# Descended from Darwin

## Insights into the History of Evolutionary Studies, 1900–1970

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Chapter 15

# Shifting Balance and Balancing Selection

## A Group Selectionist's Interpretation of Wright and Dobzhansky

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> *Great is the power of steady misrepresentation; but the history of science shows that fortunately this power does not long endure.*
>
> —Darwin, *On the Origin of Species*

> *A false statement, backed by great prestige, propagates exponentially at second and third hand.*
>
> —Wright, "Genic and Organismic Selection," *Evolution*

### Introduction

In the above quotes, both Charles Darwin and Sewall Wright bemoan the power and persistence of misinterpretation. In both cases these scientists were concerned with the treatment of their theories by the broader scientific community and the lay public. Separated by more than a century, these thoughts provide a background for the discussion of the theory of group selection as it developed in the mid- to late-twentieth century in the work of the English ecologist Vero Copner Wynne-Edwards. In this chapter I examine the ways that the work of Theodosius Dobzhansky and Sewall Wright influenced Wynne-Edwards. It is well known to biologists and historians alike that Wynne-Edwards developed a theory of group selection in the post-synthesis period that generated a heated debate. What is not so well known is that Wynne-Edwards was consciously constructing his theory in a manner he thought consistent with Wright and Dobzhansky. Indeed, Wynne-Edwards conceived of his own work as an ecological naturalist's verification of the models of Wright, consistent with the fieldwork of Dobzhansky. Although the "hardened" form of the modern synthesis may have ultimately focused research along particular individualist lines, this was not the only interpretation of the canonical works that constituted the synthesis. Wynne-Edwards is almost universally presented as an outsider in evolutionary studies, as either a misguided simpleton or an outright crank. Nevertheless, Wynne-Edwards saw himself as part of a natural continuation of the evolutionary synthesis, and he presented his work in ways that stressed his association with the architects of the synthesis, particularly Theodosius Dobzhansky and Sewall Wright. These associations were more than simply rhetorical. Wynne-Edwards derived key ideas and practices from the architects. This association is far more intimate and extensive than the secondary literature leads us to assume. Analysis of this association raises important questions about notions like "insider" and "outsider" or continuity versus breaks in the synthesis historiography.

## Biography

Vero Copner Wynne-Edwards was born in 1906 and later attended Leeds Grammar and Rugby Schools where he developed his early interest in astronomy and natural history. While at Rugby, the young Wynne-Edwards was much impressed by some visiting lecturers, including Julian Huxley. Wynne-Edwards noted in his diary, Huxley was one visitor who lectured "awfully well" (1985, p. 488). Wynne-Edwards left Rugby in 1924 with hopes of Himalayan expeditions studying alpine fauna and flora. The headmaster and his father, however, had, perhaps not surprisingly, more practical plans. The headmaster suggested the study of medicine so that Wynne could act as an expeditionary doctor, and his father suggested further formal study. In the end, Wynne entered New College, Oxford to read zoology in October of 1924 with Julian Huxley as his tutor. This relationship was to last only a year as Huxley accepted the chair of Zoology at King's College London before the end of 1925. Huxley's successor was Charles Elton (a former student of Huxley himself). According to Wynne-Edwards, Elton's influence was to be much more specific and enduring (1985, p. 490). A pioneer of animal ecology and the founder of the Bureau of Animal Population at Oxford University in 1932, Elton is credited as having lit, after their first tutorial, an interest in population ecology that burned for the rest of Wynne-Edwards's life. Much later, Elton became one of many biologists who dismissed Wynne-Edwards's theories.

Wynne-Edwards graduated with first-class honors in zoology in 1927 and became Senior Scholar of New College for 1927–1929. During this time he published several papers on the wintering behavior of starlings. In these articles thoughts on dispersion and breeding began to surface. The *British Birds* article, "The Behaviour of Starlings in Winter," is generally descriptive in nature; however, the discussion of species-level selection and nonbreeding behavior (especially in relation to the rapidly increasing population) marks them as topics of particular theoretical interest to Wynne-Edwards. He rejects the explanation provided by a preceding study that the increase of the starling population followed the advance of human agriculture in the region, which increased the availability of food. This early rejection of food supply as the limiting factor in population level foreshadows the later intense debates with David Lack. He argued that the agricultural development in the region of the southwest of England had occurred over a much longer time period than the 50 years that marked the population and range expansion of the starlings. Wynne-Edwards's rejection of the contemporary explanations was indicative of how important understanding population regulation and its connection to behavior were to him from the very beginning.

In 1930, Wynne-Edwards was offered an Assistant Professorship at McGill University in Montreal. This appointment presented one of the providential opportunities often so important in a developing scientific career. His trans-Atlantic observations led to the publication of his 1935 paper in the *Proceedings of the Boston Natural History Society*, "On the Habits and Distribution of Birds on the North Atlantic," which garnered the society's Walker Prize (Wynne-Edwards, 1935).

A later expedition to Northern Labrador produced the first clear indications of Wynne-Edwards's later work on group selection. The paper, "Intermittent Breeding of the Fulmar with Some General Observations on Non-Breeding in Sea-Birds," published in the *Proceedings of the Zoological Society of London*, marked a transition from purely observational, descriptive natural history to an approach more concerned with theory (Wynne-Edwards, 1939). In conjunction with observations of behavior at the colony, Wynne-Edwards also collected ovaries of nonbreeding females to ensure they were reproductively viable. The combination of field observations with laboratory investigation convinced him, here was a behavior simply not consistent with individual-level explanation. In this paper Wynne-Edwards laid the groundwork for later investigation of nonbreeding behavior as a mechanism for population regulation. Wynne-Edwards wrote that based on previous observations (his own, as well as others') it was estimated that only between one-third and two-fifths of the fulmars present at a particular breeding colony appeared to be engaged in reproduction. This surprising fact required explanation. If, consistent with Darwinian theory, individuals are constantly striving to increase their representation in subsequent generations, why were so many of these fulmars not reproductively active?

