"Mutual Aid" and "Animal Dispersion"

an historical analysis of alternatives to Darwin

Mark E. Borrello

ABSTRACT Petr Alekseyevich Kropotkin (1842–1921) and Vero Copner Wynne-Edwards (1906–1997) developed evolutionary theories that emphasized social groups and cooperation rather than the organism-level natural selection of standard Darwinian theory. The most important reason for their alternative interpretations was their experience as field naturalists. Kropotkin and Wynne-Edwards worked in arctic environments and were impressed by aspects of the natural world that differed significantly from those experienced by Darwin or Wallace. These field experiences led to their emphasis on mutual aid and group selection, respectively. Understanding the development of their theories helps to illuminate the continuing debates over evolutionary theory and the current resurgence of interest in group selection.

Prince Petr Alekseyevich Kropotkin and Vero Copner Wynne-Edwards developed evolutionary theories that emphasized social groups and cooperation rather than the organism-level natural selection of standard Darwinian theory. In light of the resurgence of interest in group selection theory, a comparative analysis of these two ideas is particularly compelling, as is an assessment of the factors that led them to take such a different approach to selection. As arctic

Lyman Briggs School, Michigan State University, East Lansing, MI 48825.
E-mail: borrell4@msu.edu.

Perspectives in Biology and Medicine, volume 47, number 1 (winter 2004):15–31

field naturalists, Kropotkin and Wynne-Edwards experienced nature in a significantly different fashion than either Darwin or Wallace. This, when considered against the backdrop of the emergence of biology as a discipline and their individual sociopolitical/ideological contexts, can help explain their divergence from mainstream Darwinian thought.

Kropotkin developed his theory as a response to Thomas Huxley's (1888) "gladiatorial" view of nature; over the next 20 years, his main target was August Weismann's (1889, 1904) theory of the germ plasm and the idea of the all-powerful evolutionary mechanism, natural selection acting on individual organisms. Throughout his crusade against Huxley and Weismann, Kropotkin was consistent in targeting their overemphasis on the role of individual-level selection in the evolutionary process. Likewise, Wynne-Edwards' theory of group selection, initially formulated in response to David Lack, focused on explanations for a wide range of animal behaviors, such as communal roosting in starlings and deferred breeding in fulmars, not explained by neo-Darwinian invocation of individual-level selection.

A comparison of these two theories is also of interest in the context of the development of biology. Kropotkin was writing during a period of great debate in the field (Butler 1879; Headley 1901; Kellogg 1908; Thomson 1925; Wallace 1889). Neo-Lamarckians battled neo-Darwinians, recapitulationists took on nonprogressive evolutionary thinkers, gradualists disputed saltational claims, and all of these theories were tied to larger ideological battles over the social implications of Darwinism. Wynne-Edwards' work was introduced during another important period for the development of biology, the modern synthesis (Mayr and Provine 1980; Smocovitis 1996). The transition of biology from the naturalist tradition to a more experimental approach, together with the increasing influence of genetics—and particularly population genetics—on evolutionary theory played an important role in the development of Wynne-Edwards' theory and its reception.[1]

Understanding the development of Kropotkin's and Wynne-Edwards' theories contributes a clearer understanding of the broader history of evolutionary theory and illuminates the continuing nature of the debates over evolution and the current resurgence of interest in group selection theory.

KROPOTKIN

Petr Alekseyevich Kropotkin (1842–1921) is perhaps better known to Western scholars as the leader of the international anarchist movement than as a biologist. Nevertheless, Kropotkin cultivated an interest in natural history from a young age and pursued that interest as a member of various expeditions and a

[1]The development of group selection theory in relation to the broader biological context is presented in Borrello (2002).

contributor to professional societies. Graduating first in his class in the Corps of Pages, he became the tsar's *page de chambre*, but became disenchanted with court life. Between 1862 and 1867, he traveled through Siberia as naturalist on a series of commercial and military expeditions. Kropotkin's Siberian travels, supported by the Imperial Russian Geographical Society, included a year devoted geography and to the study of Ice Age formations in Eastern Siberia. In 1866, he participated in the Olekmin-Vitim expedition, which sought an overland route to transport cattle between Chita and the Lena gold mines (Montagu 1955). Kropotkin wrote several scientific articles during these expeditions. Also during this period, he read Darwin's recently published, but not yet translated, *On the Origin of Species*.

