particular selective pressures would mean that certain phenotypes are impossible given particular selective pressures. For example, if there were selective pressures toward taller trees, ceteris paribus, it would be impossible for tree height to shorten. In other words, given a particular selective pressures, some phenotypes would be impossible. The problem with selective possibility, as with ecological possibility, is that selective pressures change. When we are talking about what is biologically possible, we are not interested in what is possible given a particular environment or selective pressures.

**Genetic (Species) Possibility**

In this sense it may be possible for a particular phenotype or phenotypic property to originate within a population, but it may be impossible for that trait to spread throughout the population due to the diluting effects of the population (even if the particular trait has a high selective value). For example, assume that polydactyl humans (humans with more that five digits) have both a high selective value and that the trait is heritable. Depending on the population size, the selective value of the trait and genetic considerations, it may or may not be possible for this trait to spread throughout the population. Thus, although an organism can exhibit a particular phenotype, it may be impossible for the phenotype to spread throughout the population. Again, I am not interested in whether a particular phenotype is likely to be spread throughout a population, but whether it is possible in the first place.

**Individual Possibility**

Finally, biology may or may not be able to explain why particular individuals have the traits that they do. There is a vein of literature debating the possibility of particular individuals to have different traits than they actually possess (Sober, 1980). Thus, biologically speaking, it may be impossible for me to have any other color eyes than the blue eyes that I have in the actual world. This kind of possibility, however, is driven by particular metaphysical commitments for rigidly identifying individuals. Namely, that a named individual, such as Jason Zinser, must have been born from his actual parents, from the actual egg and sperm used to conceive him. If all these antecedent conditions are necessary for my existence, it seems that it would be impossible for me to have different colored eyes. This form of possibility is not biological, but metaphysical. Thus, it is not really biological possibility that is being defined. Rather it is a biological explanation that is being screened off from individual possibility. When we are discussing what possible phenotypes may develop, we are not asking about individual organisms. Rather, we are asking whether such forms are possible.
Summary of the Varieties of Restricted Possibility

There are a variety of forces which coalesce to produce evolution in species: population size, heritability of a particular character, environmental pressures, physical constraints, migration of individuals to and from populations, mutation, random drift, and (most importantly) natural selection. The restricted domains of possibility described above isolate individual forces at the expense of neglecting the contribution of the other forces in shaping evolution. For example, a particular phenotype may be biomechanically possible, but impossible in a particular environment or population. There doesn’t appear to be a naturalistic manner to restrict possibility to a uniquely biological domain.

Given this unhappy diagnoses of the overall project it is easy to fall into despair. However, one must revisit what biologists actually do and why modal language is employed in the first place. Biologists rarely engage in the task of providing universal generalizations that apply to all organisms. The generalizations that come closest, think Cope’s rule or Dollo’s law, always have exceptions. Biologists aren’t concerned with establishing universal generalizations, but with the evolutionary history of particular species and how phenotypic trajectories lead to particular outcomes. Biologists do not spend much time answering questions about why there are no centaurs or unicorns; they are interested in the possibilities of existent species and lineages. We simply can’t demarcate the biologically possible organisms in any non-trivial way (as Dennett’s work nicely demonstrates). This is satisfactory because biologists are not interested in this kind of generalizable category for many of the reasons mentioned above. What they are interested in is hierarchy of forces that contribute to the evolution of existent species and phyla. It is in this spirit that I propose a restricted sense of biological possibility.

**Restricted Biological Possibility (RBP)**

It is biologically possible for lineage X to acquire phenotype \( p \) only if \( p \) is directly accessible from X, and \( p \) is an instantiation of a viable genotype.

In contrast to Dennett’s definition, RBP restricts possibility only to those phenotypes that are directly accessible to a particular lineage; species or higher taxon. The problem, again, with Dennett’s definition is that every viable genotype is accessible from any other genotype. By restricting accessibility only to genotypes that are directly accessible to a particular phenotype, genotypic variation is severely restricted. The vagaries of history, developmental constraints, etc., are transparent to Dennett’s formulation, but not to RBP.