The final move of Wynne-Edwards's career occurred in 1945 after serving in the Canadian Naval Reserve in World War II. During the war, Wynne-Edwards remained at McGill teaching electronic physics to radar mechanics in the Royal Canadian Air Force. The summer after the war, while on a trip in the Yukon, he received a letter from his wife announcing that the Regius Chair of Natural History at the University of Aberdeen had become vacant. He served as Regius Chair until 1974, and presided over the establishment of the Cultery Field Station for research in ecology, as well as providing leadership in various scientific, environmental, and ecological associations. It was at Aberdeen that Wynne-Edwards's interest in population structure and breeding behavior would develop into a full-blown theory of group selection.

## Toward a General Picture of Evolution

The first set of articles reviewed here may have been of interest to a small collection of naturalists concerned with the lives of birds; however, with the advent of the modern synthesis, Wynne-Edwards had recognized a fundamental shift in the mode of thought about evolution, which was perhaps more in line with his developing theory of group selection. The emphasis on populations in the work of Dobzhansky and Wright led to a 1955 article in which Wynne-Edwards began by questioning the Oxford ornithologist David Lack's assertion that birds reproduce as rapidly as they can.

As I have shown through the presentation of his previous work, this idea was clearly off the mark as far as Wynne-Edwards was concerned. In a paper presented the same year to the 11th International Ornithological Conference, some of his ideas regarding his developing theory were introduced in qualified terms. He wrote, "It is *theoretically possible* to regulate the numbers in the population by density dependent control of the recruitment rate alone"; and "Control of this sort *could be* largely intrinsic, that is depending for its operation on the behavior-responses of the members of the population themselves." Later in the discussion section he suggested: "A collective response by a social group to general conditions of food productivity *does not appear so very much more abstract* and improbable than the corresponding individual responses by male birds in claiming a territory" [emphasis added] (Wynne-Edwards, 1955, pp. 545–546). The concluding paragraph of this paper marks the first unequivocal statement of Wynne-Edwards's theory about the role of social behavior in limiting population:

> The theory that slowly-breeding birds have evolved a series of interrelated adaptations, giving them a great measure of autonomic control of their numbers, permits, at any rate, a rational explanation to be offered of many hitherto unconsidered or anomalous features of their breeding biology. It shows that if they were adapted to impose their own limit on the number and size of their breeding colonies (as an alternative to limiting the minimum size of individual breeding territories) they could combine optimum feeding conditions with maximum numbers. (Wynne-Edwards, 1955, p. 547)

For Wynne-Edwards this marked a first attempt to offer the "general picture of evolution" that Dobzhansky sought in 1937. He argued that his theory could account for the physiology of populations in ways that standard neo-Darwinian explanations could not, and that attention to the issues of population structure had been increasingly minimized as neo-Darwinian theory "hardened" around individual-level explanations. He was quite optimistic that his forthcoming book-length treatment would fundamentally change the field of evolutionary biology, and return the focus of biologists to the questions of population regulation and structure and their primary importance to understanding evolutionary processes. Wynne-Edwards had been intellectually motivated to pursue these questions through his formative experience as a student of Charles Elton. Despite the ongoing efforts of Elton and the other members of his Bureau of Animal Population at Oxford, the nature of population structure and maintenance remained largely unexplained. Wynne-Edwards looks to Dobzhansky's emphasis on population structure as a key idea emerging from the synthesis. It is this interest in population structure that ties his work to Dobzhansky and Wright. We tend to forget this emphasis on population structure. When looking at selection during this period, the focus moved to individuals. Wynne-Edwards maintained that population-level phenomena are key to understanding evolutionary processes. As research moved away from population structure, Wynne-Edwards seemed even more out of step.

## Into the Spotlight

Wynne-Edwards's *Animal Dispersion in Relation to Social Behavior* was published early in 1962, and was a work of epic proportions. It was comprised of 23 chapters, ran 653 pages, and covered a remarkable range of morphological and behavioral material throughout the entire animal kingdom. Wynne-Edwards essentially relied on the fieldwork of others with regard to the many species he had not studied himself. He did, however, incorporate his own ornithological work and even his early marine studies into his grand theoretical framework.

Epistemologically, Wynne-Edwards worked in a tradition of encyclopedic and largely descriptive natural history. While cognizant of the growing influence of the more experimental and quantitative approaches, he mounted what was essentially an argument by example. Contrary to the trend in biology at the time, Wynne-Edwards's work did not include a great deal of statistical analysis or more sophisticated population genetics. Although Wynne-Edwards was clearly influenced and inspired by the work of Wright and Dobzhansky he did not incorporate their population analysis in any sophisticated way. Rather, he cited their work as evidence of a trend in evolutionary theory toward the study of population structure and distribution patterns that had been previously ignored. He wrote,

> It has become increasingly clear in recent years, not only that animal (and plant) species tend to be grouped into more or less isolated populations, due very largely to the physical discontinuities of the habitat, but that this is a very important feature from an evolutionary standpoint in the pattern of their distribution (*cf.* Sewall Wright, 1938; Dobzhansky, 1941, p. 166 *et seq.*; Carter, 1951, p. 142). (Wynne-Edwards, 1962, p. 19)

By citing Wright and Dobzhansky, Wynne-Edwards sought to align himself with population geneticists whose methods and analyses had become fundamental to evolutionary theory. Wynne-Edwards also worked to distinguish his work from what he called the "traditional Darwinian heritage." He argued that the standard interpretation of natural selection, occurring at two levels, the individual (intraspecific) level and the species (interspecific), could not adequately explain the social behaviors and adaptations of interest to him. On his account, social conventions could only be maintained by groups. The fitness of these groups was a relational property, which could only be understood in terms of the evolution and adaptation of groups, not simply the aggregate of individual-level selection. Again, Wynne-Edwards cited the work of Dobzhansky and Wright as supportive of the notion that social grouping is of the utmost importance to the evolution and distribution of populations. Writing in chapter one, Wynne-Edwards attempted to carefully spell out the function of group selection:

> Evolution at this level can be ascribed, therefore, to what is here termed group selection—still an intra-specific process, and, for everything concerning population dynamics, much more important than selection at the individual level. The latter is concerned with the physiology and attainments of the individual as such, the former with the viability and survival of the stock or race as a whole. Where the two conflict, as they do when the short-term advantage of the individual undermines the future safety of the race, group selection is bound to win, because the race will suffer and decline, and be supplanted by another in which antisocial advancement of the individual is more rigidly inhibited. (Wynne-Edwards, 1962, p. 20)

The connection of Wynne-Edwards's thinking to Dobzhansky's paradox of viability is important to note. Both are arguing that natural selection works on the composite of many individuals that form social groups, and that this selection process is different from individual-level selection. Finally, they both assert that this process produces unique and evolutionarily significant results. As Dobzhansky wrote at the 1965 American Philosophical Society centenary celebration of Mendel, "For evolution is not only substitution of independent components; it is also integration of the components to form adaptively coherent systems" (Dobzhansky, 1965, p. 207). For Wynne-Edwards, Dobzhansky's emphasis on the maintenance of the genetic variability of a population in the form balancing selection was an important counterpoint to the increasing prevalence of individual-level selection explanations that had become standard in understanding population structure and animal dispersion.