Upon his return to St. Petersburg, Kropotkin continued his scientific work, gained membership to the Imperial Geographical Society, and in 1868 was awarded the gold medal for his work on the Olekmin-Vitim expedition. During this time Kropotkin also pursued his interest in radical politics. In 1872, hours after delivering a paper on the origins of the Ice Age, he was arrested for his participation in efforts to popularize revolutionary socialism among workers. While in prison, Kropotkin continued his writing, completing *Investigation of the Ice Age* in 1876. He escaped from prison and fled to England, where he pursued both science and politics: he published several articles in *Nature* and became a leader in the international anarchist movement. He was imprisoned again in France in 1882 and sentenced to five years, but was released in 1886 and returned to England.

Kropotkin continued to write about history, politics, and the natural sciences, and became a regular contributor to the popular journal *The Nineteenth Century*, the principal venue for the development of his mutual aid interpretation of Darwinian theory. Cambridge University offered him a chair in geology in 1896, but he declined because the appointment was contingent on a pledge to abstain from political activity (Todes 1989). He returned to Russia in 1917 after the tsar was deposed, and worked on his final book, *Ethics*, until his death in 1921.

Kropotkin in Siberia

Although Kropotkin's Siberian experience can be likened to Darwin's voyage on the *Beagle*, the ecosystems they encountered could not have been more different. While Darwin's voyage passed through nearly every ecological zone, some of which even resembled the Russian plains, he was most influenced by his experiences in the tropics. "The glories of the vegetation of the tropics rise before my mind at the present time more vividly than anything else," Darwin (1887) wrote in his autobiography. Kropotkin's travels ranged over Siberia, where organisms coped with a wide range of rapidly changing conditions—extreme summer heat and freak blizzards, drought and sudden torrential rainstorms.

Kropotkin's experience was clearly colored by his reading of Darwin. In the first chapter of *Mutual Aid* (1902), he wrote:

> I recollect myself the impression produced upon me by the animal world of Siberia when I explored the Vitim regions in the company of so accomplished a zoologist as my friend Poliakov was. We were both under the fresh impression of the *Origin of Species*, but we vainly looked for the keen competition between animals of the same species which the reading of Darwin's work had prepared us to expect. . . . We saw plenty of adaptation for struggling, very often in common, against the adverse circumstances of the environment, or against various enemies, and Poliakov wrote many a good page upon the mutual dependency of carnivores, ruminants, and rodents in their geographical distribution; we witnessed numbers of facts of mutual support . . . but even in the Amur and Usuri regions, where animal life swarms in abundance, facts of real competition and struggle between higher animals in the same species came very seldom under my notice, though I eagerly searched for them.

Kropotkin wrote that his experience in Siberia influenced his reaction to and understanding of Darwin's theory in four significant ways. First, the harsh environmental conditions emphasized the role of the organism's struggle against abiotic forces. Second, he saw sparse population as the common condition in nature, contradicting the Malthusian aspects of Darwin's theory. Third, where there were large numbers of animals, he was struck by the herds and colonies as cooperative communities struggling against other species and physical hardship. Finally, he observed that under the harshest conditions, where the Darwinian would expect competition to be most severe, leading to a higher level of fitness, the entire group's survival was at risk, and their overall fitness diminished (Todes 1989).

The Siberian experience played a similar role in the development of Kropotkin's ideas about evolution and ecology that Darwin's *Beagle* voyage had in his. Just as Darwin came to doubt the fixity of species, so Kropotkin became skeptical of the importance of intraspecific competition.

Theory of Mutual Aid

Daniel Todes (1989) has described the community of Russian naturalists in which Kropotkin further developed his ideas about mutual aid upon his return from Siberia. The specific event that led Kropotkin to publish his theory was Huxley's 1888 essay "The Struggle for Existence in Human Society." Ranging through natural history, anthropology, political theory, philosophy, and economics, Huxley describes the role that competition has played in human society from prehistoric "savages" up through contemporary Victorian England.

In this essay, which Kropotkin later described as "atrocious," Huxley depictes nature "on about the same level as a gladiators show. . . . [In this case, however, the] spectator has no need to turn his thumbs down as no quarter is given." In the course of the essay, Huxley clearly explains his belief in nature as a zero-sum game. The one natural urge that human society cannot override is the innate urge toward reproduction:

> Let us be under no illusion then. So long as unlimited multiplication goes on, no social organization which has ever been devised, or is likely to be devised, no fiddle-faddling with the distribution of wealth, will deliver the society from the tendency to be destroyed by the reproduction within itself, in its intensest form, of that struggle for existence, the limitation of which is the object of society.

Ultimately, Huxley's call for educational reform and workers' rights appeared quite reasonable, even to the radical Kropotkin. It was the mischaracterization of the state of nature and the argument that flowed from it that Kropotkin so vehemently rejected.

