Evolutionary Restraints

The Contentious History of Group Selection

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Introduction

Since the publication of *On the Origin of Species* in 1859, there have been questions and debates about Darwin's proposed mechanism of evolution—natural selection. Some critics of the theory have argued that Darwin merely applied the prevailing capitalist ethos of Victorian England to the natural world in an attempt to naturalize, and thereby legitimize, the system in which he himself lived and thrived. Others (most famously, perhaps, philosopher Karl Popper) have argued that the mechanism suggested by Darwinism was merely a tautology: survival of the fittest means that those who are fittest are the survivors, hence the empty phrase "the survival of the survivors." This question of tautology has been addressed extensively by biologists and philosophers of biology, and Popper ultimately changed his mind about natural selection. Historians and sociologists of science continue to explore how far prevailing social structures and attitudes influence theory development and acceptance. This book will take up another aspect of natural selection. I am interested in examining the role of group selection in evolutionary theory since Darwin, with a particular emphasis on what happens to this idea in the twentieth century. To accomplish this task in the most illuminating and focused manner, I will use the career of British naturalist Vero Copner Wynne-Edwards as the structural spine of my story. Wynne-Edwards is the perfect vehicle because it was his work that focused the attention of biologists, and especially

ecologists, on the ill-formed question of the level at which natural selection was acting.

The theory of group selection is the idea that competition in nature, which is fundamental to Darwin's mechanism of natural selection, also occurs at a level above the individual. Although most of the discussion about natural selection has been at the level of the individual, and more recently at the level of the gene, there have always been researchers committed to the idea that selection must also act on groups of individuals. This idea has been fundamental to explanations of social organization, altruistic behavior, and even the evolution of intellect and morality. In the course of this narrative, I will trace the history of this idea as its status waxes and wanes in the context of the biological sciences. I believe this history of the idea of group selection will contribute in a substantial way to our understanding of the development of evolutionary theory. This account of the history of twentieth-century biology supports a hierarchical understanding of evolutionary theory—that is to say, an understanding that natural selection occurs at multiple levels. Following the history of group selection, from its origins in Darwin's work through the professionalization and specialization of biology in the twentieth century, highlights some important trends in the biological sciences in general.

The history of group selection has been identified by several of the biologists involved in the debates as an important and as yet unattempted historical project. In his 1983 paper "The Group Selection Controversy: History and Current Status," biologist David Sloan Wilson presented his rationale for pursuing a history of the idea.[1] The criteria Wilson laid out served as a starting point for my project. First, group selection is a striking example of how scientific questions arise from attitudes normally considered outside the purview of science and shows that the development of ideas is not necessarily orderly and progressive. Second, even though the modern concept of group selection lies squarely within the older tradition, the differences that do exist must be clarified, and a historical approach is particularly appropriate. Finally, modern group selection theory is consistent with many of the theories (inclusive fitness, game theory, and reciprocity) that had been treated as rival (and mutually exclusive) explanations over the past thirty years. I heartily concur with Wilson's analysis. The history of group selection presented here will examine the work of biologists beginning with Darwin and concluding with the state of higher-level selection theory in the current literature.

The first period under consideration is the Darwinian era. In chapter 1

I use Michael Ruse's 1980 article "Charles Darwin and Group Selection" as a foil for my own interpretation of Darwin's work.[2] Contra Ruse, I will present my argument that in both *On the Origin of Species* and *The Descent of Man* Darwin explicitly allows natural selection to act at levels above the individual.[3] Of course Ruse is not alone in characterizing Darwin as an individual-level selectionist. In his 1998 book *Darwinism's Struggle for Survival*, philosopher Jean Gayon dedicated an entire chapter to what he describes as "this extremely delicate question" and continues, "The virulence of recent controversies over 'group selection' shows that this is a fundamental theoretical question as open today as it was in 1859."[4] Gayon essentially argues that Darwin was indeed an individual-level selectionist, though neither Wallace nor Spencer was.[5]

In chapter 2 I continue the analysis of evolutionary theory by examining some of the major debates over natural selection that occurred in the late nineteenth and early twentieth centuries. These two beginning chapters will set the stage for the early work of Wynne-Edwards on nonbreeding behavior in fulmars and other seabirds that will be presented in chapter 3. In his earliest papers (ca. 1927), Wynne-Edwards showed an interest in the theoretical questions arising from nonbreeding behavior of adult birds that did not fit into the standard Darwinian account of the individual's constantly striving to produce offspring. These papers foreshadowed the debate with David Lack that began in the 1950s.

The developing debate with Lack and the influence of the modern synthesis will be the subject of chapter 4. The approach to higher-level selection takes an interesting turn at this time as a result of the work of the population geneticists. The early mathematical models of Sewall Wright and Theodosius Dobzhansky were of particular significance for Wynne-Edwards. In his seminal *Genetics and the Origin of Species*, Dobzhansky introduced the paradox of viability.[6] In discussing the necessary level of variation that a population must maintain in order to remain viable, Dobzhansky wrote: "Evolutionary plasticity can only be purchased at the ruthlessly dear price of continuously sacrificing individuals to death from unfavorable mutations."[7]

The quotation above is evidence that Dobzhansky was focusing on a group-level or lineage-level trait, evolutionary plasticity or evolvability, and was interested in its importance to evolutionary theory.