The individual adaptationist accounts, represented most clearly in the work of David Lack and his group at Oxford, struck Wynne-Edwards as misguided oversimplifications of the facts of nature as he had observed them and the development of population genetics and the modern synthesis he had witnessed (Borrello, 2003). Although Lack and Wynne-Edwards had always maintained good collegial relations, they were increasingly at odds over the power of individual-level adaptive explanations to account for population regulation. By the mid-1950s Wynne-Edwards had become convinced that Lack had pushed the neo-Darwinian account to its limits. His group selection theory, he argued, fit better with the empirical data and provided a better solution to the problem. It was following the publication of *Animal Dispersion*, in the midst of what became severe criticism from much of the scientific community, that Wynne-Edwards began to look carefully at the work of Wright and attempted to incorporate the theoretical models Wright had developed into his own theory.

## Response to Wynne-Edwards and Group Selection

*Animal Dispersion* was a mixed blessing for Wynne-Edwards. While the book was quite popular and sold well, the professional response was largely critical. Even Wynne-Edwards's mentor at Oxford, Charles Elton, took a rather dim view of Wynne-Edwards's approach. In his review in *Nature* he wrote,

> The theory is set forth with enthusiasm, often pontifically, sometimes in a sort of Messianic exaltation which admits of no other important processes affecting population levels. . . . The enormous weakness of this enormous book, so full of fascinating information, so impregnated with one particular teleological bias, is that it gives no single case-history of group selection. (Elton, 1963, p. 634)

Interestingly, Elton went on to write about group selection, "I have no doubt that this process does occur and may be quite important, but this kind of selection does not only have to be related to population density and resources" (1963, p. 634). Elton's response to Wynne-Edwards's theory of group selection is typical of criticisms published in professional reviews. It also demonstrated, for Wynne-Edwards, the kind of battle he would face in trying to win acceptance for group selection. Six hundred pages of examples that could be interpreted in terms of group selection would not suffice. He very soon realized that if the theory were to stand any chance at all, he would need to develop a more sophisticated version of group selection that could not be so quickly dismissed. In another important review that contributed to Wynne-Edwards's determination to put his theory on more secure theoretical footing, the ornithologist F. W. Braestrup wrote, "the process of selection works, not only between individuals, but also between groups and between species, thus promoting characters which are to the benefit of the group, even in the face of contrary individual selection which may be kept in check by special devices. The existence of such evolutionary mechanisms is not only called for by a great many otherwise unaccountable facts, but is also in accordance with genetic evolutionary theory" (Braestrup, 1963, p. 113). In support of his claim regarding genetics, Braestrup cited Sewall Wright's by now familiar review of *Tempo and Mode*, which was published in 1945. It is clear, at least from Braestrup's point, that what Wynne-Edwards was claiming was somehow not consistent with Wright. In the notebooks, correspondence, and publications after *Animal Dispersion*, Wynne-Edwards began to work on a more careful incorporation of Wright's model of demic selection that he thought was consistent with his view.

## Populations, Demes, and Groups

The idea that natural selection operated at levels above the individual organism had been part of evolutionary theory from its inception in Darwin's *The Origin of Species*, but the invocation of "good of the group" arguments became increasingly less acceptable as the modern synthesis developed (Borrello, 2005; Richards, 1987). By the mid-1960s, with the publication of G. C. Williams's influential work, *Adaptation and Natural Selection*, group-level application of evolutionary mechanism was effectively stamped out (1966). Nevertheless, Wynne-Edwards continued to argue for the relative importance of group selection. Indeed, as my earlier analysis demonstrated, he became increasingly interested in the connection of his own ideas to those of Theodosius Dobzhansky and Sewall Wright. Dobzhansky's work identified the importance of natural population structure to the development of evolutionary theory. Wright's models emphasized the role of group membership in assessing evolutionary fitness. Wynne-Edwards sought to extend the insights of Dobzhansky and Wright into a comprehensive explanation of social behavior with his theory of group selection.

The influence of Dobzhansky on Wynne-Edwards was earlier than that of Wright. In his seminal work, *Genetics and the Origin of Species* (1937), Dobzhansky introduced the paradox of viability. In a discussion of 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" (1937, p. 127).

The above quotation is evidence that Dobzhansky was focusing on a group-level trait and was interested in its importance to evolutionary theory. The evolutionary plasticity that Dobzhansky invokes is a characteristic of a population. The increased variation of one population compared to that of a competing population conferred a fitness advantage to the more varied population even at a cost to the individuals that comprised the more varied population. These kinds of interpretations of the data produced by the population geneticists created the theoretical space within which Wynne-Edwards would pursue his 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, Mayr, and 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" (Wynne-Edwards, 1948, pp. 195–196). This passage represents Wynne-Edwards's first published attempt to connect his ideas with the new synthetic theory and particularly with Dobzhansky. I argue that as early as 1948 Wynne-Edwards was engaged in a strategy of assimilation. He began drawing links and attempting to build on them as evidenced in the passage above. This strategy was a result of Wynne-Edwards's recognition of populations (their genetics and their structure) as the core concept of the synthesis period.