Kropotkin quickly responded to Huxley's article and then spent the next 20 years publishing the developments of his theory in *The Nineteenth Century* (after 1900, published as *The Nineteenth Century and After*). Of this series, the first eight articles dealt primarily with mutual aid in human evolution; these essays were subsequently published as *Mutual Aid: A Factor of Evolution* (1902). Seven additional articles, published between 1905 and 1919, represented Kropotkin's struggle to broaden the scope of Darwinian theory contra Huxley and Weismann in a manner consistent with Darwin's intent.

In "The Theory of Evolution and Mutual Aid," Kropotkin (1910a) presented a developmental history of Darwin's theory. Through analysis of Darwin's correspondence and the changes incorporated into the various editions of the *Origin*, he offered his own theory as the logical conclusion of Darwin's theoretical development. Kropotkin argued that Darwin was initially so conservative with respect to mechanisms other than natural selection because of a simple paternal predilection for his idea, compounded by a real need to differentiate his theory of evolution from those of Lamarck and Chambers.

Kropotkin's argument addressed the apparent tension between his theory and Darwin's, which he explained was a function of Western Darwinists' commitment to the Malthusian doctrine. The shift of emphasis from Malthusian (i.e., individual) competition to one in which the organism was seen as engaging in a constant struggle for existence against environmental forces and other species, allowed an increased role for mutual aid. Citing Darwin's letters (1888), Kropotkin showed that Darwin also responded to the criticism that he had underestimated the importance of the direct action of the environment. "He gradually came, in an indirect way," Kropotkin (1910a) wrote, "to attribute less and less value to the individual struggle inside the species, and to recognise more significance for the associated struggle against the environment."

Kropotkin (1910b) argued that in the course of the struggle against the environment, species were more apt to practice mutual aid, and cooperative species would increase in numbers and outlast their individualistic rivals. In this scenario, natural selection ceases to be "a selection of haphazard variations, but becomes a physiological selection of those individuals, societies and groups which are best capable of meeting the new requirements by new adaptations of their tissues,

organs and habits. It operates largely as a selection of groups of individuals, modified all at once, more or less, in a given direction."

Kropotkin's argument regarding the direct action of the environment led to another important difference between his theory and that of the neo-Darwinians. This was the perceived difficulty for natural selection to explain the establishment of new species working from purely random variation. In essence, Kropotkin argued that variation is not purely random. The work of the biometricians had demonstrated that:

> Whether we take the sizes of the leaves of the same tree, or the stature of several thousand Englishmen at Cambridge University . . . or the contents of sugar in the beetroot, everywhere we find that the laws of variation in organic beings are the same as those with which we are familiar in physical sciences under the name of laws of errors in the theory of probabilities.

Kropotkin then deduced that if, indeed, we see some deviation from a normal distribution in a particular direction, it is the result of some permanently acting cause, in other words, the direct action of the environment. Furthermore, once there is such a cause, it obviates the need for an acute struggle between the individuals of the species to preserve the effects of variation: the acting cause itself will accumulate and increase them in the subsequent generations. Finally, Kropotkin pointed to the role of isolation in speciation as a significant development that had led to his theoretical extrapolation from the early Darwin. As naturalists came to recognize that speciation was often the result of geographical isolation, the importance of intraspecific competition and individual selection was diminished. After quoting passages from Darwin's correspondence with regard to the importance of isolation, Kropotkin asserted:

> Once we admit the successive migrations, in the course of ages, of certain species over several continents (and it seems necessary to admit them, for instance, for the series of ancestors of the wild horse), and once we realise the amount of segregation that ensued, we fully understand the necessary "absence of intermediate forms." And yet it was this absence which so much puzzled Darwin and for which he admitted "extermination" during a severe struggle for life. With isolation, such an extermination is not necessary; and probably it did not take place at all. (Kropotkin 1910a)

Kropotkin clearly felt that with a proper emphasis on the role of isolation, the importance of competition diminished. This was consistent with his own view of nature and with Darwin's original intent.

In his final article (1919), Kropotkin summarized the focus of his papers:

> A mass of researches having been made on the great fundamental question as to the part played by the direct action of the environment, I analysed them in a

> series of articles published in this review during the last seven years. Beginning with the evolution of the conceptions of Darwin himself, and most evolutionists about Natural Selection, I next gave an idea of the observations and experiments by which the modifying powers of a changing physical environment were established beyond doubt. Then I discussed the attempt made by Weismann to prove that these changes could not be inherited and the failure of this attempt. And finally, I examined the experiments that had been made to ascertain how far the changes produced by a modified environment are inherited.