With the advent of the modern synthesis, Wynne-Edwards recognized a fundamental shift in the mode of thought about evolution that was more in line with his own interests. In November 1948 he gave a paper to the

Oxford Ornithological Society, "The Nature of Subspecies," in which he discussed the importance of the shift. In his introductory remarks, he cited the work of E. B. Ford on butterflies as well as Dobzhansky's, Ernst Mayr's, and Julian Huxley's core contributions to the development of the modern synthesis. "The fundamental new idea is that populations, rather than independent individuals, are the basic units upon which evolutionary processes act."[8]

Dobzhansky also made interesting claims that the physiology of populations had been entirely neglected and at the same time was perhaps the most essential aspect of the theory of evolution.[9] In his chapter on variation in natural populations, he argued that although the origin of variation was purely physiological, when it is injected into a population it enters into the field of action of factors operating on a different level. According to Dobzhansky, "These factors, natural and artificial selection, the manner of breeding characteristic for the particular organism, its relation to the secular environment and to other organisms existing in the same medium, are ultimately, physiological, physical, and chemical, and yet their interactions obey rules *sui generis*, rules of the physiology of populations, not those of the physiology of individuals."[10]

His emphasis on higher-level selection, which he called group selection, was highly influential for Wynne-Edwards and has previously been underemphasized by authors writing about the synthesis.

The advent of this shift in attention by the population geneticists, followed by the 1954 publication of David Lack's strictly Darwinian (individual selectionist) book *The Natural Regulation of Animal Numbers,* spurred Wynne-Edwards to continue his work formulating a theory of group selection that was consistent with his field experience. The result of this work was a paper presented at the Eleventh International Ornithological Conference that introduced Wynne-Edwards's theory of group selection and rejected the standard Darwinian account represented in the work of David Lack.

The publication of Wynne-Edwards's *Animal Dispersion in relation to Social Behavior* in 1962 is widely recognized as the spark that ignited the contemporary debate over group selection theory, and the reception of this major work will be the subject of chapter 5. In *Animal Dispersion*, Wynne-Edwards expanded his theory based on his work on social behavior in birds and applied it to all animal groups. In his theory of group selection, Wynne-Edwards identified a wide variety of group-level adaptations: reproductive rate, foraging strategy, and strict population localization.

Despite the acknowledgment of the impact of the 1962 book, Wynne-Edwards often remains a footnote in the development of higher-level selection theory. Indeed, in a recent book by biologist Lee Alan Dugatkin, *The Altruism Equation: Seven Scientists Search for the Origins of Goodness*, many of the characters discussed here (including Charles Darwin, Petr Kropotkin, W. C. Allee, and William D. Hamilton) are treated in depth with respect to their contributions, but Wynne-Edwards merits only a single reference.[11]

In chapter 6 I will concentrate on the two most important critics of Wynne-Edwards's theory. First, I will present David Lack's challenge to group selection in *Population Studies of Birds*. This confrontation is particularly interesting because despite the received view that Lack clearly carried the day, closer analysis of the argument reveals that the data supporting Lack's position were surprisingly thin. In combination with the argument presented by George C. Williams in his now classic *Adaptation and Natural Selection*, however, Wynne-Edwards's theory of group selection suffered a mortal blow. This chapter will also engage some of the broader social context that influenced the reception of group selection theory. The 1960s witnessed the rise of the environmental movement and concerns about human population growth. Wynne-Edwards's arguments, presenting group selection as a mechanism of evolutionary restraint on population growth, struck a chord with a number of these groups. Finally, building on the work of historian Richard Burkhardt, I will discuss the ways group selection theory was handled by the ethologists and sociobiologists in their attempts to provide evolutionary accounts of social behavior.

The fate of Wynne-Edwards and his theory of group selection in the wake of the criticisms above and in the context of an increasing emphasis on the gene as the unit of selection is the focus of chapter 7. The increasing involvement of the philosophers of biology in the units of selection debate and the failure of Wynne-Edwards's second book, *Evolution through Group Selection*, round out the chapter and illustrate how the debate moved beyond Wynne-Edwards.

In the concluding chapter I describe Wynne-Edwards's continued attempts to advocate his theory and direct attention to the importance of group selection as an evolutionary mechanism. As we shall see, although biologists remained unconvinced by his formulation of group selection, there was an increasing acceptance of a hierarchical approach to evolutionary theory. In this chapter I will also discuss the role of ideology in the debate over group selection. The varied notions of a "group"—from

a tightly organized whole that suppresses the individual to a loose aggregate of individuals who cooperate and sacrifice for mutual benefit—have clearly influenced the arguments on both sides of this contentious issue.

How did Wynne-Edwards develop his theory? What questions was he attempting to answer that others had not resolved? In the course of this history I will trace out the development of the theory in Wynne-Edwards's early work and attempt to identify the social behaviors, the existing theories, and the broader questions about population regulation that led him to his theory of group selection. I will also place Wynne-Edwards and his theory within the context of the developments of evolutionary biology that took place throughout the twentieth century.

