Hist. Sci., xv (1977), 189-215

A BIBLIOGRAPHICAL GUIDE TO THE HISTORY OF GENERAL ECOLOGY AND POPULATION ECOLOGY

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The word 'ecology' has come to mean, for the general public, conservation, preservation, and pollution control. These activities, to the extent that they are scientifically informed, are actually applied ecology. Those interested in discussions of this literature will find useful the critical reviews by Gordon B. Dodds, Michael J. Lacey, and Donald Fleming, Ronald J. Fahl's bibliography, and also the new historical journal, *Environmental review*.[1] The scope of these reviews, and the literature discussed, is largely, but not entirely, confined to America.

The present survey of literature is limited to the science itself, which was first defined by Ernst Haeckel:

> By ecology we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to its inorganic and to its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact—in a word, ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence.[2]

As Haeckel went on to say, ecological knowledge had accumulated under the general heading of "natural history". The ecological sciences were formally organized late in the nineteenth century.

The natural history literature from Antiquity to the end of the nineteenth century is voluminous, but mostly descriptive. Finding theoretically significant discussions is often time-consuming. No doubt in the past this inhibited the development of ecology, and, in the present, the writing of its history.

GENERAL ECOLOGY

There is no general history of ecology that encompasses both pre-twentieth century natural history and modern ecology. For the period from Antiquity to about 1800 there is a very useful detailed history of environmental studies by Clarence J. Glacken, *Traces on the Rhodian shore*.[3] His perspective is that of the historical geographer. There are three ideas which are themes for his study: a designed earth, environmental influences, and man as a geographic agent. Both Glacken's discussion and references will provide a useful beginning for investigations into ecological ideas before 1800.

For the period since Darwin and Haeckel, there is coverage in some detail in a collection of *Essays on the history of ecology* by ten scholars, written in Russian with English summaries.[4] The scope is broad, there are useful references, and it is desirable to have the volume translated into a major West European language.

Edward J. Kormondy has compiled a set of papers, *Readings in ecology* (Englewood Cliffs, N.J., 1965), which encompasses the entire history of ecology, though not evenly, and some of the selections are abridged. Antiquity is represented only by Theophrastus, and the eighteenth century only by Réaumur, Linnaeus, and Malthus, with no representatives for the time between these periods. The six selections from the nineteenth century hardly do justice to the contributions made in that century, but the coverage for the period of formally organized ecology is representative. Selections are arranged under the headings of "The physical and chemical environment", "The study of populations", "The study of communities", and "The concept of the ecosystem". This book was compiled for student use and does provide a convenient source book for that purpose.

There is a comprehensive survey of animal ecology from Antiquity to 1940 in two chapters by W. C. Allee, "Ecological background and growth before 1900", and Thomas Park, "First four decades of the twentieth century", in a compendium published in 1949, *Principles of animal ecology*.[5] After almost three decades these chapters retain their value as a reference because of their broad coverage and many citations of primary sources. Charles C. Adams's *Guide to the study of animal ecology* (New York, 1913; 1977) is as valuable to the historian today as it was to the ecologist when published. Its historical value lies in its annotated subject bibliographies, which provide a reliable guide to the literature from around 1870 to 1913, with some earlier citations. Limnology, oceanography, and plant ecology are also represented.

There is no comprehensive survey of the history of plant ecology, but for the period from Antiquity to about 1850 Charles A. Browne's *A source book of agricultural chemistry* provides good indication of the progress in understanding of the relationship of plants to soil and the atmosphere. Several plant ecologists have written progress reports for the formally organized period of ecology.[6]

H. H. Trass has very recently published (in Russian) *Geobotany*:

History and contemporary trends of development, which provides a comprehensive survey of much of plant ecology. Although he does discuss Linnaeus, coverage is otherwise confined to the nineteenth and twentieth centuries. His decision to organize the chapters according to geographical regions rather than chronologically is not ideal from the standpoint of history of science, but it does have some logical justification, because regional schools of plant ecology have developed. This book, which it is also desirable to have translated into a West European language, should be consulted by those interested in plant ecology even if they do not read Russian, because it has an extensive bibliography of titles in western languages, a table of contents in English, and the best collection of portraits of ecologists of which I am aware. These fortythree portraits plus two group pictures have names given only in Russian, but for most of them life dates are also included, which assists with identification those who do not read Russian. Jack Major is preparing a review of Trass's *Geobotany* for *Ecology.* The surveys of writings on plant succession by Clements (1916), plant sociology by Du Rietz (1921), and classification of natural communities by Whittaker (1962) also provide useful general information concerning the history of plant ecology.[7]

The history of ecology in America is surveyed in two articles by myself and Robert P. McIntosh.[8] We attempted to relate developments in America both to European developments in ecology and also to the history of American culture. References to both primary and secondary sources are extensive, and our articles may be of value not only to students of ecology in America, but also to others who wish to compare American progress with that in other countries. Two articles in the Russian volume cited above (ref.4) are on the progress of ecology in the USSR. There is also an article by the eminent ecologist A. G. Tansley on "The early history of modern plant ecology in Britain", which takes some note of the work of ecologists in other countries as well. The period discussed is 1896 to 1917. Pearsall and Salisbury have more recently surveyed the development of British ecology.[9]

Drawing upon the advice of the historically oriented plant ecologist Robert P. McIntosh and animal ecologist John Lussenhop, I have assembled for republication a series of fiftyeight volumes of ecological classics and historical studies relating to ecology. The earliest works represented are Leeuwenhoek's *Select works* and John Ray's *Wisdom of God manifested in the Creation.* For the most part, the collection stops around 1930. It includes important primary sources from plant and animal ecology, oceanography, and limnology. Most of the works are in English, with a few in French and German. Although our belief in choosing them is that they are among the most significant for the general history of ecology, there are important relevant works—several by Darwin, for example—

which are omitted because they are already reprinted. Some of the volumes in the collection are papers compiled on particular topics. One volume, *History of American ecology*, reprints the above-mentioned papers on this subject by myself and McIntosh and also papers on limnology by David G. Frey and on plant ecology by E. Lucy Braun, R. H. Whittaker, McIntosh, and Ronald Tobey. The Arno Press brochure describing this collection provides an overview of literature important for the history of ecology.

Adequate studies on the contributions of individual ecologists are few. There are full biographies on Leeuwenhoek, Ray, Réaumur, Linnaeus, Buffon, Pehr Kalm, Gilbert White, Humboldt, Edward Forbes, Charles Darwin, Ernst Haeckel, and Edward A. Birge, but not all the biographies devote much attention to ecological contributions. Sellery's biography of Birge sets a welcomed example of including a chapter on Birge's contributions to limnology written by a limnologist.[10] All of the above men are included in the *Dictionary of scientific biography* (15 vols, New York, 1970-76), but even those accounts do not always provide adequate coverage of ecological contributions. Representation of ecologists in the *DSB* is moderate. Besides those named above, there are articles on Frederick (not Fritz, as listed) S. Bodenheimer, Charles E. Bessey, Richard Bradley, Frederic E. Clements, Augustin-Pyramus de Candolle, Alphonse de Candolle, Stephen A. Forbes, François A. Forel, Victor Henson, Leland O. Howard, Chancey Juday, John H. Lovell, Karl Möbius, John Murray, Andreas F. W. Schimper, Karl G. Semper, Göran Wahlenberg, J. Eugenius Warming, and Hewett C. Watson. But omitted are Charles C. Adams, John M. Coulter, William S. Cooper, Henry C. Cowles, Oscar Drude, William Derham, Gustaf E. DuRietz, Henry A. Gleason, August Grisebach, John W. Harshberger, Anton Kerner, Hermann Müller, Charles V. Riley, Christen Raunkiaer, Victor E. Shelford, and J. E. Weaver.

Apparently useful studies on ecologists often turn out to be meagre. For example, Edith Clements received a Ph.D. in botany under her husband, but her book on life with one of America's leading plant ecologists is little more than a bland travelogue. Only slightly more can be said for the autobiographies by Harshberger, Howard, and Pearse, though Harshberger's at least contains his bibliography. Fortunately, Bodenheimer's autobiography contains an excellent summary of his contributions to ecology.[11]

Detailed ecological observations were first made late in the seventeenth century by naturalists such as Leeuwenhoek and Ray, but Carl Linnaeus apparently was the first naturalist who realized the need for a coherent ecological science. He wrote an important essay, *Oeconomia naturae* (1749), which provided an outline for such a science. His "economy of nature" was a concept which had come down from Antiquity, more commonly known at present under the name "balance of nature". In the eighteenth century this concept was a useful basis around which to organize an ecological science. However, Linnaean systematics attracted more attention and overshadowed his ecological interests. Thus, his ecology did not flourish, but neither was it entirely overlooked.