Kropotkin argued that Darwinian theory had been pushed to false extremes by his followers. Again, he cited the correspondence, as well as Darwin's *Variation of Animals and Plants under Domestication* (1868), in support of his interpretation of the true nature of Darwinian theory. The primary conclusion was that the neo-Darwinians were blinded by Malthusian orthodoxy. This led to his second conclusion, that they were committed to a false polarization into Darwinist and Lamarckian camps. Finally, biologists had lost touch with the naturalist tradition and so with nature itself. According to Kropotkin, understanding the role of mutual aid was completely dependent upon field observation of animal behavior in their natural condition. In a letter quoted by Todes (1989), Kropotkin described the proper direction of evolutionary theory as he saw it, returning to Darwin's original intent and modulating the hard stance of Weissman and Huxley:

> This is a theory of evolution which, following Bacon, recognized the importance of Mutual Aid—that is, of the social instinct—for the preservation of the species, and which, with Bacon, saw in it the primordial element of Ethics. . . . This is above all a return to the Darwinism which saw in Evolution a spontaneous result of the forces of Nature, and not, as Weismann and his disciples wished, an evolution predetermined (by the mechanisms of the Universe) by means of a substance possessed of an "immortal" soul—this Hegelian creation of Weismann, his germ plasm. A theory of Evolution finally, [which describes] a physiological evolution of organs [caused] by the new functions which they perform as the organism is placed in new conditions of existence.

Although Kropotkin's ideas had little lasting influence on Western biologists, they did have an impact in Russia. Mark Adams (1968) has argued that the Russian population geneticists were responsible for bridging the gap between the naturalist and experimentalist traditions that had so concerned Kropotkin. "It is significant then," Adams wrote, "that the Russian School is one of the earliest to draw from both traditions in order to clarify the evolutionary process. . . . And by turning the techniques of genetics onto the problems of evolution in a natural setting, Chetverikov did much to heal the unfortunate gap—in effect, by creating experimental population genetics and making evolutionary theory experimental." Adams points up another of the concerns that had struck Kropot-

kin, later emphasized by the Russian geneticists, which is "that the experimental work under Chetverikov's direction, on a naturally occurring *Drosophila* population, led to the development of clear ideas concerning the influence of genetic and *environmental* backgrounds on the fitnesses and effects of genes."

WYNNE-EDWARDS

Vero Copner Wynne-Edwards (1906–1997) was the son of John Roslindale Wynne-Edwards, a canon in the Church of England and headmaster of Leeds Grammar School. He attended Leeds Grammar and Rugby, 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. According to Wynne-Edwards' diary (1985), Huxley was one visitor who lectured "awfully well." Wynne-Edwards left Rugby in 1924, with hopes of Himalayan expeditions studying alpine fauna and flora. The headmaster and his father, however, had more practical plans. The headmaster suggested the study of medicine so that he could act as an expeditionary doctor, and his father suggested further formal study. In the end, Wynne-Edwards entered New College, Oxford, in 1924, to read zoology with Julian Huxley. This relationship lasted only a year, as Huxley accepted the chair of zoology at King's College, London. Huxley's successor was Charles Elton (a former student of Huxley himself), whose influence, according to Wynne-Edwards (1985), was to be much more specific and enduring. Elton, a pioneer of animal ecology and the founder of the Bureau of Animal Population at Oxford University in 1932, is credited as having sparked, after their first tutorial, an interest in population ecology that fueled the rest of Wynne-Edwards' intellectual life.

Wynne-Edwards graduated with first-class honors in zoology in 1927, and became Senior Scholar of New College from 1927 to 1929. His earliest work was in the field of marine zoology; simultaneously, he published several papers on the wintering behavior of starlings. In these articles the earliest strains of Wynne-Edwards' thoughts on dispersion and breeding begin to surface. His 1931 article "The Behaviour of Starlings in Winter," for example, is generally descriptive in nature; however, the discussion of species-level selection and nonbreeding behavior (especially in relation to rapidly increasing population) mark them as topics of particular theoretical interest to Wynne-Edwards. He rejected the explanation, provided by a preceding study, that the increase of the starling population followed the advance of human agriculture in the region that increased the availability of food, pointing out that agricultural development in 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. This early rejection of food supply as the limiting factor in population level foreshadows his later intense debates with David Lack.

Wynne-Edwards in the Field

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 transatlantic observations led to the publication of "On the Habits and Distribution of Birds on the North Atlantic" (1935), which garnered the society's Walker Prize, the first major prize of his young career.