A joke, in a loose sense of the word, may help explain the distinction between broad biological possibility (BBP, hereafter – Dennett’s conception) and RBP. Imagine that you are lost in a city and you want to access the freeway that runs through the heart of the city. You drive toward it, but you can’t find an on-ramp. You stop at a gas station and ask the attendant, “How can I get on the highway?” The attendant responds, “Oh, you can’t get on the highway from
here!” The supposed humor in this joke is that the attendant is obviously mistaken. Of course you can get to the highway from here. After all, almost all roads in the continental USA are connected (with the exception of roads on islands, for example). What the attendant was noting was that there is no entrance in the vicinity of the station. (Like many jokes, the humor rests on abuses of conversational implications.) In our discussion of possibility, BBP would denote that all roads are connected. If you want to know if you can drive somewhere, you simply have to know if it is located on a road. Likewise, for BBP, if you want to know if \( X \) is possible, we simply have to know if there is a genotype codes for it. Accessibility is not a problem for Dennett. However, for RBP, what we are interested in is whether or not there is direct access to a particular form, like knowing whether there is direct access to the freeway.

Notice that in order for RBP to work, a starting point has to be given. We simply can’t ask if centaurs are possible, because there is no designated starting point from where we can ask if centaurs are possible. Nonetheless, centaurs may be possible given Dennett’s sense of possibility. In this way, RBP is not an alternative to Dennett’s definition, but complimentary. RBP does not establish a realm of biological possibility similar to logical or physical possibility. The project of constructing a unique domain of biological possibility in the cast of the Russian doll model is misguided. Instead, RBP indexes possibility to actual lineages. Once a starting point is designated, we can examine what is biologically possible from that point. Although, in order to understand what is biologically possible from a lineage, we have to understand how to define “directly accessibility.”

**Direct Accessibility**

\[
Y \text{ is directly accessible from } X, \text{ iff } X \text{ does not change essentially before reaching } Y.
\]

In order to know whether something is directly accessible, you first have to have a starting point. Once you have a starting point, there are certain domains of morphospace open to exploration and (most) other regions of morphospace are restricted. This move is intended to circumvent notion of “universal accessibility.” I can agree that given enough time, genetic variation, and ecological variation, all viable genomes are accessible. However, according to RBP, they no longer would be the same species. For example, let’s assume that feathered bats are possible according to Dennett’s definition; i.e., there is a viable genome in the Library of Mendel that codes for a bat with feathers. (After all, it seems that feathered bats would have a higher fitness value than the standard bat phenotype.) Would this be possible according to RBP? Although it would require empirical data to confirm this, my intuition is that it would not be possible. Existent bats could not produce the necessary variations that could lead to feathers. Importantly, this isn’t a result of selective pressures and passing through a fitness valley in order to reach a higher fitness peak where feathered bats reside. Given any selective pressure (or an absence of selective pressure) bats simply couldn’t vary in the right sort of ways; i.e., they are developmentally...
constrained from doing so. Over vast tracts of time perhaps the bat lineage could evolve feathers, but they would no longer be bats. The sense I am referring to here is the sense in which bacteria evolved into human beings. Large phenotypic transformations are obviously possible over large tracts of time.

An analogy may facilitate what, exactly, is meant by restricting biological possibility. Hurricane forecast models are a good visualization of what restricting biological space would look like. In order to get a better sense of direct accessibility, let’s examine the following diagram of hurricane forecast models.

Fig. 5.1 Forecast models for hurricane Ivan on Sept. 11, 2004 (left), and Sept. 13, 2004 (right) (NOAA).

Meteorologists at the National Oceanic and Atmospheric Administration (NOAA) have developed sophisticated forecast models for predicting hurricane paths. As they invariably stress, however, these models are imprecise. From data such as hurricane strength and speed, jet streams, pressure systems, air and water temperature, etc., they create a three-day forecast “plume” designating the probable hurricane path. These forecast “plumes,” as they are called, can be seen as metaphors for how lineages move through theoretical morphospace. The actual hurricane eye can be seen as the actual genetic variation of a particular lineage (neither the eye of a hurricane nor the genealogical nexus of a lineage are points in space, but are relatively defined regions of space). The biological analog to the forecast plumes would be the space available for evolution, or, phenotypic plumes through morphospace. Before discussing the virtues of the metaphor, I will explicate its shortcomings. The disanalogies, it turns out, are almost as informative as the analogies.

First, forecast plumes designate probable, not possible future paths. As with all weather forecasting, probabilities are usually given because weather is an epistemically stochastic phenomena. Upon examination of the two forecast plumes it is clear that they are designating probable paths. For example, in the model on the left, the Yucatan peninsula is not in the forecast plume, while the
model on the right, created two days later, the plume asymptotically approaches the Yucatan. If the plume designated possible and not probable paths, the first plume would have been mistaken, since it seems that the Yucatan peninsula was always a possibility. Although probability (in the sense of contingency) plays a major role in biological explanations, RPB is designed to have the firm bivalent boundaries typical of standard modal claims. Thus, unlike like hurricane plumes, plumes through morphospace must have firm boundaries.