CHAPTER ONE

Charles Darwin and Natural Selection

Debates over the nature and power of Darwin's primary mechanism of evolutionary change, natural selection, began with the publication of *On the Origin of Species* and continue into the present. In the sixth chapter of the first edition, Darwin addressed various difficulties his theory faced. These challenges included an oblique reference to the idea that is the subject of this story—the notion that natural selection may act at a level above that of the individual. As the study of biology has developed in the twentieth century, applications of natural selection to levels below the individual, particularly the level of the gene, have become increasingly common and comparatively unproblematic. Applications of Darwin's mechanism in the opposite direction were initially accepted as unexamined claims about the "good of the species," but as these genetic explanations became more prevalent, the higher-level explanations were increasingly seen as suspect.

Sterile Hybrids and Neuter Castes

The idea that natural selection acted at a level above that of the individual was a challenge to Darwin's theory from the beginning. Darwin himself recognized the difficulty of explaining the existence of the neuter castes of social insects by individual selection, as well as the fact of hybrid sterility.

By the end of the century, the neuter insects became the locus of an important debate over the inheritance of acquired characteristics between the neo-Darwinians, represented by August Weismann, and the neo-Lamarckians, led by Herbert Spencer.[1] Darwin's own explanation, as presented below, was based on natural selection acting on traits that were beneficial to the colony. With regard to hybrid sterility, Darwin acknowledged that sterility could be of no possible benefit to the hybrid individual and so must be incidental to other acquired differences. The benefit of the sterility of hybrids accrues not to the individual, according to Darwin, but rather to the species whose integrity is maintained (see fig. 1).

Despite the conceptual ambiguity presented here, historians of science have let this potentially fertile problem lie fallow. The only explicit historical treatment of group selection in Darwin's work was a 1980 article in the *Annals of Science* by philosopher of biology Michael Ruse.[2] His "Charles Darwin and Group Selection" was written in the midst of the sociobiology debate of the mid-1970s and early 1980s. Ruse argued that despite the claims of sociobiology's detractors, Darwin was not sympathetic to the idea of group selection except in a very few particular cases. Ruse achieved this narrow interpretation of Darwin by using modern definitions of individual and group selection that do not apply in the context of the nineteenth century. Individual selection, according to Ruse, is "selection which in some sense affects an individual's reproductive interests. This could be directly through the individual, or indirectly in some way: For instance, by kin selection, where an individual's interests are furthered through close relatives."[3]

The inclusion of kin selection here is dubious. Although Darwin was certainly aware that leaving progeny was important to the struggle for existence, kin selection in the modern sense quantifies relatedness and the benefits of aiding kin in a way that was not possible before the development of classical genetics. Furthermore, it is formally selection between groups of kin.[4]

I believe that Ruse's restrictive reading of Darwin is off the mark. This is evident from various passages from both the *Origin* and the *Descent* that more accurately present Darwin's own position with regard to selection acting at a level above the individual. The following often-quoted passage, from chapter 3 of the *Origin*, titled "The Struggle for Existence," illustrates the breadth of action that Darwin assigned to the mechanism of natural selection: "I should premise that I use the term struggle for existence in a large and metaphorical sense, including *dependence of one*

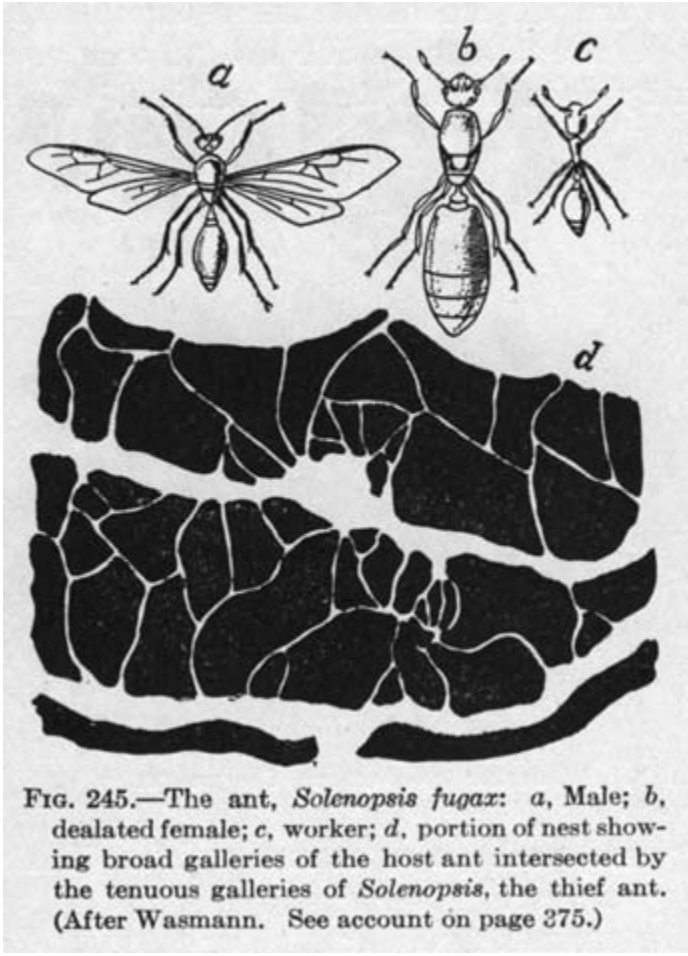

FIG. 245.—The ant, *Solenopsis fugax*: *a*, Male; *b*, dealated female; *c*, worker; *d*, portion of nest showing broad galleries of the host ant intersected by the tenuous galleries of *Solenopsis*, the thief ant. (After Wasmann. See account on page 375.)