His ecological writings are not long, but fairly numerous, and his bibliography is complex. One needs to know, in the first place, that many of his important essays were defended as theses for degrees by his students, and then published under the student's name.[12] For example, the essay on the economy of nature: *Specimen academicum de oeconomia naturae,* quod Praeside Carolo Linnaeo, submittit I. J. Biberg (Upsala, 1749). These studies, whether appearing under Linnaeus's own or his students' names, were collected and published under the title *Amoenitates academicae* (10 vols, 1749–90). Some of the most ecologically significant were translated into English in the eighteenth century, and five of these into French recently. In his introduction to the French translation, Camille Limoges has discussed a model of Linnaeus's concept of the economy of nature that seems to me to be more complex than what Linnaeus had in mind.[13] Because of the complexity and abundance of Linnaean literature, a bibliographical guide is essential. There have been several published, of which Basil H. Soulsby's is the standard one.[14]

Linnaeus stimulated interest in phenology by publishing his *Vernatio arborum* (1753) and *Calandarium florae* (1756). A half century later, Benjamin Smith Barton urged the importance of such data, believing that "calendars of flora" provided a means for collecting what is now called ecological data. Another half century later, Henry David Thoreau still thought that phenology could form the foundation for what is now called ecology.[15]

Phenology was too narrow a foundation for a comprehensive science of ecology, but shortly after Barton published his discussion, Alexander von Humboldt began publishing his phytogeographical works. Humboldt had a strong interest in ecological investigations, but generally he managed to pursue them from his orientation as a geographer. His program of research was extremely ambitious, and his writings were responsible for awakening ecological interests in most of the naturalists of the first half of the nineteenth century. In 1864 the American George Perkins Marsh explicitly proposed that room be made within geography for the study of plants and animals in relation to their surroundings.[16]

Buffon, a contemporary of Linnaeus, was the other leading naturalist of the eighteenth century. He also developed an important ecological perspective which he expressed in his writings on the natural history of mammals. Although he did not urge the development of a new ecological science,[17] his writings undoubtedly influenced Isidore Geoffroy Saint-

Hilaire. The young Geoffroy Saint-Hilaire was no doubt also very familiar with the writings of Humboldt and of his father, Étienne Geoffroy Saint-Hilaire. In 1830 Isidore began lecturing on "the interrelations of animal species and their relations with the environment".[18] These lectures were favourably received, and it would be interesting to know more about them, their background and influence. In his *Histoire naturelle générale des règnes organiques, principalement étude chez l'homme et les animaux* (3 vols, 1854–62) he described the ecological science which he had in mind under the name "ethologie", which in 1902 William M. Wheeler thought preferable to the term "oecology".[19]

Geoffroy Saint-Hilaire's perspective was advanced by Espinas,[20] but a more fundamental new direction for the ecological perspective came from Charles Darwin's theory of evolution by natural selection. Although Darwin himself took no direct steps to define and organize an ecological science, he was indirectly responsible for this occurrence. His own ecological perspective came from reading Humboldt, Lyell, and Linnaeus (in that order).[21] Ernst Haeckel, who in 1866 coined the term 'oecologie' and defined the science, realized that Darwin's theory of evolution by natural selection pointed to the importance of understanding the "relations of the organism to the environment including, in the broad sense, all the 'conditions of existence' ".[22] Darwin's theory displaced Linnaeus's economy of nature as the foundation of ecological science, though Darwin himself seems not to have fully realized the incompatibility of the two concepts.[23]

Although Haeckel has received recognition for appreciating the need for an ecological science, for coining the term 'oecologie' and providing a useful definition of it,[24] he has not generally received high marks as an ecologist himself. Stauffer and Lussenhop have examined his criticisms of the findings of the capable zoologist Victor Hensen and have both concluded that Haeckel's negative judgements of Hensen's quantitative methods and conclusions were ill founded.[25] Nevertheless, Lussenhop admits that difficulties remained with Hensen's methods, and Haeckel's own plankton studies which were the basis of his criticisms have not been evaluated by historians of ecology.[26] It is clear that, contrary to some published claims, Haeckel did have a real interest in ecology. In the controversy with Hensen he at the very least performed the valuable gadfly function of demanding greater accuracy in data and methodology from plankton investigators.

Because of Haeckel's role in founding ecology as a formal science, historians of ecology should take note of his position in the history of science in general. On the one hand, he was an imaginative, sometimes brilliant, student of morphology and phylogeny. On the other hand, he was concerned with the public dissemination of information concerning the implications of evolutionary biology for religion, philosophy, and social policy. This latter concern, which is commendable when pursued with scholarly caution and objectivity, was in Haeckel's case marred by a most unsavory nationalism, militarism, and racism. Gasman has recently claimed that Haeckel's ideological distortions of Darwinism provided an important foundation for Nazism. While one reviewer has expressed skepticism that Haeckel's *Die Welträtsel* was as influential as Gasman believes, the fact that Haeckel distorted scientific knowledge for unworthy ideological reasons seems clear.[27] Historians of ecology will want to give Haeckel his due by fully clarifying his positive contributions to ecology, but without glossing over his negative contributions either in science or in his writings for the public.

In 1959 Oehser pointed out that, in *The correspondence of Henry David Thoreau* (1958), Thoreau is quoted as having written on 1 January 1858: "Mr Hoar is still in Concord, attending to Botany, Ecology, &c with a view to make his future residence in foreign parts more truly profitable to him." This alleged use of the word ecology was eight years before Haeckel was assumed to have first coined the term. Oehser's discovery has been widely repeated in print, even being included in the 1972 supplement to the *Oxford English dictionary.* This in spite of the fact that in 1965 one of the editors of *The correspondence of Henry David Thoreau,* Walter Harding, took another look at the manuscript and concluded that the word that Thoreau wrote was "Geology", not "Ecology".[28]

In the last decades of the nineteenth century a single science of ecology did not emerge—it is arguable that it never has—but rather the sciences of oceanography, limnology, plant ecology, and animal ecology began to emerge. There is, nevertheless, a common outlook and a common body of ecological ideas that these sciences share. Although Haeckel was a zoologist and defined ecology in terms of animal ecology, his name was first taken up and developed by plant ecologists. First to use the word in the title of a book was Hans Reiter, in his *Die Consolidation der Physiognomik als Versuch einer Oekologie der Gewaechse. Mit einem Anhang: Das System der Erdkunde* (Graz, 1885). It would be interesting to know the development and content of Reiter's ideas and their influence. The British zoologist Burdon-Sanderson and the American botanist Louis Hermann Pammel both used the term 'ecology' in their published writings in 1893, and the American zoologist Stephen A. Forbes used it in 1895.[29] However, Eugen Warming deserves a substantial amount of the credit for having established the general usage of the term 'ecology' and the perspective that goes with it when he published his *Plantesamfund: Grundtraek af den ökologiske Plantegeografi* (1895; German transl., 1896).[30]

An important milestone in the maturing of a science is the establishment of societies, journals, and other institutions relating to that science.

Tansley's historical essay provides a little of this kind of information for ecology in Britain, and Robert L. Burgess is presently studying the history of the Ecological Society of America.[31] It would be useful to have similar studies on other countries as an indication of the progress of the science worldwide.

POPULATION ECOLOGY

Although population ecology only achieved prominence in the second quarter of the twentieth century, its roots go back to the beginnings of as early as 707 BC, and Babylonian records may be even earlier.[32] The earliest significant interpretations of population data are from Herodotus, and the Aristotelian writings contain the ingredients for an impressive science of population biology. Those ingredients were not, however, effectively mixed.[33] Herodotus pointed out the correlation between the ecological role of a species as a predator or prey and its reproductive rate, whereas the Aristotelians preferred to emphasize the correlation between the number of offspring and size of the species. These potentially conflicting interpretations were not, however, debated.