Secondly, once the hurricane is named, it retains its identity, which convention holds is a first name, throughout the time that the storm is organized. Species, on the other hand, will change identity over time as they evolve into other species. Thus, a problem for phenotypic plumes, but not for hurricane plumes, is where to draw boundaries. Similarly, hurricanes might not be natural kinds, whereas species, I will argue, are natural kinds. These problems will be examines shortly.

Finally, the forecast plumes have a geometrical uniformity that species plumes do not. All of the area contained in the plume above is in the potential path of Ivan; the edges of the plume are less likely while the center is of higher probability, with corresponding probabilities between the two. In phenotype plumes, there may be discontinuous regions of morphospace, where possible phenotypes exist on either side of a vacant region. The following diagrams from Albrech (1982) will illustrate the discontinuous variations that phenotypes can exhibit and identify how we can tell where vacant areas exist:

![Fig. 5.2 Phenotypic variation may cluster without intermediate (Albrech, 318).](image)

The X and Y axes represent the different dimensions that a trait can vary; e.g., egg size and egg number. The illustration represents possible clustering of phenotypic variation found in nature. Of course, the variations of organisms found in nature are never exhaustive of all of the variations that are possible.
Why is this the case? One reason is simply chance. The variations simply haven’t occurred yet. Species membership is always finite, thus the actual variation present is always a subset of possible variation. Another reason is that some variations are disadvantageous and are selected out of the population. Organisms could occupy vacant space, but they would be selected out (think of the two explanations for empty space in Raup’s shell morphospace). A final explanation is that variation is constrained by external or internal factors. For example, physical laws (like gravity) act in concert with developmental programs to limit variation, such as the case with ultimate tree height. How can we tell if the clustering is due to selection or to constraints?

Fig. 5.3 Two possible scenarios for phenotypic variation if selective pressures were removed (ibid, 318).

As the diagram illustrates, if selection is removed for a particular trait we can determine if the clustering of phenotypes is a result of selection or constraints. If selection is the limiting factor, once selective pressures are removed variations are distributed randomly, as in the bottom-left illustration. If, on the other hand, variation is restricted through constraints, the resulting pattern of variation will be clustered as in the bottom-right diagram. Therefore, if selection is responsible for the clustering effect of phenotypic variation, or if there is no clustering effect, then species plumes would expand uniformly as is the case with hurricane plumes. If constraints limit phenotypic variation irrespective of selection, then species plumes would not produce a uniformly conical shape.

Despite these concerns, there are many insightful analogies between forecast plumes and species plumes through morphospace. First, the expanding conical shape of forecast plumes is indicative of the shape that plumes through
morphospace would occupy. If we image forecast plumes as indicating possibility instead of probability, the farther the hurricane travels from its present location the more possible locations the hurricane may be. This shape reflects two traits that hurricane plumes and species plumes share. First, the farther the distance traveled from the present course, the more deviation that is possible from the current path. The width of the hurricane plume six hours from a particular point is relatively narrow compared with the width of a hurricane plume projected out two days. The same lesson can be applied to phenotypic evolution. One of the important lessons from Darwin is that variations are typically small, and evolution molds through selection over time; large phenotypic jumps in evolution are not possible, or if they occur, they are not heritable. Thus, the morphospace occupied by actual species is relatively small. However, if this space is extended in time, the space of possible phenotypic variation is broadened. Examples of this come from instances of domesticated species and artificial selection. When domesticated dogs first arose, they occupied only a fraction of the phenotypic space that contemporary dogs occupy (think of the variety of breeds that exist today). The farther in time the plume is extended from the present, the larger the plume becomes.

Secondly, there is an epistemological component to both forecast plumes and design plumes through morphospace. The kind of unpredictability of forecast models seems to be the kind of unpredictability present in evolution. Hurricane paths are causally determined. But due to the complex dynamics of the forces responsible for hurricane paths, predictions of hurricane paths are always tentative. Similarly with the evolution of species, we may not be able to predict long-term trends with precision, but that doesn’t mean that evolution is not deterministic. Environments, like the weather, are highly dynamical systems where a multitude of independent causal chains interact to form particular events.