Wynne-Edwards got his inspiration for this award-winning project on his initial voyage to McGill, aboard the Canadian Pacific Liner *Empress of Scotland* (Wynne-Edwards 1985). His ornithological observations on this trip led to the outline of the basic pattern of inshore (coastal), offshore (out to the edge of the continental shelf), and pelagic (deep water) zones of seabird distribution. This transect across the North Atlantic is an important aspect of the development of Wynne-Edwards' thoughts about nature and animal communities. He wrote:

> Nowhere on land, even in the Sahara, the prairies or the steppes of Asia, can such a vast expanse of monotony be found as on the great oceans. Because of the relatively small temperature variation at any point and the unending circulation of their waters, they present a uniformity of conditions unparalleled elsewhere on this earth. Yet it is hardly necessary to state that in spite of this prevailing sameness not all the birds primarily adapted to obtain their livelihood from the sea, even in a restricted area like the North Atlantic, belong to a single ecological community. Fulmars and cormorants, for example, might pass their whole lives without seeing one another, and could only do so at special times and places, for they belong to two communities as distinct as those of forest and fen, and their paths seldom cross. The factors which differentiate one community from another are not by any means understood, but present problems of no small interest. (1935)

The exposure to these environmental conditions contributed to the development of Wynne-Edwards' thinking about the "struggle for existence" and Darwinian selection.

A 1937 expedition to Northern Labrador produced the first clear indications of Wynne-Edwards' later work on group selection. The resulting paper, "Intermittent Breeding of the Fulmar" (1939), marked a transition from purely observational, descriptive, 19th-century-style natural history to an approach more grounded in theory. At the same time, Wynne-Edwards laid the groundwork for later investigation of non-breeding behavior as a mechanism for population regulation. Based on previous observations (his own as well as others), Wynne-Edwards noted that only between one-third and two-fifths of the fulmars present at a particular breeding colony appeared to be engaged in reproduction, a surprising fact requiring explanation. If, consistent with Darwinian theory, individuals were constantly striving to increase their representation in subsequent generations, why were so many of these fulmars not engaged in reproductive activity?

From the 1930s through the 1950s, Wynne-Edwards participated in multiple expeditions in Northern Canada. As the naturalist on the Baird Expedition to Baffin Island in 1950, he devoted 12 weeks to the collection of plants, freshwater and terrestrial animals, and above all, to a study of the breeding birds. In his report on the "Zoology of the Baird Expedition" (1952), Wynne-Edwards observed:

> Competition between individuals for space and nourishment seems commonly to be reduced to a low level among members of the arctic flora and fauna; they live somewhat like weeds, the secret of whose success lies in their ability to exploit transient conditions while they last, in the absence of serious competition. In the Arctic the struggle for existence is overwhelmingly against the physical world, now sufficiently benign, now below the threshold for successful reproduction, and now so violent that life is swept away, after which recolonization alone can restore it.

Here again, a view of nature significantly different from the tropical environments that so influenced Darwin and Wallace is distinctly described.

In 1945, Wynne-Edwards was appointed the Regius Chair of Natural History at the University of Aberdeen. There, his interest in population structure and breeding behavior developed into a full-blown theory of group selection. His earlier work may have been of interest only to a small group of naturalists concerned with the lives of birds, but 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 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."

Theory of Group Selection

Acknowledgment of the shift to population thinking, and publication of *The Natural Regulation of Animal Numbers* (Lack 1954), led to a 1955 article in which Wynne-Edwards began by quoting Lack's assertion that birds reproduce as rapidly as they can, an assessment clearly inconsistent with his own observations. Near the end of "The Dynamics of Animal Populations" (1955a), Wynne-Edwards wrote:

> It is no doubt a heritage of the Darwinian tradition that we tend to focus our attention on the struggle for existence, and the marvelous adaptations of animals for survival. . . . The struggle may sometimes be a desperate one, unsuccessful even for the fittest; but far off in the heart of its domain there may be places where, by contrast, every desirable condition of life seems to be abundantly

> fulfilled. We do not stop to reflect that in this Elysian environment there may be just as great a need of adaptations to curb the increase of numbers . . . and avert the constant threat of over-population . . . and perhaps ruin the resources of the habitat. The hardest struggle must not be identified with the best world, nor with the surest chances of survival.

Wynne-Edwards is once again in line with Kropotkin's view that the fiercest struggle can be a net loss for the group, as even the most fit individuals are damaged as a result.

In his presentation to the 11th International Ornithological Conference, some of Wynne-Edwards' ideas regarding his developing theory were introduced in qualified terms: "It is *theoretically possible* to regulate the numbers in the population by density dependent control of the recruitment rate alone. . . . 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" (1955b). In his discussion 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). The concluding paragraph of this paper marks the first unequivocal statement of Wynne-Edwards' 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 published his theory of group selection in 1959. This article, "The Control of Population Density Through Social Behaviour," presents his clear break with the neo-Darwinian emphasis on natural selection acting at the level of the individual. Wynne-Edwards asserted that most animals, by virtue of their power of movement, play a predominant role in regulating their own population densities. Although he acknowledged the role of food as almost always the critical limiting factor, he maintained that birds were largely successful in regulating their own population densities below starvation levels through social conventions. In this article, Wynne-Edwards also introduced the notion of "epideictic behavior," a term that embraces a large class of social phenomena that appear to have been evolved for the primary purpose of demonstrating population density. (Nearly all of the behavior that Kropotkin described as mutual aid would fall under this category.) Much of the behavior he described, particularly

non-breeding behavior, was interpreted by Wynne-Edwards as altruistic in the sense that the individual sacrificed immediate reproductive success for the long-term benefit of the group.