In *Genetics and the Origin of Species* (1937), Dobzhansky also made interesting claims about the physiology of populations having been entirely neglected and, at the same time, perhaps the most essential aspect of the theory of evolution. Dobzhansky argued, in his chapter on variation in natural populations, 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. (Dobzhansky, 1937, p. 120)

Dobzhansky's emphasis on higher-level selection, which he called group selection, (following Wright), was of obvious importance for Wynne-Edwards. 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. Wynne-Edwards thought that his view of social behavior as a mechanism for maintaining population levels would achieve the kind of "general picture of evolution" that Dobzhansky described in 1937:

> Since evolution as a biogenic process obviously involves an interaction of all of the above agents [gene mutation, chromosomal changes and population dynamics], the problem of the relative importance of the different agents unavoidably presents itself. For years this problem has been the subject of discussion. The results of this discussion so far are notoriously inconclusive; the "theories of evolution" arrived at by different investigators seem to depend upon the personal predilections of the theorist. One of the possible sources of this situation may be that a theory which would fit the entire living world is in general unattainable, since the evolution of the different groups may be guided by different agents. To a certain extent this possibility is undoubtedly correct. . . . Nevertheless,

> one can hardly eschew trying to sketch some sort of general picture of evolution. A very interesting attempt in this direction has been made by Wright (1931a, 1932), whose lead we may partly follow. (Dobzhansky, 1937, p. 186)

The contributions of Sewall Wright, whose earlier models influenced Dobzhansky's thinking, were ultimately even more important to Wynne-Edwards and became increasingly so as he developed his ideas.

## Balancing Selection: Individuals and Groups

Within a year of the publication of *Animal Dispersion*, Wynne-Edwards began his attempt to clarify his theory of group selection and link his work directly with the work of Dobzhansky and more especially Wright. In a paper in *Nature*, "Intergroup Selection in the Evolution of Social Systems," Wynne-Edwards again made explicit his indebtedness to and consistency with Wright:

> The general concept of intergroup selection is not new. It has been widely accepted in the field of evolutionary genetics, largely as the result of the classical analysis of Sewall Wright (1921, 1930, 1945). He has expressed the view that "selection between the genetic systems of local populations of a species . . . has been perhaps the greatest creative factor of all in making possible selection of genetic *systems as wholes* in place of mere selection according to the net effects of alleles." (Wynne-Edwards, 1963, p. 623) [emphasis added]

He went on to describe the effects of other evolutionary mechanisms working simultaneous to group selection. He acknowledged that gene frequencies within groups might alter as a result of genetic drift, "the Sewall Wright effect," and through the operation of selection at the individual level. Wynne-Edwards further argued that "population fitness, however, depends on something over and above the heritable basis that determines the success of individuals" (1963, p. 624), which led to his conclusion that social groups have highly important adaptive characteristics in their own right. In his discussion of the nature of social hierarchies as group characteristics, or "organs" of group adaptation which have no existence if the members are separated, he harkens back to the balancing selection of Dobzhansky. "The hierarchy is not the only characteristic of this kind. There are genetic mechanisms, such as those that govern the optimum balance between recombination and linkage, in which the benefit is equally clearly with the group rather than the individual" (1963, p. 624). These points represent a significant shift in the nature of Wynne-Edwards's argument for group selection. While he initially thought it might suffice to simply mention the importance of population genetics in general and the work of Dobzhansky and Wright in particular, as early as 1963 he began making specific use of their work. He concluded this paper, writing,

> Relatively simple genetic mechanisms can be evolved whereby the door is shut to one form of selection and open to another, *securing without conflict the maximum advantage from each*; and since neighbouring populations differ, not only in genetic systems but in population parameters (for example, mean fecundity) and in social practices (for example local differences in migratory patterns in birds, or in tribal conventions among primitive

> men), there is no lack of variation on which intergroup selection can work. (1963, p. 626) [emphasis added]

The tie to the architects of the synthesis and genetics was explicit. Of the eleven citations included in this paper, three are to Wright (1929, 1930, 1945), one is to J. B. S. Haldane (1932), and one is to Sturtevant (1938). This represents a response to his critics that while he may have presented a number of compelling examples in *Animal Dispersion* he did not provide a compelling theoretical framework within which to pursue further research on group selection. Wynne-Edwards became increasingly aware of the necessity for rigorous genetic arguments as the focus of the attacks on his theory shifted almost exclusively to the genetic level. This attack was most forcefully presented by John Maynard Smith in his development of the haystack model, which is discussed below. For the present, it is most important to note that in this paper Wynne-Edwards explicitly acknowledged the importance of other evolutionary mechanisms (e.g., drift and individual selection) although this is often unrecognized. Similar to Wright, who felt the need to defend his own ideas against persistent misinterpretation along the same lines (as evidenced by the quote at the outset of this chapter), Wynne-Edwards argued that group selection and individual selection need not be opposing evolutionary forces, nor did group selection require, on his account, a decrease in individual fitness. Of course, the responsibility of the misrepresentation lies not only with the audience but also with the author.

Wynne-Edwards's explicit effort to connect lapsed only a couple of years later. In a 1965 paper in *Science*, "Self-Regulating Systems in Populations of Animals," he reverted to the assertions presented in his original argument and dropped references to population genetics altogether. In the midst of the development of kin selection theory and individual-level game theoretic explanations for social behavior, he was no longer sure that Wright and Dobzhansky could provide the necessary support and so retreated to his initial position, namely, neo-Darwinian theory is flawed and group selection is the answer. He wrote unequivocally, "Antisocial behavior among individual members, although it may advance their own interests, is by definition potentially detrimental to the survival of the group. It appears to have been firmly and almost universally suppressed by natural selection, acting at this overriding level. Total compliance with the social code, even when this entails the restriction or inhibition of fertility, exclusion from food and shelter, expulsion from the habitat, or summary death to the individual concerned, is consequently the routine of social life" (Wynne-Edwards, 1965, p. 178). This retrenchment did not last. The following year Wynne-Edwards presented a paper at a conference with Dobzhansky as the keynote speaker. The theme of the conference, organized by the Russell Sage Foundation, was "Biology and Behavior" with a focus on genetics. Dobzhansky's address, "Genetics and the Social Sciences," focused on the relation between evolutionary theory and ideas regarding social mobility. In his paper, Dobzhansky stressed the importance of genetic variation in populations and connected some recent experimental work on *Drosophila* to the role of social mobility in human evolution. According to Dobzhansky, social mobility (which gives rise to positive assortative mating) enhances the fitness of the population groups between which it occurs and leads to the higher likelihood of genotypes that would be less common given random mating. Dobzhansky offered the following hypothetical example:

> Suppose, then, that a certain special ability (for example, musical talent) is the result of simultaneous possession of several genes, each of which has only limited effect separately. The frequencies of each of these genes in the population may be low. If so, under random mating the probability of a genotype arising which carries all such genes may be minute. The situation changes with free social mobility, which brings into a class or a profession the individuals that carry at least some of the genes that qualify these carriers for success in this profession. Positive assortative mating will then be able to produce accumulation of such genes in some individuals, raising their ability in their special field. (Dobzhansky, 1968, p. 142)

This example resonated with Wynne-Edwards and corroborated his thinking with regard to the importance of population structure and breeding patterns.