FIGURE 1. Social insects. David Starr Jordan and Vernon Kellogg, *Evolution and Animal Life: An Elementary Discussion of Facts, Processes, Laws and Theories relating to the Life and Evolution of Animals* (New York: D. Appleton, 1907).

being on another and including (which is more important) not only the life of the individual, but success in leaving progeny."[5]

Later in the *Origin*, Darwin's statements on higher-level selection dealt mostly with the social insects. Darwin recognized the difficulty that the neuter insects, with their distinct morphology and habits, presented for his theory, and in typical Darwinian style he did his best to explain and defuse this potentially devastating case.

> How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure; for it can be shown that some insects and other articulate animals in a state of nature occasionally become sterile; and if such insects had been social and it had been *profitable to the community* that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection.[6]

The passage above illustrates Darwin's commitment to the mechanism of selection despite the lack of a clear theory of heredity. The question of the evolution of the neuter insects became fundamental to the ongoing debate over the inheritance of acquired characteristics. Both Lamarckian supporters of use inheritance and neo-Darwinian selectionists used the case to show the insufficiency of the other side's theory. I offer the following lengthy quotation from the *Origin* to demonstrate Darwin's position with regard to the evolution of various castes among the social insects.

> I believe that natural selection, by acting on the fertile parents, could form a species which should regularly produce neuters, either all of large size with one form of jaw, or all of small size having jaws of widely different structure; or lastly, and this is our climax of difficulty, one set of workers of one size and structure, and simultaneously another set of workers of a different size and structure; a graduated series having been first formed, as in the case of the driver ant, and then the extreme forms, from being the most useful to the community, having been produced in greater and greater numbers through the natural selection of the parents which generated them; until none with an intermediate structure were produced.
>
> Thus as I believe, the wonderful fact of two distinctly defined castes of sterile workers existing in the same nest, both widely different from each other and from their parents, has originated. We *can see how useful their production may have been to a social community of insects,* on the same principle that the division of labour is useful to civilised man.[7]

Even though these passages come from the chapter in the *Origin* titled "Instinct," there is no explicit reference to the inheritance of instinct. Rather, Darwin described the morphological traits of the neuter castes and explained them in terms of their usefulness to the community. In an excellent recent review of this problem, historian Thomas Dixon has argued that Darwin's "community selection explanation of the evolution of well adapted neuter insects provided one important example of a case

FIG. 228.—The Portuguese man-of-war, *Physalia*, with men-of-war fishes, *Nomeus gronovii*, living in the shelter of the stinging feelers. (Specimens from off Tampa, Fla.)

FIGURE 2. Colonial organism. David Starr Jordan and Vernon Kellogg, *Evolution and Animal Life: An Elementary Discussion of Facts, Processes, Laws and Theories relating to the Life and Evolution of Animals* (New York: D. Appleton, 1907).

that could not be explained by Lamarckian inheritance of modifications produced by use and disuse."[8] Dixon's analysis, consistent with the account I develop here, challenges the characterization of Darwin by scholars such as Helena Cronin, who present "those twentieth-century biologists who invoked group selection as departing from 'the individual-level orthodoxy of Darwin, Wallace and their contemporaries.' "[9] In the case of the social insects, however, instinct was clearly recognized as an important factor in the evolution of the social systems. This idea was more carefully developed in *The Descent of Man*, which I will discuss below, but the following quotation gives some indication of Darwin's position in the *Origin* with regard to instinct in the social insects: "Thus, I believe it has been with social insects: a slight modification of structure, or instinct correlated with the sterile conditions of certain members of the community has been *advantageous to the community*: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification."[10]

It is clear from a careful reading of the selections from Darwin's work that he indeed conceived of the mechanism of natural selection as functioning at the level of the community. This is especially clear in the case of the social insects but was also part of Darwin's theory with regard to communal organisms such as the Portuguese man-of-war and the coral polyp and also true of higher social animals.

The final passage from the *Origin* comes from chapter 6, "Difficulties on Theory." In this chapter Darwin discussed various phenomena that he recognized as potentially contradictory to his theory. Through the broad application of the mechanism of natural selection—that is to say, application to the group rather than the individual—Darwin's theory can encompass even the most self-destructive of "adaptations." "We can perhaps understand how it is that the use of the sting should so often cause the insect's own death: for if on the whole the power of stinging be *useful to the community*, it will fulfill all the requirements of natural selection, though it may cause the death of some few members."[11]

Social Insects and Social Instincts

In *The Descent of Man,* we see Darwin shifting emphasis from the social insects to the social instincts. Generally he continued to use social insects

for the model of the evolution of social instincts, but he also included the social behavior of primates and other higher animals. This shift in emphasis acted as an accelerant to the debates generated by Darwinian theory. In *The Descent of Man*, Darwin was explicitly drawing the connection between the moral faculties of man and the social instincts of the lower animals.