The next major contribution to population biology came when the mathematician Leonardo Fibonacci asked in his *Liber abbaci* (1202; 2nd ed., 1228) how many pairs of rabbits could be produced from one pair in one year, given that rabbits mature in one month and that each pair produces one pair per month? Although his data were chosen for mathematical convenience rather than being derived from observation, this was the first demonstrated calculation of the rate of increase for a species.[34] The next such effort known to me was Denis Petau's attempt in 1627 to calculate the possible rate at which the world had been populated after the flood of Noah. This was the first mathematical investigation into human demography. Sir Thomas Browne (1646), John Graunt (1662), and Sir Matthew Hale (1677) were among the other early speculators on this problem. Both Browne and Hale attempted to strengthen their case by appealing to data on the rates at which animal populations can increase.[35]

Graunt founded demography and statistics with the publication of his *Natural and political observations . . . made upon the bills of mortality* (London, 1662). His discovery of the statistical regularity of the occurrence of the sex ratio and his data on the life expectancy of people at different ages were potentially applicable to animal populations as well. He also showed some interest in animal demography by reporting to the Royal Society on the growth in length of salmon and the rate of population increase of carp.[36]

Antoni van Leeuwenhoek shortly thereafter began sending his microscopic observations to the Royal Society of London. His statement in 1676 that he had observed several thousand animalcules in a single drop of water was met with incredulity. He was thus stimulated to devise a method of counting them. He later used his technique to estimate the numbers of sperm and eggs in fish, crabs, and other animals. Still later, he calculated on the basis of observations the rates of increase of mice and various insects. These quantitative studies were the most extensive that had ever been made upon animal populations, and Leeuwenhoek must be considered an important founder of population ecology.[37]

His contemporary, Denis Dobart, a French botanist, made somewhat similar calculations on the lifetime seed production of an elm tree in 1700, which Richard Bradley translated into English.[38] During the eighteenth century William Derham (1713) and Buffon (1749 and later) both wrote on human as well as animal populations, thereby advancing both subjects. Other notable naturalists of the century, including Réaumur and Linnaeus, also made useful contributions to the stock of information on population biology.[39]

The main theory applied to this information was the balance of nature (discussed in the following section). Among the important questions relating to population biology were spontaneous generation[40] and the possibility of the extinction of species.[41] Leeuwenhoek had published evidence that the knowledge of life histories of insect pests might help control their population. Outbreaks of insect plagues in crops or forests often led to interest in the relationship between insect numbers and environmental conditions.[42]

Around the beginning of the nineteenth century Alexander von Humboldt wrote on both animal and human populations as part of his extensive survey of both the natural and human resources of Latin America. He was interested in the populations of domestic cattle as well as wild edible turtles, because he saw the necessity of controlling the harvest of both. Probably every naturalist in the first half of the nineteenth century read Humboldt's *Personal narrative* of his travels, and some of them picked up an interest in population biology. Although Humboldt read and recommended Malthus's *Essay on the principle of population,* he seems to have had reservations about Malthus's ideas. Population pressure and the resulting competition played no role in Humboldt's thinking.[43]

Before the nineteenth century one can find interesting isolated observations on competition, but competition was not clearly distinguished from predation. Malthus did not clarify this situation, merely stating that the populations of plants and animals, unlike man's, are held stable by natural checks. Augustin Pyramus de Candolle was apparently the first to realize that population pressure and competition might be important for the geographical spread of plant species (1820), and he may have got the idea after he talked with Malthus in 1816. Charles Lyell, however, deserved the credit for having developed so well de Candolle's idea to explain both the spread and extinction of species.[44] Although virtually all of Lyell's population data came from the literature, and although he lapsed a few times into simplistic explanations, the discussion of population ecology in vol. ii of his *Principles of geology* (1832) was the best account before Darwin. It is clear from Lyell's references that his thinking on the subject was indebted to Linnaeus, Humboldt, and de Candolle.

Darwin's theory of evolution was built upon the facts that all species produce varying offspring and more of them than can survive, and upon the assumption that this leads to a struggle for existence, with only the fitter surviving. In Lyell's discussion population ecology had become more significant for biology than it had been before, but Darwin made it a central part of a scientific revolution. It is therefore of interest to know the influences upon his thinking, the content and evaluation of his writing, and his influence concerning population ecology.

Darwin's letters, notebooks, his *Journal of researches* (1839), and the three manuscript versions of the work that in 1859 became *The origin of species* provide extensive evidence for the development of his thoughts.[45] It seems clear that Humboldt's *Personal narrative* of his travels in Latin America awakened Darwin's interest in population biology before the voyage of the *Beagle,* and that Lyell's *Principles of geology* had shown Darwin in 1832 much of the ecological significance of population pressure. Darwin read, probably on Humboldt's recommendation, Malthus's *Essay on the principle of population* on 28 September 1838.[46] He then realized the important role that population pressure must play in the change of species. Around 1876 he remembered this aspect of the development of his theory as follows:

> In October 1838, that is, fifteen months after I had begun my systematic enquiry, I happened to read for amusement Malthus on *Population,* and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species. Here, then, I had at last got a theory by which to work. . . .[47]

There has been much discussion about the precise debt which Darwin owed to Malthus,[48] and this is relevant to the history of population ecology and the history of the theory of competition in nature.

No less controversial is the evaluation of what Malthus himself contributed to population biology. His main positive contribution was simply calling attention to the fact that population tends to grow faster than the food supply. His famous argument of the geometric increase of population *vs* the arithmetic increase of food was poorly documented and misleading. He did not develop any new mathematical description of population phenomena.[49] The hypothesis which he developed, he confined to man and did not apply to nature.

The origin of species is, of course, about evolution, and not primarily about population biology. It does not, therefore, contain a systematic survey of the latter. Andrewartha and Birch have observed that "Darwin based his argument on rate of increase ($r=b-d$) but most of his examples referred to the influence of environment on death rate".[50] Darwin did explain the importance of population dynamics for evolution, particularly in ch. 4 on natural selection and in chs 11 and 12 on geographical distribution (chs 12 and 13 in 6th edition).

Perhaps because Darwin only used population biology as a supporting argument, it does not appear that the *Origin* stimulated during the following few decades many studies on the subject. Nevertheless, Andrewartha and Birch continue: "Most of the theories that have emerged during the first half of the twentieth century have reflected Darwin's emphasis on survival rate." A similar claim can be made for competition theory: Darwin made fundamental contributions to the subject; there was a long time lag before further research was undertaken; but when ecologists began to study the subject again, they picked up where Darwin left it.[51]

The development of population biology from 1860 to 1895 is poorly known. There may be little to know. There is a continuous development of human demography and statistics throughout the eighteenth and nineteenth centuries,[52] and some biologists in the nineteenth century may have absorbed some of this knowledge. Allee's discussion gives that impression, but without demonstrating it.[53] What seems more likely is that, with the increasing quantification of other sciences and the increasing sophistication of mathematics, biologists who studied mathematics and other sciences learned to apply mathematical reasoning to biological problems.[54] That this was the case for Mendel seems well established.[55] His contemporary, Francis Galton, who was one of the founders of biometry, was fond of mathematics as a student. His biographer, Karl Pearson, had the impression that Galton simply brought a fertile mathematical mind to the investigation of a wide variety of biological problems, and that he was not heavily indebted to prior investigators when developing mathematical analyses of the problems he studied.[56] The other biometricians who associated with Galton, the mathematician Pearson and the zoologist Walter F. R. Weldon, were both attracted to the subject by reading Galton's *Natural inheritance* (1889).[57]

The prominent botanist Carl Nägeli in 1874 published an original study on plant competition that was indeed stimulated by Darwin's theory. For this study Nägeli developed mathematical descriptions of the frequency of the competing forms. Unfortunately, this promising start was as uninfluential as Mendel's paper on heredity.[58] The German zoologist Victor Hensen developed sampling techniques to estimate the numbers of earthworms in a given area of land (1877) and the numbers of fish eggs and plankton in the Baltic Sea and Atlantic Ocean (1884–1912).[59] His controversy with Haeckel over the validity of his sampling techniques is discussed above. The French naturalists Bellevoye and Laurent (1897) and Marchal (1897) developed mathematical descriptions of insect population dynamics.[60] If there is any continuity of influence among these diverse efforts, it has yet to be demonstrated.