A final analog between hurricane plumes and plumes through morphospace is the role that history plays in each. Looking at the two forecast models of Ivan, you can see that at one time the Florida Keys were in the forecast plume, but two days later the Keys were no longer in the forecast plume. Again, let’s assume that hurricane plumes represent possibility, not probability. Thus, at one point the hurricane could have hit the Florida Keys, but after the hurricane’s path shifted, the path through the Keys was no longer possible. This is similar to the biohistorical sense of biological possibility that Dennett invoked and subsequently rejected. Some phenotypic variations, such as six-limbed mammals, were possible from a distant point in history. However, once the four-limbed design path was ingrained within mammalian architecture, six-limbed mammals are no longer possible.

The following illustration is of a hypothetical phenotypic plume through theoretical morphospace.
Fig. 5.4 A plume through theoretical morphospace. E is the actual phenotypic variation of a hypothetical species or lineage. E₁ and E₂ are possible phenotypes that may be acquired; the arrows indicate the limit of possible variation. V₁ and V₂ are potential vacant regions which are inaccessible due to developmental constraints (see above). D₁ and D₂ are accessible from E in the long run, but they are not directly accessible from E; they are members of a different species or lineages.

The phenotypic variation of the actual species, represented by E, is not a point in morphospace but a cluster of points representing the actual variations of organisms found in nature. The plume, defined by the arrows extending out from E, represent the possible variations organisms of a particular species may acquire. For example, E₁ or E₂ are possible, non-actual phenotypes that are directly accessible from E. What determines whether species will acquire E₁, E₂ or remain with phenotype E? In other words, how can we predict which phenotype will be acquired, or once a phenotype is acquired, how can we explain how that phenotype was arrived at? In order to explain the “threads of actuality” within the phenotypic plume we have to invoke the standard host of forces responsible for shaping the evolutionary trajectories of lineages, such as natural selection, mutation, population size, random drift and the migration of individuals to and from a population. These forces converge to produce the actual phenotypes from a set of possible phenotypes. As mentioned earlier, the actual selective forces placed on a species are contingent. For example, if you move organisms from one ecosystem into another, organisms will be exposed to different selective pressures. However, the concept of phenotypic plumes suggests that there are only so many ways that species can vary given any possible selective pressure.

The thought that variation is limited for particular species is not new. Julian Huxley, the grandson of T. H. Huxley, commonly known as Darwin’s Bulldog, claimed:

It is quite conceivable that every species tends to produce varieties of a limited number and kind, and that the effect of natural selection is to favor
the development of some of these, while it opposes the development of others, along their predetermined lines of modification (Julian Huxley, quoted in Spurway, 1949).

Expressing a similar sentiment, Spurway argued:

Each species has its own characteristic potential for variation, thus speciation modifies not only the anatomy and physiology of a species, but it’s evolutionary future (1949, 7).

These accounts describing the limitation of variation within species are similar to my account of RBP. However, from a philosophical viewpoint, these accounts are incomplete. In order for RBP to be philosophically grounded, the definition requires a defense of biological essentialism in order to fix species, or lineages, at a particular location within the broader realm of biological possibility. Remember that the definition of RBP was in reference to direct accessibility, which, in turn, was defined in terms of essentialism. Without such an account, possibility claims will not work for the following reason: even if phenotypic plumes are fixed to particular species, and variation (through mutation or selection) is limited, the particular phenotypic plume is contingently fixed through historical events. History, in other words, needs to be incorporated into an account of possibility in order to fix plumes to a particular location within morphospace. For example, recall Dennett’s rejection of biohistorical possibility. He claimed that although six-limbed mammals may not be possible from current mammalian design plan, it could have been the case that mammals have six limbs had historical events been otherwise. Thus, in order to be metaphysically sound, my account of RBP relies on an account of biological essentialism. Lineages need to be fixed essentially to their particular location within morphospace in order to fix their respective phenotypic plumes.

Biological Essentialism

The questions surrounding biological essentialism are too complex to receive the proper attention in this dissertation. In order to properly defend an account of biological essentialism a careful treatment of biological classification as well as a host of metaphysical issues would have to be discussed. Nonetheless, I will sketch several accounts which defend a version of biological essentialism against the prevailing anti-essentialist consensus in evolutionary biology. Before defending biological essentialism, I will have to describe the standard account of essentialism and the motivation for the anti-essentialist arguments in biology. Elliot Sober, a critic of essentialist tendencies in biology, describes essentialism in the following way:

Essentialism is a standard philosophical view about natural kinds. It holds that each natural kind can be defined in terms of properties that are
possessed by all and only the members of that kind... A natural kind is to be characterized by a property that is both necessary and sufficient for membership (1980, 145).