In his own paper published in the proceedings of the conference, Wynne-Edwards was again explicit regarding the connection of his theory to the work of Dobzhansky writing, “no one has done more than Dobzhansky to analyze the kind of spatial and temporal organization that typically exists in animal species” (Wynne-Edwards, 1968, p. 160). He further argued that this spatial and temporal organization was consistent with his theory of group selection. According to Wynne-Edwards,

> We find no evidence of selection to maximize ferocity toward rivals in a group . . . any more than there is an inevitable trend towards higher fecundity . . . Each of these characters varies in a given population over a range of values, which must obviously fit the requirements for survival of the group as a whole. The characters are immune to quick selective changes that could give an antisocial hereditary advantage to the individual, because their physiological control is immensely complex and their genetic basis perhaps even more so . . . Polygenes and heterosis can negate any immediate hereditary advantage to the progeny of an individual, and if somehow antisocial self advantage does make a breakthrough and increases the fitness of the individual, it will sooner or later lead to the extinction of the group. (Wynne-Edwards, 1968, p. 162)

Wynne-Edwards concluded the paper in what was becoming a typical fashion, bold assertion of the supremacy of group selection. “The facts demonstrate unequivocally that adaptations have arisen, capable of modifying the fitness of the individual in the overriding interests of group survival. To deny this, it seems to me, is to bury one’s head in the sand” (Wynne-Edwards, 1968, p. 163). He continued to focus on those elements of population genetics research that conformed to his ideas and to dismiss those that did not. For example, he criticized the general consensus that had built around Haldane’s claim that genes for altruism seemed unlikely to spread, as “an oversimplified concept” (Wynne-Edwards, 1968, p. 161).

Perhaps the most important result of this conference for Wynne-Edwards was a discussion he had with Dobzhansky. Wynne-Edwards recalled in his autobiographical memoir, “In private afterward, while we were discussing the implications of my own paper on population control and social behavior in animals, he [Dobzhansky] put a specific challenge to me. ‘Don’t you think you could sort this thing out once and for all?’ ‘This thing’ was how group selection (which has vexed geneticists for half a century) could take place, and lead to the evolution of collaboration and altruism and statistical kinds of genetic adaptation as well” (Wynne-Edwards, 1985, p. 510).

Wynne-Edwards followed this recollection with the claim that albeit too late for Dobzhansky, who died in 1975, he had finally developed the answer.

## Rethinking Group Selection

Between the conference in 1966 and the announcement in his 1985 memoir of an answer to the problem of group selection, Wynne-Edwards continued to think about group selection, but did not publish much. After his retirement from Aberdeen in 1974 he seemed nearly ready to give up on group selection. The increasing focus on individual and genic level selection had led him to what Richard Dawkins described as a "magnanimous recantation" regarding group selection in 1977. Wynne-Edwards wrote,

> In the last 15 years many theoreticians have wrestled with it [group selection] and in particular with the specific problem of the evolution of altruism. The general consensus of theoretical biologists at present is that credible models cannot be devised, by which the slow march of group selection could overtake the much faster spread of selfish genes that bring gains in individual fitness. I therefore accept their opinion. (1977, p. 19)

The recantation was short-lived, as Dawkins described in the revised edition of *The Selfish Gene*, "magnanimous these second thoughts may have been, but unfortunately, he has had third ones: his latest book re-recants" (Dawkins, 1989, p. 297).

What led Wynne-Edwards back to group selection was a combination of new and old ideas in biology that he was grappling with in his notebooks. He was well aware of the work of W. D. Hamilton on kin selection, John Maynard Smith's development of the haystack model, and Robert Trivers's theory of reciprocal altruism, all of which presented serious challenges to his theory of group selection. In his personal notebooks from the late 1960s and 1970s, Wynne-Edwards attempted to develop answers to these challenges. Again, he looked to Dobzhansky, and with increasing interest, to Wright for support of his theory. After reading Hamilton's 1964 paper, Wynne-Edwards wrote in his notebook that it was inadequate to explain the evolution of social adaptations on the basis of individual advantage as Hamilton had done. Given that the benefit did not accrue to the individual, it was not possible for selection acting on the individual to produce this group result. Wynne-Edwards copied a passage from Dobzhansky's 1951 paper, "Mendelian Populations and Their Evolution," that read: "In other words, natural selection enhances the adaptedness of the Mendelian population as a whole, at the price of the continuous production of some less well adapted individuals" (Dobzhansky, 1951, p. 581). This passage connected some of the most recent theorizing against Wynne-Edwards's ideas (i.e., inclusive fitness theory) with the earlier work of Dobzhansky. Wynne-Edwards interpreted Dobzhansky's work as not supportive of kin selection theory, because the populations he described were not necessarily comprised of closely related individuals. The "benefit" of genetic variation could not be ascribed to the individual because it was a characteristic of populations. The second set of new and old ideas that led to Wynne-Edwards's re-recanting were the new work on group selection being developed by Michael Wade and David Sloan Wilson and his rediscovery of Wright.