Darwin's most straightforward presentation of the evolution of the social instincts came in chapter 3, "Moral Sense." In this passage Darwin argued that the inheritance of the social instincts was of the utmost importance to the later development of the human society and, furthermore, that the development of these instincts was for the good of the community over and above the advantage to the individual. "Finally, the social instincts which no doubt were acquired by man, as by the lower animals, *for the good of the community*, will from the first have given him some wish to aid his fellows, and some feeling of sympathy."[12]

Here we see Darwin's explanation of the human need to offer aid to another in terms of the selective benefit this behavior confers on the community, in the same way that the existence of the sterile caste maintains the selective advantage of the hive. In the next chapter, "On the Manner of Development of Man from Some Lower Form," Darwin pointed out that in the case of the social animals, selection acting at the level of the community could have indirect effects on individuals: "With strictly social animals, natural selection sometimes acts indirectly on the individual, *through the preservation of variations which are beneficial only to the community.* A community including a large number of well-endowed individuals increases in number and is victorious over other and less well-endowed communities; although each separate member may gain no advantage over the other members of the same community."[13]

Darwin went on to illustrate the point with the example of the social insects, describing pollen-collecting behavior and the sting of worker bees in addition to the jaws of the soldier ants. According to Darwin's argument, these apparatuses and behaviors were of no direct advantage to the individual; rather, they served the community and were maintained by natural selection acting on the level of the community.

The final passage from the *Descent* that I will include here illustrates the importance Darwin assigned to the social instincts. "All this implies some degree of sympathy, fidelity and courage. Such social qualities, *the paramount importance of which to the lower animals is disputed by no one*,

were no doubt acquired by the progenitors of man in a similar manner, namely, through natural selection, aided by inherited habit."[14]

It follows that if these instincts are as important to the evolution of social groups as Darwin insisted, and if the selection of these instincts often occurs at a level above that of the individual, then higher-level selection is an important factor in Darwinian evolutionary theory. In this way Darwin explicitly equated selection among communities with natural selection—a very different stance from that of later authors, like George C. Williams, who equate only individual selection with natural selection (as I will discuss in chapter 6). Despite Ruse's claim to the contrary, it is apparent that for Darwin there was at least some possibility for his mechanism to function above the level of the individual. At best, Ruse is using a modern definition of kin selection retroactively in evaluating the past. As worst, he is misdefining kin selection in order to "rescue" Darwin from the "error" of group selection.

Darwin's ambiguity on this question of levels at which the mechanism might work contributed to an intellectual environment where claims about "the good of the species" or "the benefit of the community" were accepted unexamined. From the end of the nineteenth century through the first decades of the twentieth, biologists' characterization of this adaptation or that behavior, which had clearly evolved for the benefit of the species or community or group, were generally accepted.

Early Context: The Darwinian Revolution?

Despite a generation of scholarship dedicated to examining the state of Darwinian theory at the end of the nineteenth century, there remained deep disagreements on some very basic points. To what extent was Darwin's work an echo of the Victorian capitalist ethos? What was the actual influence of Malthus on Darwin? What is the meaning of evolution? Was Darwinian theory progressive? These questions, among many others, have fueled the Darwin industry for decades.[15]

Peter Bowler's *The Non-Darwinian Revolution: Reinterpreting a Historical Myth* provides an excellent analysis of the complexity of the situation with regard to evolutionary theory in the period under consideration. Bowler has spent his career examining the varied evolutionary ideas that were being espoused throughout the community of evolutionary thinkers. Bowler's point (and one that is well taken) is that most evolutionists at the

end of the nineteenth century and the beginning of the twentieth were not Darwinians, often despite their claims to the contrary.

In *The Non-Darwinian Revolution*, Bowler described the continuing influence of Lamarck's ideas about the importance of use and disuse, Ernst Haeckel's idea of recapitulation—which was closely linked to the idealist and transcendentalist origins of the developmental view of nature—and other scientific and philosophical concepts to illustrate the intellectual confusion that reigned during this period. Bowler also dedicated a chapter to social Darwinism, which he argued was often closer to social Lamarckism. (Bowler argued that if social thinkers wanted people to strive to get ahead, Darwinian theory gave them no grounds to make any effort. Either they had the advantageous traits or they did not. The Lamarckian notion of inheritance of acquired characteristics made quite a bit more sense.) Hence the ultra–social Darwinist Herbert Spencer, as classically presented in Richard Hofstadter's *Social Darwinism in American Thought,* is a misconception. According to Bowler, Spencer's ideas about evolution's improving society were often more Lamarckian than Darwinian.