The effort to describe mathematically the rate of infection in epidemic diseases began, according to Ronald Ross, with William Farr (1866), and there is a line of influence from him to G. H. Evans (1873–74) and John Brownlee (1906–15). Presumably, Ross benefited in some way from this tradition in his own mathematical models of malaria and other epidemics (1911–17), though his historical preface stressed the difference between his work and that of these predecessors rather than the similarity. Ross's work, in turn, provided the starting point for the biomathematician Alfred J. Lotka's own studies in mathematical epidemiology.[61]

Mathematical studies of biological problems had become significant enough by 1901 for Karl Pearson and Francis Galton to found the successful journal *Biometrika*. During the first two decades of the twentieth century various biologists applied statistics to estimating the numbers of organisms in aquatic or terrestrial areas, but it was not until the 1920s that there were significant new advances in the mathematical descriptions of population dynamics. A movement in this direction was led in America by Lotka and Raymond Pearl and in Italy by Vito Volterra. Both Lotka and Volterra were trained in physics and mathematics and then became interested in the quantitative analysis of biological problems. Pearl was a zoologist whose interest in population analysis developed while studying under Pearson. It was due largely to their work and leadership that statistical techniques from demography were applied to animal populations and the beginnings were made toward developing new mathematical approaches for animal demography.[62] William Streifer's review of models in population ecology is to some extent historically organized and therefore is a valuable assistance in putting this subject into perspective.[63]

From 1907 to 1917 Pearl was head of the department of biology at the Maine Agricultural Experiment Station, where he conducted poultry breeding experiments. In 1918 he went to Johns Hopkins University and organized a department and laboratory of statistics for biology and medicine. There, in 1921, he began with Sylvia L. Parker a long series of experiments on the duration of life of *Drosophila melanogaster*, the familiar fruit fly of genetics studies. Their pioneering studies established both demographic and genetic properties of the experimental populations. Their work must be viewed, therefore, as the beginning of the interaction between population genetics and population ecology. Furthermore, their experiments set the example for the experimental investigation of population ecology.[64]

In 1928 Royal N. Chapman adopted the experimental approach to investigate the environmental resistance to population increase, using the flour beetle, *Tribolium confusum*. Thomas Park, in turn, began to study the population of this species in the laboratory, and he has been responsible for much of the American interest in this approach. The Russian biologist G. F. Gause also began to study the populations of organisms, such as yeast and *Paramecium* in the laboratory to test Pearl, Volterra, and Lotka's mathematical descriptions of increase, competition, and predation. In Australia, A. J. Nicholson attempted to integrate his observations in nature with laboratory experiments.[65]

Neither the observations in nature nor the laboratory experiments clearly established what prevented the potential growth of populations from being realized. Population ecology became a controversial subject, resembling Kuhn's description of a pre-paradigm science.[66] Two conflicts in particular arose in the '30s and continued to be debated into the '70s. These are the interrelated questions of whether populations are controlled by density-dependent or density-independent factors and whether two similar species can compete for long in the same niche.

The leading opponents of the importance of density-dependent factors have been H. G. Andrewartha and L. C. Birch, whose well-known arguments were presented in their encyclopedic work, *The distribution and abundance of animals* (Chicago, 1950). This book is probably still the most exhaustive single work ever published on population ecology. They argued that "the division of environment into 'density-dependent' and 'density-independent factors' is misleading because all the evidence indicates that there is no component of environment such that its influence is likely to be independent of the density of the population" (p. 17). For example, the individuals which survive adverse weather conditions might be the ones that found the limited number of sheltered places. Instead of relying upon the above dichotomy of factors, they put forward stochastic models to explain population dynamics.

> Because any substantial area is inevitably heterogeneous it is realistic to consider that a natural population comprises a large number of

> subpopulations or local populations existing more or less separately from one another. This condition occurs partly because of the heterogeneity of the terrain and partly because of chance events that fall unevenly on the local populations in the local situations.[67]

The dichotomy between density-dependent and density-independent factors was suggested by Howard and Fiske (1911). The terms, however, were not theirs, but were later applied to their concepts by H. S. Smith (1935). Others whom Andrewartha and Birch cite as responsible for the popularity of this concept are W. R. Thompson, Nicholson, Chapman, Charles Elton, and G. C. Varley.[68] To their list (1954) should be added David Lack, whose *Natural regulation of animal numbers* also appeared in 1954. Lack later summarized his arguments favouring density-dependent regulation and his objections to Andrewartha and Birch's counter-arguments.[69] I have found his discussion a more easily comprehended introduction to the controversy than Andrewartha and Birch's, but, whether or not others share my experience, one must read both points of view fully to appreciate the conflict. Further airings of the different perspectives are conveniently available in the *Cold Spring Harbor symposia on quantitative biology*, xxii (1957), entitled *Population studies: Animal ecology and demography* and in Ian A. McLaren (ed.), *Natural regulation of animal populations* (New York, 1971), papers 1–5.

McLaren, in his introduction, claimed that "Probably in the eyes of many ecologists, this controversy has been resolved". J. Merritt Emlen in his recent textbook reviewed the controversy and commented that "The problem has been neatly resolved by Horn (1968)".[70] Horn developed a mathematical model which expresses both density-dependent and density-independent factors that limit population growth. If this resolves the controversy, it is only by the capitulation of Andrewartha and Birch. Their capitulation has indeed been reported in another recent textbook: "since Birch's paper (1962) the argument can be considered settled. Birch now accepts that populations will frequently be limited in a density dependent way, though he argues there will be some exceptions."[71] However, it does not appear that Birch's 1962 concession differs much from his and Andrewartha's words of 1954, quoted above. Their latest account of the controversy (1973) seems to differ from their 1954 account primarily in their use of Den Boer's concept of spreading the risk (1968) in support of their position.[72]

It has sometimes been suggested that controversies in population ecology occur between ecologists who study different groups of animals and attempt to over-generalize from their findings. No doubt this has occasionally added heat to controversy, but since entomologists have held different positions in the above controversy, the above suggestion cannot provide the basic key to the problem.

Regarding this controversy, it has been mentioned above that the earliest interest in population ecology was stimulated by outbreaks of locust or rodent plagues. The mystery of the locust has been solved. Its outbreaks are controlled by the weather.[73] Rodent cycles have been more difficult to elucidate. Krebs and Myers have recently reviewed the currently plausible explanations: (a) food, (b) predation, (c) weather, (d) stress, (e) behaviour, and (g) genetics. While they were able to shed much light on the cycles using four decades of research data, they could not make a final choice among the above possibilities. They suspected, however, "that studies of the heritability of reproductive capabilities, growth potentials, and behaviour of microtines will be the key to unlocking the mystery of rodent cycles".[74]

COMPETITION

Until the publication of Darwin's *Origin of species,* the only comprehensive theory of population ecology was the balance of nature concept. Within this theoretical framework, to the extent that competition was recognized by naturalists, particularly Linnaeus and Buffon, it was viewed as a means by which one species prevented another from destroying the balance. Before the nineteenth century, competition was not clearly distinguished from predation and most naturalists were unwilling to believe that species had become extinct. Around 1800, the consensus shifted toward belief in extinction and in 1820 the botanist Auguste Pyramus de Candolle discussed a new function of competition—as a factor in the spread of species. In 1832 Lyell extended this argument and discussed competition as a cause of extinction. In 1859 Darwin explained how the extinction of certain populations within a species could lead to the change of the species. His *Origin of species* must, therefore, be taken as the source of the competitive exclusion principle.[75] No one seems to have investigated Garrett Hardin's suspicion that the principle might be buried away in the economic writings of Simonde de Sismondi (1773–1842), perhaps because of the lack of evidence that he influenced Darwin's thoughts in a way similar to Malthus.[76]

The sporadic studies on plant competition before 1929 have been surveyed by Frederick E. Clements, John E. Weaver, and Herbert C. Hanson in *Plant competition, an analysis of community functions* (Washington, 1929), ch. 1. The history of studies on plant competition is being surveyed anew by James White of the University of Dublin. Although Clements and his associates appreciated the importance of competition for ecology and evolution, and although they set a good example for ecologists in the investigation of competition, and although Russian botanists were also advancing the subject,[77] from the 1930s through the '60s competition was of much greater interest to animal than to plant ecologists.