## Making Group Selection Wright

In 1986 Wynne-Edwards published his second book, *Evolution Through Group Selection*. This was to be his definitive account of the power of group selection in shaping evolutionary history. Much of the book was dedicated to an interpretation of the long-term research on the red grouse that had been conducted at the Culterty Field Station, which Wynne-Edwards had worked to establish in the late 1950s. The grouse research would stand as the detailed example or case study of the role of group selection in maintaining population levels that many of Wynne-Edwards's critics had demanded since the publication of *Animal Dispersion*. Equally important to Wynne-Edwards's strategy to establish the fundamental importance of group selection was the incorporation of Sewall Wright's shifting balance model into his own work. His notebooks demonstrate an increasing level of interest in Wright throughout the 1970s, which culminated in the 1986 book. His definitive 1986 work included a chapter on evolution in structured populations that drew heavily on Wright's shifting balance model. Wynne-Edwards states at the beginning of the chapter, "On the genetical side, however, it appears that the classical assumptions about panmixis in mating systems are seldom if ever borne out by the facts, at least in the vertebrates; and in birds and mammals including primitive races of man, mating is often regulated and contrived—often as in the red grouse being exogamous and patri- or matrilocal as the case may be" (Wynne-Edwards, 1986, p. 200). Wynne-Edwards went on to discuss how structuring of populations could readily serve to restrict gene flow between groups or demes. The importance of population structure was that it performed two important functions; one ecological, the other evolutionary. The ecological function, to ensure the rewards of resource husbandry were transmitted to subsequent generations, had long been the focus of Wynne-Edwards's work on group selection. In *Evolution Through Group Selection*, Wynne-Edwards had finally turned explicitly to the evolutionary function of population structure, and that turn led directly to Wright's shifting balance theory. He wrote,

> My own ideas about both functions [ecological and evolutionary] have of course been reached by following ecological and sociobiological paths; but there is an older and more powerfully and persistently argued theory that has led to very much the same conclusions, with regard to the evolutionary conclusions alone, in the work of Sewall Wright (e.g., 1931, 1940, 1945, 1949, 1968–1978, 1980). (Wynne-Edwards, 1986, p. 203)

He emphasized that Wright's argument was based on the usual premise that evolutionary change is mediated by changes in gene frequency and these changes were due to mutation, selection, migration, and chance. He was particularly interested in the characters of organisms that exhibited continuous variation. As these characters are largely polygenic, they provided the variation of fine adjustment and they represented, for Wynne-Edwards, the main systems of demic differentiation. In structured populations, then, it was selection and chance that were the most powerful evolutionary forces. "In such small units the individuals that actually survive to breed will be rather few in number, and subject therefore to appreciable sampling errors, giving rise to corresponding variances between units even though the units may have been originally derived from the same base population" (Wynne-Edwards, 1986, p. 204). In his discussion of Wright's work Wynne-Edwards went on to describe Wright's adaptive landscape and included the now famous illustration from his 1932 paper. Wynne-Edwards then cited Wright's 1940 paper, where he wrote,

> Under this condition neither does random differentiation proceed to fixation, nor adaptive differentiation to equilibrium, but each local population is kept in a state of continual change. A local population that happens to arrive at a genotype that is peculiarly favorable in relation to the general conditions of life of the species, i.e. a higher peak combination than that about which the species had hitherto been centered, will tend to increase in numbers and supply more than its share of migrants to other regions, thus grading them up to the same type by a process that may be described as intergroup selection. (Wright, 1940, p. 175)

This introduction of Wright's focus on population structure culminating in his description of intergroup selection led then to Wynne-Edwards's reading of Wright's 1980 paper on "Genic and Organismic Selection." Wright's 1980 paper came to Wynne-Edwards like manna from heaven. Wynne-Edwards began his analysis of the 1980 paper pointing out that much like his own, Wright's theory had frequently been misrepresented and the paper was meant to set things straight. This indeed was the same motivation behind Wynne-Edwards's second book. What was particularly fascinating for Wynne-Edwards was that their ideas were so similar and that they had been "misunderstood" in similar ways, as well. Wynne-Edwards argued,

> Populations structured on Wright's model could store a much greater genetic variability than panmictic populations of the same size; and not only might better adapted stocks emerge in the manner just described, but when the environmental changes of wider than local importance occurred the probability would be correspondingly greater that preadapted units were already in existence, from which mass selection and expansion could take place. In his expressive phrase (Wright, 1980, p. 841) "creativity is raised to the second power" in populations structured in this way. (Wynne-Edwards, 1986, p. 206)

Here again we see Wynne-Edwards homing in on Wright's insights regarding population structure in an attempt to connect them with his own. This was perhaps the most important function for the 1980 paper in Wynne-Edwards's eyes.

In Wright's attempts to clarify his own ideas to the community of evolutionary biologists, Wynne-Edwards saw an opportunity to show the consistency of his own thought with Wright's and thereby salvage his theory from oblivion. Wynne-Edwards was particularly keen to show that his theory, like Wright's, need not always be considered as working in opposition to individual-level selection. Given the earlier critiques of Williams and Maynard-Smith, this was an especially important point of clarification for Wynne-Edwards. He cited Wright gleefully:

> He [Wright] concludes the paper by saying that several recent authors who have discussed group selection for group advantage at length, have rejected it as of little or no evolutionary significance, and seem to have concluded that natural selection is practically wholly genic. "None of them discussed group selection for organismic advantage to individuals, the dynamic factor in the shifting balance process . . . although it is not fragile at all, in contrast with the fairly obvious fragility of group selection for group advantage, which they considered worthy of extensive discussion before rejection." My task is obviously to show

> that the group selection I advocate is not essentially different from Wright's in raising average individual fitness, and is not fragile either. (Wynne-Edwards, 1986, p. 207)

Wynne-Edwards's extensive reliance on Wright in *Evolution Through Group Selection* was preceded by a decade of reading and annotating his work and connecting it to the work of Dobzhansky and the Chicago ecologist Warder Clyde Allee, with whom Wright had worked through the middle part of his career. Indeed, while working on the manuscript for the book, Wynne-Edwards had corresponded with Wright regarding Allee. Wynne-Edwards was interested to hear Wright's thoughts on Allee's use of Wright's population structure models as a functional explanation of undercrowding in laboratory populations of invertebrates. He wrote to Wright that this was a "remarkable stroke of intuition" and that he had recently come to the same conclusion himself. Wright responded that he was certain that he and Allee had discussed these matters at the time, but could not recall the nature of the conversations beyond what had been published in *Principles of Ecology*. He went on to write,

> I was interested in learning that you are writing a sequel to your 1962 book. I touched on the subject of the conditions under which selection for group advantage would prevail over an associated individual disadvantage in a review of Simpson's *Tempo and Mode of Evolution*. I overlooked then a discussion by Haldane in his 1932 book on evolution. Our modes of attack on the problem were different but our conclusions were much the same: possible, but rather fragile, under changing conditions. I came to appreciate the importance of this question much more fully after reading your 1962 book. I have no doubt that group selection has prevailed in many cases. I discussed it (much too briefly) in *Evolution and the Genetics of Populations*. (Sewall Wright to Wynne-Edwards, March 11, 1983, Box 16 File 2, Wynne-Edwards Papers, Queens University Archive)

This letter must have provided great satisfaction for Wynne-Edwards and spurred him to complete the manuscript the following year.