A stock example of natural kind essentialism is that gold is essentially atomic number 79. It is essential that gold has atomic number 79, but only accidental that it has the particular color, malleability, or other descriptive properties. It's the “hidden” microstructure of gold rather than the “obvious” macrostructure that makes a particular chunk of ore gold. Furthermore, the causal powers of gold are related to its microstructure. Therefore, the standard account of essences claims that they:

1) are necessary and sufficient properties; they are not accidental;
2) must be explanatory; essences are responsible for the traits typically associated with the members of that kind
3) are intrinsic properties;
4) help predict those properties associated with that kind (Sober 1980; Ereshefsky, 2006).

In this sense, one of the goals of science is to discover the essences of natural kinds in the physical world; to determine what the essence of natural kinds are and the causal powers that emanate from their essence.

While this interpretation of science may have captured much of what physical sciences pursue, it has not worked well for the biological sciences. Through the influence of Mayr (1963) and Hull (1965), evolutionary biology has taken a decidedly anti-essentialist turn. Species membership, it is argued, is not attained through a shared common property. There are no traits that, for example, all and only Homo sapiens possess. There is a shared history between all human beings, but there are no shared physical properties. Even if there are shared properties, these properties would be accidental. Given time and variation, there would be members of that species which do not possess a particular traits.

This leads to a second argument against biological essentialism which is that species evolve. The argument is as follows (Ereshefsky, 2006):

Natural kinds are immutable
Species evolve
Therefore, species are not natural kinds

Gold, for example, cannot change into another element. If it is broken into its constituent parts and assembled into other elements, it ceases to be gold. However, species can evolve into different forms without changing essentially.

The anti-essentialist turn in biology is reflected in the classificatory and explanatory commitment of biologists. Biological classification is accomplished through historical relationship between organisms and more coarse-grained
hierarchies, such as families, genus, etc., not through phenotypic or genetic set of properties. Furthermore, biological explanations are typically population level explanations, which do not rely on the nature of individual organisms (Sober, 1980; Walsh, 2006).

In spite of these arguments, there have been attempts to defend essentialism and natural kinds within biology. I will sketch two of these attempts and argue for a weak form of biological essentialism.

**Historical/Relation Essences**

In a recent paper, Samir Okasha (2002) advances a modified account of essentialism defended by Saul Kripke (1980) and Hilary Putnam (1975). Kripke and Putnam defend a causal theory of reference, where natural kinds are identified through their essential microstructure. Differing from the descriptive theory of reference, which claims that natural kinds are identified via their descriptive properties, the causal theory of reference claims that the descriptive properties of natural kinds are a product of their essential microstructure. Under the causal theory of reference, the essence of water is $H_2O$, not the set of descriptive qualities of water, such as the liquidy stuff flowing through rivers, potable, freezes at $0^\circ$ Celsius, etc. (This reflects the distinction between nominal and real essences exposed by Locke, where nominal essences are external, observable features and real essences are hidden and internal.) This distinction is often motivated by the Twin Earth thought experiment. Imagine a world similar to earth in all respects, except that the liquidy stuff flowing through rivers and streams was not composed of $H_2O$, but of $XYZ$. In this case, argue Kripke and Putnam, the stuff flowing through rivers on Twin Earth is not water, but some other substance. Why? Because the essence of water is $H_2O$, and since the microstructure of the “watery stuff” on Twin Earth has a different microstructure, it is not water. The story is a bit more complicated, but for our purposes, we can leave the details out.

Kripke and Putnam both use biological examples to motivate an essentialism for biology. For example, Kripke argues that “tigers” have an essence – the DNA microstructure that is common to all and only tigers. As indicated above, biologists argue that this misrepresents the biological data. Specie members do not share a common microstructure. Agreeing with the prevailing biological thought, Okasha does not argue that all members of a species share a common microstructure. Rather, he argues that all members of a species share a historical/relational property. To defend this view, Okasha examines the prevailing species concepts. Although there are a host of intermediary positions, he distinguishes four general kinds of species concepts: phonetic, biological species concept, ecological, and phylogentic. Phoenetic species concepts assign species membership based on overall similarity of phonetic properties. The biological species concept, developed by Mayr, argued that the membership criteria for species was interbreeding, either potential or actual (Mayr vacillated on this point). The ecological species concept distinguishes membership criteria on the basis of the particular ecological niche that organisms occupy. Finally, phylogenetics distinguishes species by their
evolutionary history. Accordingly, species are the smallest monophyletic groups; i.e., groups in which all of the members have a shared common ancestor.