Wynne-Edwards illustrated his hypothesis by analogy with human behavior. He examined the problem of over-fishing and argued that "under a system of free enterprise, [man] is in grave danger of impairing the resource by taking too big a harvest, depleting the stock, and entering upon a spiral of diminishing returns." The way to avoid this situation, he suggested, was through the conclusion of an agreement, binding participants to limit the catch to the long-term optimum figure. This analogy was generalized as a natural and inherent attribute of the relationship between every kind of hunter and its staple prey. It is easy to understand how this analogy, which suggests very complex intentionality to members of bird populations, would arouse immediate suspicion on the part of naturalists working to further "scientize" natural history and ecological fieldwork.

Wynne-Edwards sketched out how population density acts as a conventional buffer between the animals and over-exploitation of their food supply. He argued that the territory system, in conjunction with social hierarchies or peck order, was capable of imposing a ceiling on population numbers and eliminating direct competition for food. The final paragraph succinctly recapitulates his argument:

> The hypothesis put forward here, therefore, suggests that animals have become adapted, with varying success, to control their own population densities, limiting them at the optimum level—this being the level that offers the best living to the largest number, consistent with safeguarding the food-supply from damage from so-called over fishing. It suggests that the result is achieved by interposing artificial, conventional goals as substitutes for direct competition for food.

Social behavior, especially in the form of conventional competition, was presented as the causal mechanism in the regulation of population density.

Wynne-Edwards' *Animal Dispersion in Relation to Social Behavior* (1962) was the culmination of more than three decades of professional work in natural history, particularly in avian ecology and behavior. The preface offered insights into the development of the work and some warnings about a theory so wide-ranging and unconventional; the author was clearly aware that it would stir controversy. The book was to be presented as "one long argument" linking the subjects of population and behavior, and its structure was designed to contain enough factual evidence to support the theory in each of its widespread ramifications. Wynne-Edwards noted that his new theory was fraught with important philosophical implications. Perhaps not surprisingly, the examination of social behavior of animals provided the clearest indication yet of the "closeness of man's kinship with his fellow animals." Wynne-Edwards' prefatory comments were akin to those of Darwin in the *Origin*, emphasizing a style of argument that reflects his close connection to the naturalist tradition.

Animal Dispersion includes a recapitulation and expansion of Wynne-Edwards' 1959 argument by analogy with the over-fishing example; this analogical argument clearly mimics Darwin's examination of artificial selection as the analog to natural selection in the *Origin*. Here Wynne-Edwards laid out his theory and connected it to previous thought about animal population and social behavior, and he also identified the fundamental differences he perceived to exist between his theory and that of the neo-Darwinians. He asserted that some mechanism must constantly restrain populations, while in the midst of plenty, from overexploiting their resources. He rejected the application of such terms as "free enterprise" and "unchecked competition" to natural populations on observational grounds, and invoked instead the concept of the balance of nature.

> One of our first guiding principles, however is that undisguised contest for food inevitably leads in the end to over-exploitation, so that a conventional goal for competition has to be evolved in its stead; and it is precisely in this—surprising though it might appear at first sight—that social organisation and the primitive seeds of all social behavior have their origin. This is a discovery (if it can be so described) of the greatest importance to the theory. (14)

According to Wynne-Edwards, a society, in its most primitive function, was merely an organization capable of providing conventional competition. The existence of conventional competition diminished direct competition for food or other resources and thereby assured the persistence of the social group through the avoidance of overexploitation.

Wynne-Edwards also took pains to differentiate his own theory from the traditional "Darwinian heritage." He cited the standard interpretation of Darwinian natural selection, which occurs at two levels—the individual (intra-specific) and the species (inter-specific)—and argued that neither of these cover the social adaptations of interest (i.e., non-breeding behavior or deferred maturity). According to Wynne-Edwards, it required a group of individuals to maintain social conventions, and he cited the work of Theodosius Dobzhansky and Sewall Wright as supportive of the notion that social grouping is fundamental to both the evolution and distribution of populations. Wynne-Edwards also attempted to spell out the function of group selection:

> Evolution at this level can be ascribed, therefore, to what is here termed group-selection—still an intraspecific 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 the 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. (20)

Thus, an important part of the fundamental reassessment that Wynne-Edwards advocated was a broadening of the terms "social behavior" and "social group." While previously biologists had limited the use of these terms to a very limited list of species, especially the social insects and some higher animals, Wynne-Edwards pushed for an understanding of sociality that included nearly every species of the animal kingdom.