The following day, Wynne-Edwards wrote a letter to Michael Wade at the University of Chicago, informing him of his forthcoming book and requesting permission to reproduce figures from Wade's 1977 paper in *Evolution*. Wynne-Edwards wrote enthusiastically of how Wade's experimental work provided "strong practical support" and "impressive elucidatory powers in accounting for the evolution of statistically (i.e., group) adapted genetic mechanisms, including the tight control of dispersal, and the separation of the two dimorphic sexes" (Wynne-Edwards to Michael Wade, March 12, 1983; letter in Borrello's possession). Wynne-Edwards had clearly identified Wade's work as a continuation and verification of Wright's model importantly consistent with his own. Indeed, Wade concurred, in a review of *Evolution Through Group Selection* in *Evolution*:

> Many of the studies of population structure in other organisms over the past decade have been presented in a conceptual vacuum, as though population structure per se, in the absence of any evolutionary perspective, had some intrinsic meaning. Wynne-Edwards must be acknowledged for his thorough presentation of the red grouse as a model for the population structure component of Wright's shifting balance theory. (1988, p. 1116)

The following year, Wynne-Edwards's use of Wright's model was carefully examined by Gregory Pollock, in a 1989 paper in the *Journal of Evolutionary Biology*. As Pollock noted,

> Beneath his [Wynne-Edwards's] dogmatic theme of population regulation lies a struggle to articulate intuitions underlying the concept of population heterogeneity: the roles of population structure, group definition and absolute fitness in evolutionary thought. (Pollock, 1989, p. 206)

Pollock argued that Wynne-Edwards, although often considered "a spurned father of contemporary evolutionary thought," was connecting his work to the ideas that motivated both Dobzhansky and Wright and represented some of the most important developments of the modern synthesis. Contrary to the claims of his critics, Wynne-Edwards's view of the evolutionary significance of population structure was consistent with Wright and not accurately presented by Maynard-Smith's haystack model. Recall that for Wynne-Edwards, a population was

> typically self perpetuating, tending to be strongly localized and persistent on the same ground, illustrated by the widespread use of traditional breeding sites . . . preserving the integrity of their stock. Isolation is normally not complete, however. Provision is made for an element of pioneering and infiltration into other areas; but the gene flow that results is not commonly fast enough to prevent the population from accumulating heritable characteristics of its own. (Wynne-Edwards, 1963, p. 624)

For Wynne-Edwards, group selection consists of differential reproduction of in-groups. These groups were not the spatially isolated groups posited by Maynard-Smith's haystack model. Rather, they were consistent with the demes that Wright described. Pollock went on to present Wynne-Edwards's 1986 version of group selection theory as "a pioneering extension of Wright's shifting balance metaphor to selection of socially induced fitness effects in viscous populations, difficult to express in the kin/group taxonomy of Maynard Smith" (Pollock, 1989, p. 210). Pollock cited Wynne-Edwards's (1972) Herbert Spencer Lecture to counter claims that Wynne-Edwards's cooperative view of nature was naively utopian, then went on to point out how our own position within a social context can ultimately be better understood in terms of the Wrightian/Wynne-Edwardsian description of populations:

> Humans are themselves embedded in a Wrightian viscous population, where behavioral proximity, measured as the relative allocation of interaction among individuals, replaces spatial proximity. Cooperation is the product of a fragmented social environment and, for this very reason, is itself heterogeneously distributed. We are socially viscous creatures, creating islands of solstice [*sic*] within Malthusian necessity. (Pollock, 1989, p. 218)

## Remaining Outside

We might not be surprised to find that, despite Wynne-Edwards's attempt to create an island of solace and the recognition of some contemporary theorists of his connection to Dobzhansky and Wright, group selection remained outside the mainstream of evolutionary thinking even after the publication of *Evolution Through Group Selection*. Into his late eighties, Wynne-Edwards continued to publish and advocate for the importance of group selection to evolution. Moreover, he continued to emphasize the connection of his own work to Wright's. In a 1991 article in *The Ecologist*, he cited Wright's review of *Tempo and Mode*, writing,

> Neo-Darwinian evolutionists, however, hold firm to the belief that natural selection can operate only on individual organisms, and that all the adaptations and advances which evolution has witnessed must have arisen by that process alone. . . . Theoretical defects on this scale again point to the existence of a second, slower process of innovation and natural selection, with self-perpetuating groups or sub-populations as the separate units on which selection works. The theoretical conditions required to make group selection work have been well understood for many years (i.e., Wright, 1945). (Wynne-Edwards, 1991, p. 138)

In the final publication of a career that had begun in the 1920s Wynne-Edwards made one last appeal for his theory. Once again, Wright and the relative significance of population structure played a prominent role.

> Long ago Sewall Wright (1931) published his visionary concept of an adaptation that could immeasurably increase the speed and versatility of evolution. Wright evidently believed that this structural adaptation was real, although he never attempted to confirm it in the field. It seems remarkable that what started as an extremely perceptive intuition, rejected by other evolutionists at the time as unbelievable, should turn out, half a century later, to exist in factual detail in the real world as a widespread phenomena. (Wynne-Edwards, 1993, pp. 7–8)

Again he cited Wade's work with *Tribolium* and his own analysis of the red grouse research as empirical evidence for the importance of population structure to the evolution of any social organism (Wynne-Edwards, 1993, p. 10). Wynne-Edwards was not content with the state of evolutionary theory in the mid- to late-twentieth century and spent his career attempting to illustrate its shortcomings and describe his alternative. Although he has generally been thought to have been working completely outside the mainstream with little connection to "serious biological thinking" this analysis demonstrates otherwise.