Since the rise of laboratory population studies, there have been doubts expressed about the relevance of experimental results to the understanding of populations in nature. These doubts are relevant to the controversy that developed over the competitive exclusion principle. The principle is derived from Darwin's theory of evolution by natural selection, but it was G. F. Gause (1934) who first focussed the attention of ecologists on the concept. It was not for another decade, however, that debate over the concept arose, at a symposium on the ecology of closely allied species sponsored by the British Ecological Society on 21 March, 1944.[78] The debate has been over, first, the possibly tautological character of the principle (which would make it unfalsifiable) and, second, how important competition actually is in nature. There are excellent reviews of this controversy.[79]

Also relevant to competition theory are two concepts which have pre-twentieth century roots, but which have been developed mostly in this century—niche and territory. Naturalists have been aware of ecological diversity and the association of particular species with particular habitats since Antiquity, and these are the facts upon which the niche concept is built. Nevertheless, Joseph Grinnell first used the term niche to indicate the subdivision of the habitat occupied by a particular species (1904). Charles Elton popularized the term in his *Animal ecology* (1927) as indicating the role of species in food chains, and G. Evelyn Hutchinson defined niche in terms of set theory to encompass all relevant environmental factors, such as food, shelter, temperature, and humidity (1957). Bernard Altum (1868) and Eliot Howard (1920) are the most important founders of territory studies. It has become clear that many kinds of animals compete for breeding territories, but the extent to which this limits the increase of the numbers of a species has been less easily determined and continues to be debated.[80]

BALANCE OF NATURE

The balance of nature concept can be traced back to Herodotus and Plato and is probably much older than that. It was the first organizing principle for ecology, but until the time of Linnaeus it functioned as a background assumption. He made the concept, under the name of the economy of nature, the basis of his outline of an ecological science (1749). The general assumption was that God had created all species with definite survival mechanisms, including reproductive potential, longevity, and defence mechanisms which insured the immortality of each species. It was also assumed that species do not change. Ecological diversity insured that each species had a place and means to live, and that any temporary imbalance in numbers would be brought into check by predation, weather, shortage of food, or other factors.

The first notable challenge to the concept was the shift in the consensus of naturalists concerning the extinction of species. However, since the concept was not explicitly defined, this challenge went unnoticed by most naturalists. The fundamental challenge came, however, from Darwin's theory. However, as mentioned earlier, he did not fully realize the extent to which his theory did challenge Linnaeus's economy of nature concept. Stephen A. Forbes actually developed in 1887 a balance of nature concept that incorporated the theory of natural selection.

The title of his paper, "The lake as a microcosm", is a reminder of the fact that since the time of Plato various authors had defended a particular view of the balance of nature in which the organisms in nature were said to be parts of an integrated whole in the same way that organs or cells are integrated into a functioning organism. Both the general balance of nature concept and the special superorganism concept survived into the twentieth century without having been subjected to serious scrutiny or even much suspicion. I have surveyed the history of both concepts in a paper entitled "Changing concepts of the balance of nature" (ref. 23). However, since the appearance of that paper in 1973, I have come to realize that my treatment of developments during the last one hundred years was too brief to do full justice to them. I have also made additional discoveries and have read some relevant sources which I had not seen before publication. I therefore made a number of revisions before this article was translated into Russian for publication,[81] and I have plans to publish further on the subject in English in a history of ecology being coauthored with Robert P. McIntosh.

Among the additions and changes to my survey the following should be mentioned. The earliest known author to suggest differential longevity among species as a factor in the balance of nature is now Alexander of Aphrodesias (*fl.* 2nd–3rd century AD) rather than Sir Thomas Browne (1646).[82] Stephen A. Forbes was indebted to Herbert Spencer's theory of population in developing his own synthesis of the balance of nature and natural selection.[83] Frederic E. Clements did not, as I hypothesized, abandon in the face of criticism his superorganism concept.[84] Twentieth century developments relating to the balance of nature which deserve more consideration than provided in my survey are stability theory,[85] group selection,[86] and altruism.[87] Michael T. Ghiselin's polemical discussion of the history of the superorganism concept is an interesting supplement to my survey, including as it does a much broader selection of authors from the twentieth century than I did.[88]

Finally, A. J. Jansen has published "An analysis of 'Balance in nature' as an ecological concept".[89] His paper is organized logically rather than historically, but his conclusions are similar to · mine. He surveys many recent works which I did not cover, and his article provides useful insights into the many perspectives that have developed concerning the meaning of the balance of nature.

REFERENCES

1. Gordon B. Dodds, "The historiography of American conservation, past and prospects", *Pacific Northwest quarterly,* lvi (1965), 75-81. Michael J. Lacey, "Man, nature, and the ecological perspective", *American studies,* viii (1970), 13-27. Donald Fleming, "Roots of the new conservation movement", *Perspectives in American history,* vi (1972), 7-91. Ronald J. Fahl, *North American forest and conservation history, a bibliography* (Santa Barbara, 1976). *Environmental review* is edited by John Opie, College Hall, Duquesne University, Pittsburgh, Pa, 15219, USA.
2. Haeckel, "Ueber Entwickelungsgang und Aufgabe der Zoologie", *Jenaische Zeitschrift für Naturwissenschaft,* v (1869, pub. 1870), 353-70; reprinted in Haeckel's *Gesammelte populäre Vorträge aus dem Gebiete der Entwickelungslehre* (Strauss, Bonn, 1879), ii, 17. English translation quoted from W. C. Allee, Alfred E. Emerson, Orlando Park, Thomas Park, and Karl P. Schmidt, *Principles of animal ecology* (Philadelphia and London, 1949), p. [v].
3. Clarence J. Glacken, *Traces on the Rhodian shore: Nature and culture in Western thought from ancient times to the end of the eighteenth century* (Berkeley and Los Angeles, 1967).
4. Institute for the History of Science and Technology, Academy of Sciences of the USSR (Moscow, 1970). The papers are as follows: Georg Uschmann, "E. Haeckel's definition of the ecology concept" (pp. 10-21), G. A. Novikov, "Hundred years of Ernst Haeckel's ecology" (pp. 22-76), G. P. Dementiev, "Russian founders of ecology" (pp. 77-88), S. S. Schwartz, "On the history of the main ideas in the modern ecology" (pp. 89-105), N. P. Naumov, "Advances of the population concepts in animal ecology" (pp. 106-46), P. M. Rafes, "Development of biogeocoenose theory" (pp. 147-94), A. G. Voronov, "Development of phytocoenosis theory" (pp. 195-222), L. V. Tchesnova, "Development of the biocoenosis doctrine and its practical applications in the works of Soviet parasitologists" (pp. 223-52), V. N. Gutina, "L. Pasteur and origin of ecological microbiology" (pp. 253-67), and R. Th. Hecker, "History and contents of paleoecology" (pp. 268-84). I thank Vassily Babkoff for providing me with a copy of this book.
5. *Op. cit.* (ref. 2), chs 2-3. See also Alister Hardy, "Charles Elton's influence in ecology", *Journal of animal ecology,* xxxvii (1968), 3-8.
6. Charles A. Browne, *A source book of agricultural chemistry* (Waltham, Mass., 1944; New York, 1977). H. C. Cowles, "The work of the year 1903 in ecology", *Science,* xix (1904), 879-85. W. F. Ganong, "The cardinal principles of ecology", *Science,* xix (1904), 493-8. Howard S. Reed, "A brief history of ecological work in botany", *Plant world,* viii (1905), 163-70, 198-208. Henry A. Gleason, "Twenty-five years of ecology",

Brooklyn Botanical Garden memoirs, iv (1936), 41-49. Robert P. McIntosh, "Plant ecology, 1947-1972", *Missouri Botanical Garden annals*, lxi (1974), 132-65.

7. Hans H. Trass, *Geobotanika. Istoriia i Sovremennye Tendentsii Razvitiia* (Leningrad, 1976). I thank Robert L. Burgess for bringing this book to my attention. Frederic E. Clements, *Plant succession: An analysis of the development of vegetation* (Washington, 1916), chs ii and vii. Gustaf E. Du Rietz, *Zur methodologischen Grundlage der modernen Pflanzensoziologie* (Vienna, 1921; New York, 1977). Robert H. Whittaker, "Classification of natural communities", *Botanical review*, xxviii (1962), 1-239; reprinted New York, 1977.
8. Egerton, "Ecological studies and observations in America before 1900", in *Issues and ideas in America*, ed. Benjamin J. Taylor and Thurman J. White (Norman, Oklahoma, 1976), 311-51. Robert P. McIntosh, "Ecology since 1900", *ibid.*, 353-72.
9. Arthur G. Tansley, "The early history of modern plant ecology in Britain", *Journal of ecology*, xxxv (1947), 130-7. W. H. Pearsall, "The development of ecology in Britain," *ibid.*, lii (suppl.) (1964), 1-12. E. J. Salisbury, "The origin and early years of the British Ecological Society", *ibid.*, 13-18. P. D. Lowe, "Amateurs and professionals: The institutional emergence of British plant ecology", *Journal of the Society for the Bibliography of Natural History*, vii (1976), 517-35.
10. G. C. Sellery, *E. A. Birge, a memoir* (Madison, 1956), including C. H. Mortimer, "E. A. Birge, an explorer of lakes", pp. 163-211.
11. Edith Gertrude Schwartz Clements, *Adventures in ecology: Half a million miles . . . from mud to macadam* (New York, 1960). *The life and work of John W. Harshberger, Ph.D., an autobiography* (Philadelphia, 1928). Leland O. Howard, *Fighting the insects, the story of an entomologist, telling of the life and experiences of the writer* (New York, 1933). A. S. Pearse, *Adventure . . . trying to be a zoologist* (Durham, 1952). Frederick S. Bodenheimer, *A biologist in Israel: A book of reminiscences* (Jerusalem, 1959).
12. William T. Stearn, "An introduction to the *Species plantarum* and cognate botanical works of Carl Linnaeus", in Linnaeus, *Species plantarum, a facsimile of the first edition, 1753* (2 vols, London, 1957), i, 51-64.
13. Carl Linnaeus, *Miscellaneous tracts relating to natural history, husbandry, and physick, to which is added the calendar of flora,* transl. Benjamin Stillingfleet (London, 1759; 2nd ed., 1762; 3rd ed., 1775; New York, 1977). Linnaeus, *Select dissertations from the Amoenitates Academicae,* transl. F. J. Brand (London, 1781; New York, 1977). Linnaeus, *L'Equilibre de la nature: Oratio de telluris habitabilis incremento (1744), Oeconomia naturae (1749), Politia naturae (1760), Curiositas naturalis (1748), Cui bono (1752)*, transl. Bernard Jasmin, introduction and notes by Camille Limoges (Paris, 1972). Limoges has also discussed the use of political analogy in the development of Linnaeus's ideas on the economy of nature: "Economie de la nature et idéologie juridique chez Linné", *XIIIth International Congress of the History of Science proceedings* (Moscow, 1974), section ix, 25-30.
14. Basil H. Soulsby, *A catalogue of the works of Linnaeus (and publications more immediately relating thereto) preserved in the libraries of the British Museum (Bloomsbury) and the British Museum (Natural His-*