By 1909, the centennial of Darwin's birth and fifty years after the *Origin*, almost everyone agreed that life evolved, but there was no such agreement on a mechanism. There remained the unsolved problems of variation and heredity, and further complicating matters, physicists' and geologists' estimates of the age of the earth were not providing sufficient time for Darwin's gradualistic account. Even the concept of species was still vague, which created problems for evolutionary theory at the most fundamental level. Meanwhile, new fields in the life sciences arose as older areas of study were modified or abandoned. Weismann and Hugo de Vries, although they themselves did not do research in the field, saw the solution to the problem of inheritance in colloidal chemistry, the study of large molecules that were the basis of life and of how to identify, understand, and analyze them. Physiology, and the work of Jacques Loeb among others, was reshaping biology along mechanistic and experimental lines.[16] Major advances had occurred in plant hybridization techniques. The opening of the American West led to the discovery of major fossil fields and fueled rapid growth of paleontology. The biometricians, led by Darwin's cousin Francis Galton, developed techniques for analyzing inheritance and correlating traits.[17]

The neo-Darwinians were matched by neo-Lamarckians in nearly all of these pursuits. American paleontologists such as Edward D. Cope and Alpheus Hyatt did not see proof of natural selection in the fossil record

and maintained a belief in the inheritance of acquired characteristics. Experimental physiologists Paul Kammerer and Charles-Édouard Brown-Séquard performed experiments that supported Lamarckian claims of the inheritance of acquired characteristics. These disputes provide the context for Petr Kropotkin's development of his theory of mutual aid, which I will discuss in chapter 2. In the next section we will examine some general biological texts from the turn of the century in order to gain greater insight into the state of Darwinian theory and, more specifically, the application of natural selection above the level of the individual.

Weismann's Germplasm

August Weismann's collection of lectures, *The Evolution Theory*,[18] provided a transition from the consideration of higher-level selection in general to a more specific treatment of selection in the case of the social insects. This two-volume work consists of thirty-six lectures given at Freiburg im Breisgau over almost as many years. Weismann's lectures presented the neo-Darwinian position disparaged by the followers of Spencer at the turn of the century and described the all-sufficiency of natural selection as the mechanism of evolution.

Besides offering an engaging history of evolution that began with Empedocles and traveled through the works of Goethe and Erasmus Darwin, the first volume introduced Darwinian theory, as well as Weismann's own theory of the germplasm.

Two lectures in the second volume of *The Evolution Theory* are of particular relevance here. Lectures 23 and 24, both of which treat the inheritance of functional modifications, reveal Weismann's position on the role of selection in the evolution of social insects. In the course of his lecture Weismann asked about the behavior and morphology of the neuter insects: "How can all these peculiarities have arisen, since the workers do not reproduce, or do so only exceptionally, and, in any case, are incapable of pairing, and therefore — among bees at least — only produce male offspring?"[19]

Weismann went on to answer his own question, asserting that obviously it could not be through the transmission of the effects of use and disuse, because the workers had no offspring to whom anything could be transmitted.

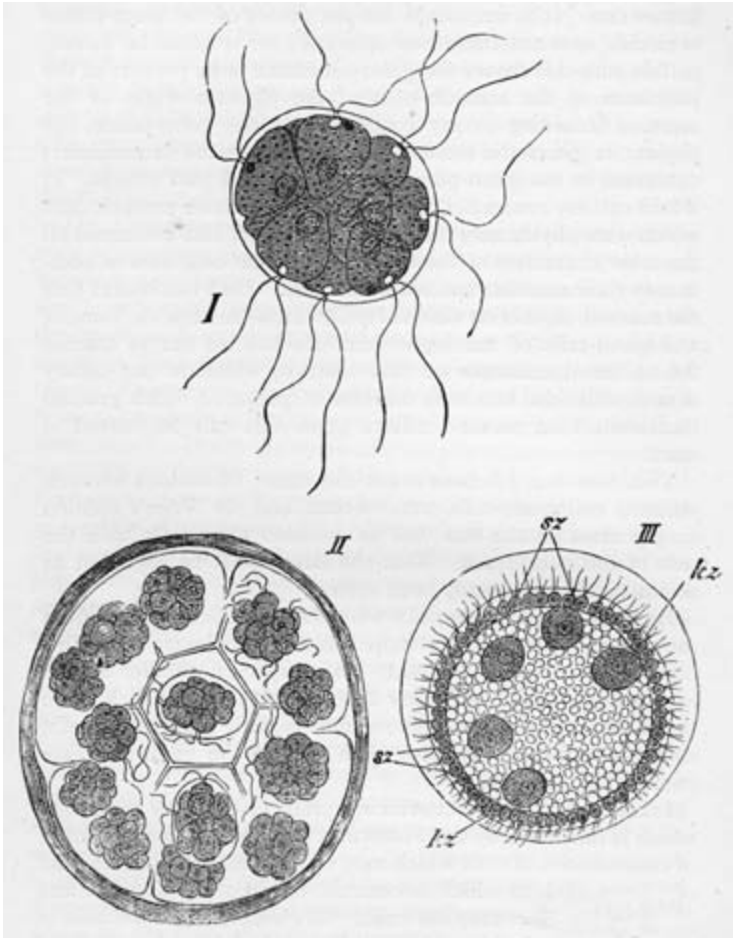

FIGURE 3. Superorganism? August Weismann, *The Germ-Plasm: A Theory of Heredity* (New York: C. Scribner's Sons, 1893), 214.