To be certain, classificatory debates within biology are alive (the most recent issue of *Nature*, March 15, 2007, is dedicated to these problems). Nonetheless, Okasha notes a similarity between all of the species concepts, with the exception of the phonetic species concept – which, as Okasha notes, has since gone out of favor. The biological species concept, the ecological species concept and phylogenetics all require a historical/relational property common to all members. According to Okasha, Kripke and Putnam are correct in attributing essentialism to species members, but are mistaken in thinking that it is a microphysical property. Rather, all conspecifics have a relational property in common: according to the biological species concept, all and only members of a species can interbreedability; according to the ecological species concept, all and only members of a species share a common ecological niche; according to phylogenetics, all and only members of a species share a common ancestor.

Kripke, therefore, was correct in arguing that “tigers” have an essential property, but wrong in that it was a microphysical property. If Okasha is correct, “tigers” have an essential relational property (which particular relational property, depends on what species concept ultimately becomes the received view). Like the example with gold, one can run a Twin Earth thought experiment with tigers. On Twin Earth, there are beings that are physically isomorphic with tigers, but they are not “tigers” because they lack the essential relational property that tigers on earth possess.

**Aristotelian Essences**

Walsh (2006) defends an alternative account of biological essentialism, which he claims is a modern version of Aristotelian essentialism. According to Aristotle, species membership is determined by a set of common, immutable properties which are essential for species membership. (Obviously, Aristotle did not think that species evolved.) Walsh argues that recent advancements in developmental biology suggest that members of species share a set of developmental mechanisms which are responsible for channeling variation in specific ways. Thus, the immutable properties are developmental mechanisms responsible for restricting (and promoting) variation. In support of his view, Walsh quotes Rudolph Raff:

> (the processes that control evolution)... provide internal, non-random evolutionary variation. Such variation is sorted by the internal requirement to maintain integrated function and by external selection on resultant phenotypes. Because of the internal requirement that modified ontogenies be functional, only a subset of all theoretically possible phenotypes will be generated (325).

The particular ways in which organisms are constructed, limit the subsequent kind of variations that are permitted. Therefore, Walsh argues, species essences are indispensable for biological explanations:
...evolutionary developmental biologists deploy their conception of an organism’s natures in ways that are remarkably similar to the ways in which Aristotle deployed the concept of an organism's nature – viz. to explain: (i) the presence of features (ii) recurrence of traits (iii) the resemblance among organisms (442).

Essentialism and RBP

The different kinds of essentialism expounded by Okasha and Walsh are not in conflict with each other. For example, let’s examine a particular species such as Homo sapiens. All humans have a relational property in common with each other: we share a common niche, we can interbreed, or we share a common ancestor. However, this is not all that we share. Humans also share a similar construction and, as a result, are limited in the kinds of variations individuals can possess. In arguing against biological essentialism Sober claimed, “two individuals belong to the same natural kind in virtue of their similarity, not in virtue of their history” (1980, 145). However, in the case of species, history is the cause of similarity. According to Okasha, membership criteria of species are relational properties which are fixed, in part, by history. Furthermore, as a result of having a shared history, members of a species have a shared developmental program which limits and directs evolution.

As mentioned earlier, a thorough defense of essentialism cannot be presented here, and, perhaps, a convincing account may not yet exist. Nonetheless, an account of essentialism is required for RBP to be grounded, but it need not be as robust as traditional forms of essentialism. For example, a critic might point out that relational essences differ from Kripkean type essences in that historical properties are not intrinsic properties, but relational. A chunk of ore, irrespective of its history, can be examined to see if it is, say, gold. However, a token organism could not be examined to determine its essence, since its essence is a historical property – if there was a tiger and a tiger* in a room, and one was from Twin Earth, we could not distinguish between the two. I do not find this criticism troublesome, however. If the project of essentialism is to discover what properties all and only members of a species share, then the above accounts have achieved this, despite their break with the tradition concept of essentialism.