tory) (*South Kensington*) (2nd ed., London, 1933; *index* by C. Davies Sherborn, 1936). For a guide to literature on Linnaeus, see the account of him by Sten Lindroth in *Dictionary of scientific biography*, viii (1973), 374-81. Important, but unlisted by Lindroth, is G. Einar Du Rietz, "*Linné som Myrforskare* (Linné as Paludologist)", *Uppsala Universitets Arsskrift*, v (1957), 1-80 (English summary, 60-80) and Du Rietz, "Linnaeus as a Phytogeographer", *Vegetatio*, vii (1957), 161-8.

15. For further discussion and references, see Egerton (ref. 8).

16. Humboldt is discussed below in the section on population. George Perkins Marsh, *Man and nature; or, Physical geography as modified by human action* (1864; cited from new ed., Cambridge, Mass., 1965), 53.

17. Philosophy of science rather than ecology is the main focus in Robert Wohl, "Buffon and his project for a new science", *Isis*, li (1960), 186-99. Concerning Buffon's bibliography, see Jacques Roger on Buffon in *Dictionary of scientific biography*, ii (1970), 576-82.

18. Franck Bourdier on Isidore Geoffroy Saint-Hilaire, *Dictionary of scientific biography*, v (1972), 358-60; quotation on 358.

19. Charles C. Adams, *Guide to the study of animal ecology* (New York, 1913; New York, 1977), 19. William Wheeler, "'Natural history', 'œcology' or 'Ethology'?", *Science*, xv (1902), 971-6. F. Dahl, "Die Ziele der vergleichenden 'Ethologie' (d.i. Biologie im älteren engeren Sinne)", *Verhandlungen des V. Internationalen Zoologen-Congresses zu Berlin, 1901* (Jena, 1902), 296-300. C. J. van der Klaauw, "Okologische Studien und Kritiken: II. Zur Geschichte der Definitionen der Okologie, besonders auf Grund der Systeme der zoologischen Disziplinen", *Sudhoffs Archiv für Geschichte der Medizin und der Naturwissenschaften*, xxix (1936), 136-77; see 139-40, 155-6.

20. Alfred V. Espinas, *Des sociétés animales: étude de psychologie comparée* (Paris, 1877; New York, 1977). See also J. van der Hoeven and H. G. Bronn, who are discussed by van der Klaauw (ref. 19), 137-9.

21. Egerton, "Humboldt, Darwin, and population", *Journal of the history of biology*, iii (1970), 325-60. Robert C. Stauffer, "Ecology in the long manuscript version of Darwin's *Origin of species* and Linnaeus' *Oeconomy of Nature*", *American Philosophical Society proceedings*, civ (1960), 235-41. Peter Vorzimmer, "Darwin's ecology and its influence upon his theory", *Isis*, lvi (1965), 148-55. Frederic E. Clements, "Darwin's influence upon plant geography and ecology", *American naturalist*, xliii (1909), 143-51.

22. Ernst Haeckel, *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie* (2 vols, Berlin, 1866), ii, 286-7. English quotation from Robert C. Stauffer, "Haeckel, Darwin, and Ecology", *Quarterly review of biology*, xxxii (1957), 138-44; see p. 140.

23. Egerton, "Changing concepts of the balance of nature", *Quarterly review of biology*, xlviii (1973), 322-50; see 341-2.

24. Van der Klaauw (ref. 19), Uschmann (ref. 4), and on Haeckel in *Dictionary of scientific biography*, vi (1972), 6-11.

25. Stauffer (ref. 22), 141-3. John Lussenhop, "Victor Hensen and the development of sampling methods in ecology", *Journal of the history of biology*, vii (1974), 319-37; see 328-30. Also useful for this debate is James

Johnstone, *Conditions of life in the sea: a short account of quantitative marine biological research* (Cambridge, 1908; New York, 1977). Concerning another of Haeckel's oceanographic controversies, see Philip F. Rehbock, "Huxley, Haeckel, and the oceanographers: The case of *Bathybius haeckelii*", *Isis,* lxvi (1975), 504-33.

26. Ernst Haeckel, "Report on the Radiolaria collected by H.M.S. *Challenger* during the years 1873-1876", xviii (in 2 vols) of *Report on the scientific results of the Voyage of H.M.S. Challenger during the Years 1873-76 . . . ,* ed. John Murray (London, Edinburgh, Dublin, 1887). Haeckel's criticism of Hensen (which have been discussed by Stauffer and Lussenhop, ref. 25) is in his *Plankton-Studien. Vergleichende Untersuchungen über die Bedeutung und Zussammensetzung der pelagischen Fauna und Flora* (Jena, 1890), transl. George Wilton Field, "Planktonic studies: A comparative investigation of the importance and constitution of the pelagic fauna and flora", *Report of the U.S. Commission of Fish and Fisheries* (1891), 565-641. Haeckel's conclusions from his "Report on the Radiolaria" and the English translation of his "Planktonic studies" are reproduced in *Early marine ecology,* ed. Frank N. Egerton (New York, 1977).

27. Daniel Gasman, *The scientific origins of National Socialism: Social Darwinism in Ernst Haeckel and the German Monist League* (New York and London, 1971). Reviewed by C. A. Culotta in *Isis,* lxiii (1972), 587-8.

28. *The correspondence of Henry David Thoreau,* ed. Walter Harding and Carl Bode (New York, 1958), 502. Paul H. Oehser, "The word 'Ecology' ", *Science,* cxxix (1959), 992. Walter Harding, "Thoreau and 'Ecology': Correction", *Science,* cxlix (1965), 707.

29. John S. Burdon-Sanderson, "Biology in relation to other natural sciences", *Smithsonian Institution annual report* (1893), 435-63; see p. 439. Also in *Nature,* xlviii (1893), 464-72 and *British Association for the Advancement of Science report* (1893), 3-31. Louis Hermann Pammel, *Flower ecology* (Carroll, Iowa, 1893) and *Ecology* (Carroll, Iowa, 1903). I thank Robert P. McIntosh for calling these works by Pammel to my attention. Stephen A. Forbes, "On contagious disease in the Chinch-bug (*Blissus leucopterus Say*)", *Nineteenth report of the state entomologist on the noxious and beneficial insects of the State of Illinois* (Springfield, 1895), 16-18.

30. R. J. Goodland, "The tropical origin of Ecology: Eugen Warming's jubilee", *Oikos,* xxvi (1975), 240-5. I thank Robert P. McIntosh and Robert L. Burgess for bringing this article to my attention.

31. Tansley (ref. 9). Robert L. Burgess talked on the history of the Ecological Society of America at the December 1976 meeting of the History of Science Society, Philadelphia.