Weismann continued his explanation by asserting that these varied forms of neuter insects, which exhibited complex behaviors, were the result of natural selection. Essentially, Weismann argued that the inhabitants of the hive were members of the same family and that selection acted on the sexual members of the hive that produced the better workers. In the case of bees, selection acted on the individual queen. Today this would be recognized as family selection if the queen is singly mated, but if she is

multiply mated, or joined by other queens, it is a type of kin selection that has been shown to be among-group selection.[20]

Given Weismann's theory of the continuity of the germplasm, it is perhaps not surprising that he would offer this explanation. Nevertheless, one might argue that there is room for some selective force to act on the level of the group, given the following passage from the same chapter. "A colony whose queen was unsatisfactory in this respect [producing good workers] could not hold its own in the struggle for existence, and only the best colonies and the best hives would survive, that is, through their descendants."[21]

It appears from the passage above that, although Weismann is committed to the position that selection acts on variations in the germplasm, somehow the fitness of the hive or colony is an important factor along the lines of Thomson's sieves, discussed below. The idea of higher-level selection is often presented in the context of more general studies of Darwinian theory of the period. The social insects, however, were often invoked as the model for studies of complex behavior and sophisticated social systems that might require higher-level selection. With this in mind, chapter 2 will focus on the varied positions taken by evolutionary biologists considering the social insects, and on the concepts of the superorganism and of mutual aid. Before turning to a discussion of these concepts, I will analyze some general treatments of the state of evolutionary theory. I have selected these works as representative of the very broad interpretation of evolutionary theory common to the period and specifically for their treatment of higher-level selection.

Higher-Level Selection in General Biological Texts

The first of these texts, *Evolution and Animal Life*, by David Starr Jordan and Vernon Lyman Kellogg, was published in 1907.[22] David Starr Jordan is well known (especially at Indiana University, where the biology building bears his name) as an ichthyologist and field naturalist of the first order. His work led to the naming of more than 2,500 species of fish. After serving as president at Indiana University for five years, Jordan became the first president of Leland Stanford Junior University. Vernon Kellogg joined the faculty at Stanford in 1894 as a professor of entomology and became head of the department the next year. This text, according to the authors, attempted to "provide a lucid account of the processes of evolution so far

as they are understood." The book did not discuss the evolution of plants because both of the authors were trained as zoologists. Nevertheless, *Evolution and Animal Life* is useful as an example of a general biology text of the period. The material covered was generated from the lectures Jordan and Kellogg used in introductory biology courses at Stanford University.

The subtitle of this work, *An Elementary Discussion of Facts, Processes, Laws and Theories relating to the Life and Evolution of Animals,* gives one a fair sense of its scope. Jordan and Kellogg began with a chapter on the definition of evolution and concluded twenty-one chapters later with a discussion of man's place in nature. Although the authors were certainly supporters of Darwin, their position with regard to the mechanism of natural selection was not absolute.

Chapter 4, "Factors and Mechanism of Evolution," included the subsection "Lamarckism and the Inheritance of Acquired Characters." In this chapter, Jordan and Kellogg asserted that, although they considered natural selection to be the predominant mechanism in the course of evolution, Lamarckism must not be omitted. This was especially true in the context of development. The authors also included an entire chapter (11) on the inheritance of acquired characteristics. The message with regard to Lamarckism here is less clear. Jordan and Kellogg seem to want to downplay the importance of Lamarckian ideas as much as possible; however, they also want to avoid any direct affiliation with the *Allmacht* stance of the neo-Darwinian Weismann. Jordan and Kellogg went on to discuss the role of mutual aid and communal life in chapter 18, which provides some indirect insight into their position with regard to selection acting on groups.

In this chapter the authors treat the social insects but do not make specific reference to the role of natural selection in the development of insect social systems. They do, however, emphasize the importance of the group, especially in the case of bees. For example, the discussion of the worker bee concentrates primarily on its morphological differences from the other members of the hive; however, it also describes the contribution of the worker as more important to the community than to the individual itself. "And all work done by the workers is strictly work for the whole community; in no case does the worker bee work for itself alone; it works for itself only in so far as it is a member of the community."[23]

At the end of the chapter, in which they include examples of a number of dependent relationships, including symbiosis and parasitism, Jordan and Kellogg acknowledge the importance of communal and social life in the animal world and, more specifically, the important advantages it

provides in the struggle for existence. "The advantages of communal or social life, of cooperation and mutual aid, are real. The animals that have adopted such a life are among the most successful of all the animals in the struggle for existence."[24]

Although there is never any discussion of the mechanism at work here, it appears that the authors are quite close to Darwin's own position with regard to selection working at higher levels. Their social context may have played a role in their closing comments for this chapter. After extolling the virtues of community and cooperation, the American zoologists, teaching at Stanford University in the great western region of the United States, felt compelled to qualify their claims. "Its great advantages are, however, balanced by the fact that mutual help brings mutual dependence. The community or society can accomplish greater things than the solitary individuals, but cooperation limits freedom, and often sacrifices the individual to the whole."[25]

Jordan and Kellogg, though convinced of the importance of the group in nature, would not deny the equally important role of the individual, especially in a free and democratic society like the United States.

The following year Vernon Kellogg published *Darwinism Today*.[26] In this work he attempted to provide a balanced discussion of the varied evolutionary theories of the time and included some interesting passages on the efficacy of the mechanism of natural selection. Here again he attempted to locate himself close to Darwin with respect to the role of natural selection in evolution. Even though Kellogg admired the work of Weismann and other neo-Darwinians, he cautioned that they had gone too far.