The remainder of *Animal Dispersion* is the catalogue of facts promised in the preface. Like Darwin, Wynne-Edwards rarely cites others with regard to theory or interpretation, but he freely introduces their observations and fieldwork in support of his hypothesis. For example, throughout the text, Wynne-Edwards reinterprets Lack's field observations and data in support of his own theory.

The fate of *Animal Dispersion* is better known than is the history of Wynne-Edwards' development of group selection theory. In 1966, George C. Williams published *Adaptation and Natural Selection*, a critical response that effectively prevented any consideration of the theory of group selection for nearly a decade. In the mid-1970s, however, Michael Wade and David Sloan Wilson revised and revived the theory of group selection, and the debate over its role in evolutionary processes persists (Sober and Wilson 1998; Wade 1976, 1977, 1978, 2001; Wilson 1975, 1977, 1980, 1983, 2000; Wilson and Sober 1994). Wynne-Edwards continued to publish, and wrote another book-length treatment of group selection in 1986, however, this book was considered merely a repeat of the 1962 work and garnered little interest. Wynne-Edwards' last article, "A Rationale for Group Selection" (1993), clearly illustrates a continued commitment to group selection and recalls the sympathetic memory of the theory of mutual aid.

> Group adaptations such as programmed dispersal have evolved through the survival of the fittest groups. Groups, like human teams, consist of individuals whose quality is all important: groups that have the highest proportion of efficient, cooperative members and the lowest proportion of incompetent or selfish ones tend to survive best.

CONCLUSION

How should one view nature in light of evolutionary theory? Where Huxley, Weismann, and Lack see the struggle of each against all to procure resources to provide for themselves, Kropotkin and Wynne-Edwards are witness to a cooperative struggle by social groups against the environment. Where Huxley, Weismann, and Lack see harsh elements increasing intraspecific competition, Kropotkin and Wynne-Edwards observe a state of depleted resources that threatens the survival of the entire group.

Despite their differences, both groups lay claim to the Darwinian heritage. Kropotkin's Siberian experience, the Russian naturalist tradition, and even his anarchist politics clearly influenced his non-Malthusian view of nature. These

elements, compounded by the state of Darwinian theory in the early 20th century, provided ample support and theoretical space within which to develop his theory.

For Wynne-Edwards, too, the impact of his field experience led to his theory of group selection, although the initial influence of the modern synthesis and an emphasis on population thinking may also have contributed to these ideas. The hardening of the synthesis around the mechanism of natural selection acting at the level of the individual, however, did not bode well for the long-term survival of his theory.

The analysis of these two theories may help to illuminate the broader context of the development of Darwin's theory. Because the debate over the validity of group selection and its role in the evolutionary process continues, historians have an opportunity to contribute to ongoing discussion of the hierarchical nature of evolutionary theory. Furthermore, this history can be useful to students of biology: many of the common misunderstandings of evolution are a direct result of the misapplication of natural selection at the level of the individual.

References

Adams, M. B. 1968. The founding of population genetics: Contributions of the Chetverikov school, 1924–1934. *J Hist Biol* 1(1):23–39.

Borrello, M. E. 2002. Vero Copner Wynne-Edwards and the history of group selection theory. Ph.D. diss., Indiana Univ.

Butler, S. 1879. *Evolution, old and new*. London: Harwick and Bogue.

Darwin, C. 1859. *On the origin of species*. London: John Murray. Rpt. Cambridge: Harvard Univ. Press, 1964.

Darwin, C. 1868. *The variation of animals and plants under domestication*. 2 vols. London: John Murray.

Darwin, C. 1887. *The autobiography of Charles Darwin 1809–1882*. Ed. N. Barlow. New York: Norton.

Darwin, C. 1888. *Life and letters of Charles Darwin*. Ed. F. Darwin. London: John Murray.

Headley, F. W. 1901. *Problems of evolution*. New York: Thomas Y. Crowell.

Huxley, T. H. 1888. The struggle for existence in human society. In *Evolution and ethics*. London: Macmillan, 1894.

Kellogg, V. 1908. *Darwinism today: A discussion of present-day criticism of the Darwinian selection theories*. New York: Henry Holt.

Kropotkin, P. A. 1902. *Mutual aid: A factor of evolution*. Rpt. Boston: Extending Horizons Books, 1955.

Kropotkin, P. A. 1910a. The theory of evolution and mutual aid. *Nineteenth Century* 67: 86–107.

Kropotkin, P. A. 1910b. The direct action of environment on plants. *Nineteenth Century* 68:58–77.