32. Masayasu Konishi and Yosiaki Itô, "Early entomology in East Asia", *History of entomology,* ed. Ray F. Smith, Thomas E. Mittler, and Carroll N. Smith (Palo Alto, California, 1973), 1-20; see p. 5. Bruno Meissner, *Babylonien und Assyrien* (2 vols, Heidelberg, 1920-25), i, 195-6; ii, 213, 237. I thank Otto Neugebauer for locating these references to Meissner.

33. Frank N. Egerton, "Ancient sources for animal demography", *Isis,* lix (1968), 175-89. Egerton, "Aristotle's population biology", *Arethusa,* viii (1975), 307-30.

34. Leonardo Fibonacci, *Liber abbaci*, sec. 3, in *Scritti di Leonardo Pisano*, ed. B. Boncompagni (2 vols, Rome, 1857-62), i, 283-4. English transl. in D. J. Struik, *A source book in mathematics, 1200-1800* (Cambridge, Mass., 1969), 2-3 and in Frederick S. Bodenheimer, "An early study in population dynamics", *Archives internationales d'histoire des sciences*, xi (1958), 27-28. The problem is also discussed by Kurt Vogel in his account on Fibonacci in *Dictionary of scientific biography*, iv (1971), 604-13; see pp. 606-7.
35. Frank N. Egerton, *Observations and studies of animal populations before 1860, a survey concluding with Darwin's Origin of species* (Ph.D. dissertation, University of Wisconsin, 1967), ch. 2 on the mathematical aspects of this problem. For other aspects, see Egerton, "The longevity of the Patriarchs, a topic in the history of demography", *Journal of the history of ideas*, xxvii (1966), 575-84.
36. Frank N. Egerton on Graunt in *Dictionary of scientific biography*, v (1972), 506-8.
37. Frank N. Egerton, "Leeuwenhoek as a founder of animal demography", *Journal of the history of biology*, i (1968), 1-22. The authoritative edition of Leeuwenhoek's letters is that edited and annotated by a Committee of Dutch Scientists, *Collected letters of Antoni van Leeuwenhoek*, of which eight volumes have thus far been published (Amsterdam, 1939-68). However, vol. viii only extends to 1692, and at the present pace of publication, it will take another three decades to complete. Since the later letters are often more ecologically significant than the earlier ones, I have decided to reprint Samuel Hoole's translation of *The select works of Antony van Leeuwenhoek* (2 vols, London, 1798-1807; New York, 1977). This translation is the only English version of most of the later letters.
38. Frank N. Egerton, "Richard Bradley's understanding of biological productivity: A study of eighteenth-century ecological ideas", *Journal of the history of biology*, ii (1969), 391-410; see pp. 394-401 on Dodart's computation and its influence.
39. Egerton, *Observations* (ref. 35), ch. 3, pp. 99-269 on John Ray, William Derham, Richard Bradley, René de Réaumur, Friedrich Lesser, Pierre Lyonet, Carl Linnaeus, Charles Bonnet, Charles de Geer, Comte de Buffon, John Bruckner, Joseph Townsend, William Smellie, Erasmus Darwin, and others.
40. Aram Vartanian, "Spontaneous generation", *Dictionary of the history of ideas*, iii (1973), 307-12. Jean Rostand, *La genèse de la vie: Histoire des idées sur la génération spontanée* (Paris, 1943). Edmund Oskar von Lippmann, *Urzeugung und Lebenskraft. Zur Geschichte dieser Probleme von den ältesten Zeiten an biz zu den Anfängen des 20. Jahrhunderts* (Berlin, 1933). Nils von Hofsten, "Skapelsetro och Uralstringshypoteser före Darwin", *Uppsala Universitets Arsskrift* (1928), 1-73 and English summary, "Ideas of creation and spontaneous generation prior to Darwin", *Isis*, xxv (1936), 80-94. Sten Lindroth, "Uralstringen. Ett kapitet ur Biologiens äldre Historia", *Lychnos* (1939), 159-92. D. M. Balme, "Development of biology in Aristotle and Theophrastus: Theory of spontaneous generation", *Phronesis*, vii (1962), 91-104. Pierre Louis, "La génération spontanée chez Aristotle", *Colloques XIIe congrès international d'histoire des sciences* (Paris, 1968), 291-305. Paul Brien, "La

génération des êtres vivants dans la philosophie épicurienne", *ibid.*, 307-21. Carlo Castellani, "Le problème de la *generatio spontanea* dans l'oeuvre de Fortunio Liceti", *ibid.*, 323-40. Everett I. Mendelsohn, "Philosophical biology *vs* experimental biology: spontaneous generation in the seventeenth century", *XIIe congrès international d'histoire des sciences* (1968), *Actes*, IB (Paris, 1971), 201-26. Discussion of these four papers, *ibid.*, 189-200, 227-9. Carlo Castellani, *La storia della generazione. Idee e teorie dal diciasettesimo al diciottesimo secolo* (Milan, 1965). Castellani, "L'Origine degli infusori nella polemica Needham-Spallanzani-Bonnet, con alcuni Documenti inediti", *Episteme*, iii (1969), 214-41; iv (1970), 19-36. John Farley, "The spontaneous generation controversy (1700-1860): The origin of parasitic worms", *Journal of the history of biology*, v. (1972), 95-125. Farley and Gerald L. Geison, "Science, politics and spontaneous generation in nineteenth-century France: The Pasteur-Pouchet debate", *Bulletin of the history of medicine*, xlviii (1974), 161-98.

41. John C. Greene, *The death of Adam: Evolution and its impact on Western thought* (Ames, Iowa, 1959), see listings in index under "Species, extinction". Loren Eiseley, *The firmament of time* (New York, 1960), 35-51. Frank N. Egerton, "Studies of animal populations from Lamarck to Darwin", *Journal of the history of biology*, i (1968), 225-59; see pp. 227-30.

42. Egerton, "Ancient sources" (ref. 33), 175-9. F. Schwerdtfeger, "Forest entomology", in *History of entomology*, ed. Ray F. Smith, Thomas E. Mittler, Carroll N. Smith (Palo Alto, Calif., 1973), 361-86.

43. Egerton (ref. 21).

44. Egerton (ref. 41), 231-40. Egerton, "The concept of competition in Nature before Darwin", *XIIe congrès international d'histoire des sciences* (1968), *Actes*, viii (Paris, 1971), 41-46. Conway Zirkle, "Natural selection before the 'Origin of species'", *American Philosophical Society proceedings*, lxxxiv (1941), 71-123.

45. Many of Darwin's letters have been published; many others have not. Those published in special Darwin collections, as well as Darwin's other works, are listed by R. B. Freeman, *The works of Charles Darwin, an annotated bibliographical handlist* (London, 1965). Frederick Burckhardt is currently preparing a complete "Collected letters of Charles Darwin", but this edition, unlike many of the others, will not include the letters written to Darwin. John C. Greene, "Reflections on the progress of Darwin studies", *Journal of the history of biology*, viii (1975), 243-73. Gavin de Beer on Darwin in *Dictionary of scientific biography*, iii (1971), 565-77.

46. Egerton (ref. 21), 333. Gavin de Beer, ed., "Darwin's Notebooks on transmutation of species. Part VI. Pages excised by Darwin", *Bulletin of the British Museum (Natural History), historical series*, iii (1967), 129-76; see p. 162 (Darwin's third notebook, 134-5).

47. *The autobiography of Charles Darwin, 1809-1882, with original omissions restored*, ed. Nora Barlow (New York, 1959), 120.

48. Peter J. Bowler, "Malthus, Darwin and the concept of struggle", *Journal of the history of ideas*, xxxvii (1976), 631-50. Th. Cowles, "Malthus, Darwin, and Bagehot: A study in the transference of a concept", *Isis*, xxvi (1936), 341-8. Gavin de Beer, "The origins of Darwin's ideas on evolution and natural selection", *Royal Society of London proceedings*, B, clv (1961),

321-38; see pp. 328-31. Loren Eiseley, *Darwin's century: Evolution and the men who discovered it* (Garden City, 1958), 178-82. Barry G. Gale, "Darwin and the concept of a struggle for existence: A study in the extrascientific origins of scientific ideas", *Isis,* lxiii (1972), 321-44; see pp. 335-42. Michael T. Ghiselin, *The triumph of the Darwinian method* (Berkeley, 1969), 48-49, 59-61, 256-58. Sandra Herbert, "Darwin, Malthus, and selection", *Journal of the history of biology,* iv (1971), 209-17. Gertrude Himmelfarb, *Darwin and the Darwinian revolution* (London, 1959), 132-9. Joel S. Schwartz, "Charles Darwin's debt to Malthus and Edward Blyth", *Journal of the history of biology,* vii (1974), 301-18. Peter Vorzimmer, "Darwin, Malthus, and the theory of natural selection", *Journal of the history of ideas,* xxx (1969), 527-42. Robert M. Young, "Malthus and the evolutionists: The common context of biological and social theory", *Past & present,* no. 43 (1969), 109-45.