## What Is a Synthesis? *The Synthesis*?

Questions regarding the nature, content, and meaning of the synthesis have motivated historical inquiry since at least the late 1950s (Tax, 1960, vols. 1–3).

Both biologists and historians have generated volumes, conducted symposia, and engaged in debates regarding the construction of the appropriate historical narrative and the identification of the key contributions (Mayr & Provine, 1980). The modern synthesis has been described in a number of ways: the integration of theories from a wide range of fields (Darden, 1986), the cooperative organizational solution to discipline building (Cain, 1993), a conscientious effort on the part of working scientists to unify biology (Smocovitis, 1994, 1996), a hardening of biological investigation and explanation around the idea of individual-level adaptation (Gould, 1983), and a constriction of biology consistent with the mathematical models of Fisher, Haldane, and Wright (Provine, 1978, 1992). This volume will add to these interpretations and offer new narratives and definitions. The aim of this essay is to present a bit of history not often connected to the standard narrative and to illuminate the extent to which the invocation of "the modern synthesis" became an important legitimizing tool for biological ideas and theories.

The question regarding the level at which natural selection occurs has been a primary concern of biologists since the publication of *On the Origin of Species*. As Darden points out in her 1986 paper in *Integrating Scientific Disciplines*, Theodosius Dobzhansky was particularly attuned to the importance of these multiple levels and their role in the process of evolution. As Darden nicely illuminated, they consist of mutations and chromosomal changes at the level of the individual, selection, migration and isolation occurring at the level of the population, and finally, fixation of the diversity attained at the preceding levels occurring at the species level (Darden, 1986, p. 114). In the same volume, John Beatty pointed out that Dobzhansky achieved another kind of synthesis that was equally important. He argued that in addition to thinking of Dobzhansky's contribution as a synthesis of theories operating at multiple levels, we must also understand his work as a synthesis of theory and observation. Beatty cited Lewontin to this effect, writing,

> The contribution of Dobzhansky's experimental and field studies to the synthesis, [is] "The successful melding of the theory of gene frequency change with the known facts of genetic variation . . . marks the first real synthesis in biology of a complex mathematical theory with a large body of observation and experiment." (1986, p. 128)

Beatty went on to argue that evolutionary biologists did not go into the field or into their labs simply to test the synthetic theory. Rather, they first wanted to measure the values of the variables of the theory in particular cases. Second, they wanted to extrapolate from the values of the variables in particular cases to the overall relative importance of the various possible modes of evolutionary change (Beatty, 1986, p. 128). According to Beatty, evolutionary biologists around the time of the synthesis had the goal of understanding the *relative* importance of the various possible modes of evolutionary change. It is in terms of this framework that I have analyzed the attempts of one biologist concerned with a particular mode of evolutionary change; that biologist was Vero Copner Wynne-Edwards and the mode of evolutionary change he advocated was group selection.

Both William Provine and John Beatty have argued that the synthesis did indeed harden around the mechanism of natural selection. But they also cautioned against making too much of this (Beatty, 1992; Provine, 1992). Provine wrote: "There were about as many different versions of the evolutionary synthesis as there were major evolutionary biologists associated with it[.]" (Provine, 1992, p. 169). He went on to point out that while the hardening process continued into the early 1960s what was really characteristic of the synthesis was a constriction of biology around a small number of variables (i.e., effective population size, population structure, random genetic drift, levels of heterozygosity, mutation rates, migration rates, etc.) considered important in the evolutionary process. While these variables were not new to evolutionary research, the idea that evolution depended on so few of them was (Provine, 1992, p. 177). This according to both Beatty and Provine allowed for multiple paths of research to emanate from the core of the synthesis. According to Beatty, "We cannot let the 'constriction' and 'hardening' of the synthesis blind us to the diversity of possible evolutionary agents being discussed in the fifties, sixties and seventies and to the incredible room still left for controversy about these actual modes of evolution" (Beatty, 1992, p. 188). My analysis of Wynne-Edwards's work clearly reflects this image of the synthesis. Wynne-Edwards was certainly different from some, but clearly developed his work consistent with and as an extension of the core synthesis ideas.

## Conclusion

From Wynne-Edwards's initial notice of Dobzhansky's emphasis on the various modes of selection that play important evolutionary roles in his 1937 book and its connection to the importance of population structure, to the emphasis in his later work on the similarity of his own theory to Wright's, it becomes clear that many in the biological community have underappreciated the connection between Wynne-Edwards's model of group selection and theoretical population genetics. Wynne-Edwards saw himself as an outsider certainly, particularly set against the individual selectionist theory of the Oxford zoology department. He nevertheless presented himself as working within the boundaries of the modern synthesis and the parameters of population genetics as developed by Wright and Dobzhansky.

Wynne-Edwards's career should be seen as a sustained plea for the relative significance of group selection as a mechanism of evolution. The reception of Wynne-Edwards's work and the ensuing debate over group selection illuminates and supports elements of Gould's hardening thesis; there was indeed an increasingly individualist, adaptationist point of view that became standard. It is important for historians, however, to be sensitive to the fact that this hardening was neither universal nor instantaneous. Wynne-Edwards, drawing on thinking from both the American and British communities of evolutionary biologists, was more pluralist than we are led to expect from the hardening thesis. By stressing the idea of hardening Gould invents an orthodoxy, thereby automatically marginalizing Wynne-Edwards. If we look carefully at Wynne-Edwards's work we see that while he challenged the individualist orthodoxy that was fundamental to the hardening of the synthesis, he was equally convinced his theory was consistent with the selectionist emphasis that was just as important to postsynthesis evolutionary theory. Wynne-Edwards thought his work rose naturally from the population genetics and was consistent with the developments of the modern synthesis. If we embrace Beatty and Provine's characterization of the synthesis, Wynne-Edwards is no longer a marginal character. Rather, he is more accurately identified as another branch on the evolutionary family tree.

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