

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.