Kropotkin, P. A. 1919. The direct action of the environment and evolution. *Nineteenth Century* 85:70–89.

Lack, D. 1954. *The natural regulation of animal numbers*. Oxford: Oxford Univ. Press.

Montagu, A. 1955. Introduction. *Mutual aid: A factor of evolution*, by P. Kropotkin. Boston: Extending Horizons Books.

Mayr, E., and W. B. Provine, eds. 1980. *The evolutionary synthesis: Perspectives on the unification of biology*. Cambridge: Harvard Univ. Press.

Smocovitis, V. B. 1996. *Unifying biology: The evolutionary synthesis and evolutionary biology*. Princeton: Princeton Univ. Press.

Sober, E., and D. S. Wilson. 1998. *Unto others: The evolution and psychology of unselfish behavior*. Cambridge: Harvard Univ. Press.

Thomson, J. A. 1925. *Concerning evolution*. New Haven: Yale Univ. Press.

Todes, D. P. 1989. *Darwin without Malthus: The struggle for existence in Russian evolutionary thought*, ed. R. Burian et al. New York: Oxford Univ. Press.

Wade, M. J. 1976. Group selection among laboratory populations of Tribolium. *Proc Natl Acad Sci USA* 73:4604–4607.

Wade, M. J. 1977. Experimental study of group selection. *Evolution* 31:134–53.

Wade, M. J. 1978. A critical review of the models of group selection. *Q Rev Biol* 53:101–14.

Wade, M. J. 2001. Group selection: The adaptive process in genetically subdivided populations. In *Encyclopedia of genetics*, ed. S. Brenner and J. H. Miller. San Diego: Academic Press.

Wallace, A. R. 1889. *Darwinism*. 2nd ed. London: Macmillan, 1923.

Weismann, A. 1889. *Essays upon heredity and kindred biological problems*. Oxford: Clarendon Press.

Weismann, A. 1904. *The evolution theory*. London: Edward Arnold.

Williams, G. C. 1966. *Adaptation and natural selection*. Oxford: Oxford Univ. Press.

Wilson, D. S. 1975. A theory of group selection. *Proc Natl Acad Sci USA* 72:143–46.

Wilson, D. S. 1977. Structured demes and the evolution of group-advantageous traits. *Am Naturalist* 111(977):157–85.

Wilson, D. S. 1980. *The natural selection of populations and communities*. Menlo Park, CA: Benjamin/Cummings.

Wilson, D. S. 1983. The group selection controversy: History and current status. *Annu Rev Ecol Systematics* 14:159–87.

Wilson, D. S. 2000. Cooperation, altruism and multilevel selection. In *Evolutionary ecology: Synthesis and perspectives*, ed. C. W. Fox, D. A. Roff, and D. J. Fairbairn. Oxford: Oxford Univ. Press.

Wilson, D. S., and E. Sober. 1994. Reintroducing group selection to the human behavioral sciences. *Behav Brain Sci* 17:585–654.

Wynne-Edwards, V. C. 1931. The behaviour of starlings in winter. *British Birds* 24:346–53.

Wynne-Edwards, V. C. 1935. On the habits and distribution of birds on the North Atlantic. *Proc Boston Soc Natl Hist* 40(4):233–346.

Wynne-Edwards, V. C. 1939. Intermittent breeding of the fulmar (*Fulmarus glacialis*), with some general observations on non-breeding in sea-birds. *Proc Zoolog Soc London* 109: 127–32.

Wynne-Edwards, V. C. 1948. The nature of subspecies. *Scottish Naturalist* 60:195–208.

Wynne-Edwards, V. C. 1952. Zoology of the Baird expedition. *Auk* 69(4):353–91.

Wynne-Edwards, V. C. 1955a. The dynamics of animal populations. *Discovery* (Oct.):433–36.

Wynne-Edwards, V. C. 1955b. Low reproductive rates in birds, especially sea-birds. *Acta 11th Int Congress Ornithol* 540–47.
Wynne-Edwards, V. C. 1959. The control of population density through social behaviour: A hypothesis. *Ibis* 101:436–41.
Wynne-Edwards, V. C. 1962. *Animal dispersion in relation to social behavior*. Edinburgh: Oliver and Boyd.
Wynne-Edwards, V. C. 1985. Backstage and upstage with Animal dispersion. In *Leaders in the study of animal behavior: Autobiographical perspectives*, ed. D. Dewsbury. London: Associated University Presses.
Wynne-Edwards, V. C. 1986. *Evolution through group selection*. Oxford: Blackwell Scientific.
Wynne-Edwards, V. C. 1993. A rationale for group selection. *J Theor Biol* 162:1–22.