A similar criticism could be raised against Walsh’s version of essentialism. Gold has a clear essence – atomic number 79. Members of species, according to Walsh, have developmental essences that bias variation. However, what, exactly, is a developmental essence? Is it a particular genetic sequence, or linkage between genes? Is it a particular developmental modularization? In other words, can we precisely identify the essences of particular species? Regardless of whether or not such precision can be achieved, I agree with Walsh in that variation is restricted for each particular species. To reiterate the quote from Raff above, “only a subset of all theoretically possible phenotypes will be generated.”
In summary, versions of biological essentialism are being revived. Although these accounts may differ from traditional accounts of essentialism, I believe that the differences are a reflection of the differences between the physical and the biological sciences. It is intuitive to me, given Darwinian evolution, that the essential properties of specie membership are historical or relational. Furthermore, given the recent advancements in developmental biology, it also seems intuitive that organisms are constructed in such a manner that variation is restricted. Relating this to the project at hand, these two forms of essentialism relate to RBP by fixing species locations within the broader morphospace (through relational essences) and define the phenotypic plume (through developmental essences). If one agrees to the historical and developmental accounts properties above, but does not feel compelled to call either a version of essentialism.

The Actual and the Possible

In order assess the impact of RBP, let’s revisit the motivating examples. In chapter one, I described three kinds of modal claims in biology: impossibility claims (e.g., ultimate tree height); hypothetical biological spaces (e.g., Raup’s shell morphospace and Thomas’s skeletal design space); and metaphors that rely on possible, non-actual organisms (e.g., Gould’s “rewinding the tape of life” metaphor). Now we are in a position to assess which claims receive biological and philosophical support.

Starting with the latter examples first, I will examine the use of modal claims in metaphors. There are several metaphors which share a common theme. Gould’s “rewinding the tape of life” metaphor, Dennett’s “Library of Mendel” and Dawkin’s “Museum of all Possible Organisms” and “total theoretical morphospace” all exhibit an interesting similarity. As I noted when theses examples were first raised, although the authors find it necessary to raise such metaphors, with the exception of Dennett, no authors attempt to describe the limitations to their metaphors. Which hypothetical organisms reside in the Museum of All Possible Animals, and which do not? How can we tell the difference?

I believe that Dennett’s self-acknowledged failure to capture the contents of the Library of Mendel in an interesting way indicate why these spaces are undefined and uninteresting; namely, because there is no systematic way to describe the limits to phenotypic variability in any systematic manner when looking from a broad perspective. Trying to define a realm of biological possibility in the same sense that there is a realm of physical possibility is misguided. In other words, the “Russian Doll” model of modality is not conducive to a biological domain. Physical possibility relies on physical laws, which are universal. Biology, however, has no such laws. Unlike physics, evolutionary biology is a historical discipline, and it is the historical nature which is one of the sources for the inability to define a broad biologically possible domain. A second reason why no author goes on to successfully define what is biologically possible (in a broad, or global sense) is that there are no systematic way to describe what
is possible. What is biologically possible depends on the context in which it is being raised. With the realization that defining a uniquely biological domain of possibility is misguided, my project shifted to discover if there were any interesting, natural ways in which possibility could be contextualized. The result, which is RBP, is captured in the following diagram:

Fig. 5.5 The difference between restricted (or, local) biological possibility and broad (or global) biological possibility.

Broad Possibility captures the sense of possibility used in the metaphors of Gould, Dawkins and Dennett in describing what is biologically possible given any possible outcome. For example, if we could replay the “tape of life” an infinite number of times, we could determine what the area of broad biological possibility. Broad possibility, I contend, cannot be described in a systematic, non-trivial way.

What is interesting, both empirically and theoretically, is to restrict possibility to a particular point (or tightly defined region) within morphospace. It makes philosophical sense to do this when we are using the names of species or larger lineages. As I have previously argued, there is an essential connection between names (such as a particular species or higher-level lineage) and regions of morphospace. Once an area or starting point is designated, we can ask what is possible from that location. This is exactly what biologists are doing when they are making impossibility claims. Ultimate tree height, for example, is contextualized to existent tree morphology. When biologists discuss what is impossible, it is almost always from a particular species or lineage.