Kellogg argued that although Weismann had provided substantial refutation or alternative explanations for every example of inheritance of acquired characteristics, he nevertheless had to modify his own position on the *Allmacht* of natural selection in light of the work of Karl Wilhelm von Nägeli and Yves Delage on the "swamping" of favorable variations.[27]

With regard to selection's acting at a level higher than the individual, Kellogg deferred to Thomas Hunt Morgan's argument against natural selection's giving rise to sterile castes in the social insects. In *Evolution and Adaptation* Morgan had argued that the neuter castes were perhaps not adaptive at all and were merely the result of a nonlethal mutation.[28] Initially, the mutation theory provided an account of the origin of new variations that were distinct enough to be of evolutionary significance and

were also heritable. Morgan espoused this position, in direct opposition to Weismann and the neo-Darwinian overemphasis on natural selection as the creative force in evolution. Morgan's position on natural selection continued to develop in the first decades of the twentieth century, and by the time he wrote *The Scientific Basis for Evolution* in 1932, he had come to accept natural selection in concert with a modified mutation theory.[29]

Ultimately it is difficult to discern exactly where Kellogg stands on Darwinism. Reflecting the contemporary atmosphere while at the same time constructing it, he considered a multitude of possibilities with regard to evolutionary theory. His book provides an archetypal illustration of the state of affairs described by Bowler in *The Non-Darwinian Revolution*.

The structure of *Darwinism Today* is particularly illustrative of the state of Darwin's theory almost fifty years after the *Origin*. The book begins, inauspiciously for Darwin's theory, with the chapter "Introductory: The Deathbed of Darwinism." The second chapter is dedicated to an exposition of the distinction between evolution and Darwinism, and the following three chapters are headed "Darwinism Attacked." In a section in chapter 4 subtitled "How Real Is Personal Selection?" Kellogg asserts: "I may say baldly that no such vigour of individual selection based on variation in colour, in pattern, in venation and other wing characters, in hairs and in numerous other structural characters, as demanded by the needs of selection theory, is to be detected. . . . in other words, just as much variation exists after enduring the selective rigour of the struggle as existed before."[30]

Here Kellogg's sympathy for Darwin's theory seems to have disappeared. The following chapters (6 and 7) are headed "Darwinism Defended," and then Kellogg presents a discussion (comprising two full chapters) of alternative evolutionary theories. In the concluding chapter, "Darwinism's Present Standing," Kellogg essentially returns to the Darwinian fold and to the position he took with Jordan in *Evolution and Animal Life*. He asserts that despite the ongoing debate over many of the particulars, natural selection must still be considered the final arbiter in descent.

Thomson's Sieve

In James Arthur Thomson's *Concerning Evolution* we get perhaps the most Darwinian picture of evolution considered to this point.[31] Thomson,

a professor of natural history at Aberdeen University and the translator of Weismann's work, derived this book from a series of lectures presented at Yale University in 1924. His object, according to the preface, was to show that the evolutionary view of nature and of man provided an enriching and encouraging account, contrary to popular understanding. This was not to be an exclusively Darwinian reading of evolution; in a section headed "Self-Regarding and Other-Regarding," Thomson quoted Spencer on the importance of mutual aid. "As Herbert Spencer said: 'From the dawn of life altruism has been no less essential than egoism. Self-sacrifice is no less primordial than self-preservation.'"[32]

Throughout his book, Thomson emphasized the importance of what he called Darwin's subtlety with regard to the idea of the struggle for existence. He introduced the notion of selective sieves acting on different aspects of an organism and at different levels (sieve of the quest for food, sieve of the physical environment, sieve of the animate environment, sieve of courtship). Although these ideas are not developed into a systematic theoretical structure, they nevertheless indicate Thomson's sympathy for the idea of selection acting at multiple of levels. He made specific reference to selection acting at the level of society in his chapter on organic evolution: "Moreover, under the shelter of society there is a possibility of new departures which would be speedily eliminated by the sieves which apply to ordinary, more or less individualistic, life. At different levels of animal society there will be a different pattern of sieve."[33]

Clearly, altruistic behavior, which would be difficult to explain by a selective sieve operating at the individual level, could be effectively explained given another selective sieve operating at the level of the societal group. The altruistic group, having the higher fitness owing to cooperative effort, would outlive the group of selfish individuals.[34]

Thomson's work was essentially Darwinian—that is to say, selectionist but more teleological than Darwin himself might have liked. Most relevant for our purposes, Thomson clearly supports the action of selection at the group level.

Through the analysis of these selected texts it becomes apparent that Weismann had a far-reaching effect on the development of evolutionary theory in general around the turn of the century. Many biologists, although convinced of evolution and sympathetic to Darwinism, remained skeptical regarding the mechanism of natural selection. How and where the mechanism worked was unclear, and the idea was inconsistently applied. Clearly there was difficulty making progress from Darwin's nineteenth-century

heredity theory to the more transitional one represented by Weismann. This difficulty was initially compounded by views like Morgan's and by the challenge that faced theorists attempting to sort out the evolution of the sterile castes of the social insects. In the next chapter we will see how these ideas regarding the social insects and superorganisms laid the foundation for further investigation into the possibility of higher-level selection.