Recently, biologists have begun to define restricted biological space in a manner similar to RBP. Stadler et. al. (2001) argue for such a position.
The current implementation of Neo-Darwinian model of evolution typically assumes that the set of possible phenotypes is organized into a highly symmetric and regular space equipped with a notion of distance, for example, a Euclidean vector space... If phenotypes are organized according to genetic accessibility, the resulting space lacks a metric and is formalized by an unfamiliar structure, known as a pre-topology... We propose to extend the explanatory level for phenotypic evolution from fitness considerations alone to include the topological structure of phenotypic space as induced by the genotype-phenotype map (241).

In a similar move, Eble (2003) describes a more accurate conception of morphospace, called “developmental morphospace.” Unlike Raup's shell morphospace which is symmetrical and based on geometric variation, developmental morphospace is non-symmetrical (not based on geometrical variations, but on developmental constraints) and indexed to a particular specie or lineage. Thus, in order to illustrate a hypothetical biological space that reflects actual possibilities, morphospaces must be constructed non-uniformly according both internal and external constraints of the particular lineage being described. As Stadler et. al. and Eble argue, we can only determine what is possible, once we (1) determine a location within the broader realm of morphospace and (2) examine the constraints of a particular lineage. Once these two parameters are defined, we can create a phenotypic plume through morphospace and determine what is RBP.

Different kinds of explanations are required for actual versus possible phenotypes. In other words, the explanation for the actual trajectories taken by lineages differs from the explanation for what trajectories were possible. Actual phenotypes are explained by the actual forces which shape phenotypes: natural selection, population dynamics, and random drift are forces which sculpt actual organisms. These forces, however, must operate within the realm of possible phenotypes. Possibility is not defined by these forces, but by constraints. In their canonical paper on the subject, Maynard Smith et. al. (1985) define developmental constraints as:

... a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system (266).

They go on to define the sources of developmental constraints as:

...properties of materials, requirements governing storage and retrieval of information employed during development, particular features of the evolutionary determined pathways of development exemplified by a group of organisms, and mathematical structure pertaining to the class of complex systems within which a given developmental system falls (266).
Unlike laws of nature, constraints are not universal. For example, every organism must obey physical laws, such as gravity. However, gravity does not present the same constraints to all organisms. In an insightful, if not disturbing, quotation, famed biologists J.B.S. Haldane (1985) notes the contextual differences to the universal force of gravity:

To the mouse and any smaller animal it presents practically no dangers. You can drop a mouse down a thousand-yard mine shaft; and, on arriving at the bottom, it gets a slight shock and walks away. A rat is killed, a man is broken, a horse splashes. ...so the resistance to falling in the case of the small animal is relatively ten times greater than the driving force (3).

What I take from this is that even physical forces, which are universal, must be interpreted within a particular context to determine what is biologically possible. No species can “violate” the law of gravity, but the impact that gravity has on phenotypic space depends on the context. This brings us to the first set of motivating examples, which were the impossibility claims. Gravity, it was argued, is the limiting factor in tree height. Given their hydraulic transportation system, trees cannot pump water to foliage over 122 meters high. However, this depends on the particular hydraulic system used by actual trees. If trees allocated water differently, gravity wouldn’t pose the same challenge. Even universal constraints must be contextualized to the actual in order to determine the possible.

**Conclusion**

In the beginning of the chapter I outlined several requirements for a framework for biological possibility: it must accurately reflect biology; it must provide a procedure to determine what is possible; it must be metaphysically sound; and it must be interesting. I think that my account of RBP meets all of these requirements. Biologists are interested in constraints, both internal and external, that channel evolution. In defense of RBP I’ve described the work of many biologists who argue that variation in restricted. By leaning on recent accounts of biological essentialism, it is metaphysically plausible to index actual species to a particular location within the larger morphospace. This is also consistent with the most accepted forms of biological classification. Finally, RBP is informative, indeed necessary, to give complete evolutionary explanations. As I have argued, in order to explain the actual, we need to make reference to the possible.
REFERENCES


BIOGRAPHICAL SKETCH

Jason Zinser received his BA in philosophy and psychology from the University of Wisconsin at Stevens Point in 1997. He went on to receive a MA in philosophy from Texas A&M University in 2000, where he completed his thesis on “evolutionary epistemology” under the guidance of Colin Allen. He began his PhD at Florida State University in 2001, where he studied under Michael Ruse. Jason has presented papers at numerous conferences, including several internationally. Also, Jason has published several articles on topics ranging from bioethics, media ethics, artificial intelligence, and evolutionary theory. At the time of this publication, Jason has accepted a visiting faculty position at the University of North Florida.