49. Harald Westergaard, *Contributions to the history of statistics* (London, 1932; New York, 1968), 125-9. Michael Drake, "Malthus on Norway", *Population studies,* xx (1966), 175-96. David V. Glass, ed., *Introduction to Malthus* (London and New York, 1953). Harold A. Boner, *Hungry generations: The nineteenth-century case against Malthusianism* (New York, 1955). Kenneth Smith, *The Malthusian controversy* (London, 1951).
50. H. G. Andrewartha and L. C. Birch, "The history of insect ecology", in Smith, Mittler, and Smith (ref. 32), 229-66; see p. 242.
51. Frank N. Egerton, "Charles Darwin's analysis of biological competition", *XIIIth international congress of the history of science* (1971), Proceedings, ix (Moscow, 1974), 71-77.
52. Westergaard (ref. 49). Philip M. Hauser and Otis Dudley Duncan, eds, *The study of population, an inventory and appraisal* (Chicago, 1959), part II.
53. Allee (ref. 2), 25-27.
54. P. V. Terentiev, "The sources of biometry" (Russian with English summary), *Iz Istorii Biologii,* iii (1971), 124-34. Some background though no direct assistance with this question, might be obtained from some of the papers from the Conference on the History of Quantification in the Sciences, *Isis,* lii, no. 168 (June, 1961), 133-354.
55. Robert C. Olby, *Origins of Mendelism* (New York, 1966), 109-14. Jirí Jindra, "A possible derivation of the Mendelian series", *Folia Mendeliana,* no. vi (1971), 71-74.
56. Karl Pearson, *The life, letters and labours of Francis Galton* (3 vols in 4, Cambridge, 1914-30), i, 142 ff.; ii, 12. Ruth Schwartz Cowan, "Francis Galton's statistical ideas: The influence of eugenics", *Isis,* lxiii (1972), 509-28; see p. 512 ff. Robert de Marrais, "The double-edged effect of Sir Francis Galton: A search for the motives in the biometrician-Mendelian debate", *Journal of the history of biology,* vii (1974), 141-74.
57. William B. Provine, *The origins of theoretical population genetics* (Chicago, 1971), ch. 2. Churchill Eisenhart on Pearson in *Dictionary of scientific biography,* x (1974), 447-73. Ruth Schwartz Cowan on Weldon, *ibid.,* xiv (1976), 251-2.
58. Carl Nägeli, "Verdrängung der Pflanzenformen durch ihre Mitbewerber", *Akademie der Wissenschaften, München, Mathematisch-Physikalischen Classe, Sitz.* iv (1874), 109-64. The lack of influence of this paper was noted by G. F. Gause, *The struggle for existence* (Baltimore, 1934; New

York, 1971), 6. For a two-paragraph summary in English of Nägeli's paper, see Frederic E. Clements, John E. Weaver, and Herbert C. H. Hanson, *Plant competition, an analysis of community functions* (Washington, 1929), 8.

59. Victor Hensen, "Die thatigkeit des Regenworms (*Lumbricus terrestris* L.) für die Fruchtbarkeit der Erdbodens", *Zeitschrift für Wissenschaft: Zoologie,* xxviii (1877), 354-64. This article is cited several times by Charles Darwin, *The formation of vegetable mould through the action of worms, with observations on their habits* (London, 1881; New York, 1899). Stauffer (ref. 22). Lussenhop (ref. 25).

60. Ad. Bellevoye and J. Laurent, "Les plantations de pins dans la Marne et les parasites qui les attaquent", *Société d'Etude des Sciences naturelles de Reims bulletin,* v (1896), 70-126. Paul Marchal, "L'équilibre numérique des espèces et ses rélations avec les parasites chez les insectes", *Société Biologique* [Paris] *comptes rendus,* xlix (1897), 129-30. Marchal, "The utilization of auxiliary entomophagous insects in the struggle against insects injurious to agriculture", *Popular science monthly,* lxxii (1908), 352-419. Bellevoye and Laurent's paper and Marchal's 1908 paper are reprinted in *Ecological studies on insect parasitism,* ed. Frank N. Egerton (New York, 1977).

61. Ronald Ross, "An application of the theory of probabilities to the study of *a priori* pathometry", *Royal Society of London proceedings,* A xcii (1916), 204-30; Pt 2, coauthored with Hilda P. Hudson, *ibid.,* A xciii (1917), 212-40; bibliography, Pt I, 230. For Ross's more extensive bibliography, see his *Memoirs, with a full account of the great malaria problem and its solution* (New York, 1923), 526-36. On Lotka, see the account by Norman T. Gridgeman in *Dictionary of scientific biography,* viii (1973), 512. Lotka's bibliography is included in the reprint of his *Elements of physical biology* (Baltimore, 1924), retitled *Elements of mathematical biology* (New York, 1956), 442-7. Papers by Ross (1911) and Lotka (1912) are reprinted in Egerton (ref. 60). For a more recent discussion of the ecology of malaria epidemiology, see Fredeick S. Bodenheimer, *Animal ecology to-day* (The Hague, 1958), 92-98.

62. Francesco M. Scudo, "Vito Volterra and theoretical ecology", *Theoretical population biology,* ii (1971), 1-23. I thank John Lussenhop for bringing this article to my attention. E. Volterra on Vito Volterra, *Dictionary of scientific biography,* xiv (1976), 85-88. H. S. Jennings, "Raymond Pearl, 1879-1940", *National Academy of Sciences biographical memoirs,* xxii (1943), 295-347. Franklin Parker on Pearl, *Dictionary of scientific biography,* x (1974), 444-5. Allee, Emerson, Park, Park, and Schmidt (ref. 2), ch. 20.

63. William Streifer, "Realistic models in population ecology", *Advances in ecological research,* viii (1974), 199-266.

64. Allee, Emerson, Park, Park, and Schmidt (ref. 2), 61. Bodenheimer (ref. 61), 67-82.

65. Gause (ref. 58). An indication of A. J. Nicholson's work, which also includes references to some of his earlier papers, is "The role of population dynamics in natural selection", in *The evolution of life, its origin, history, and future,* ed. Sol Tax (3 vols, Chicago, 1960), i, 477-521. Nicholson has summarized his ecological goals and achievements in a personal communication to me.

66. Thomas S. Kuhn, *The structure of scientific revolutions* (Chicago, 1962; 2nd ed., 1970), ch. 2.
67. Andrewartha and Birch (ref. 50), 249.
68. Leland O. Howard and William F. Fiske, *The importation into the United States of the parasites of the Gipsy Moth and the Brown-tail Moth . . .* (Washington, 1911; New York, 1977). W. R. Thompson, "A contribution to the study of biological control and parasite introduction in continental areas", *Parasitology,* xx (1928), 90-112; reprinted in Egerton (ref. 60). Royal N. Chapman, *Animal ecology, with especial reference to insects* (New York, 1931; reprinted 1977). Allee, Emerson, Park, Park, and Schmidt (ref. 2), 331-3. Andrewartha and Birch, *The distribution and abundance of animals* (Chicago, 1954), 16-19.
69. David Lack, *Population studies of birds* (Oxford, 1966), 281-99. For density-dependent arguments on insects, see M. E. Solomon, "Analysis of processes involved in the natural control of insects", *Advances in ecological research,* ii (1964), 1-58. See also Naumov's general survey (ref. 4).
70. J. Merritt Emlen, *Ecology: An evolutionary approach* (Reading, Mass., Don Mills, Ontario and London, 1973), 269. Henry S. Horn, "Regulation of animal numbers: A model counter-example", *Ecology,* xlix (1968), 776-8; reprinted in McLaren, ed., *Natural regulation of animal populations* (New York, 1971), 51-57. In a personal communication, Robert P. McIntosh has expressed doubts about the validity of Horn's reasoning and the significance of his paper.
71. Mark Williamson, *The analysis of biological populations* (London, 1972), 29.
72. Andrewartha and Birch (ref. 50), 250-1. P. J. Den Boer, "Spreading of risk and stabilization of animal numbers", *Acta biotheoretica,* xviii (1969), 165-94.
73. Bodenheimer (ref. 61), 86-92. Bodenheimer (ref. 11), 201-17. Boris Uvarov, *Grasshoppers and locusts: A handbook of general Acridology* (Cambridge, 1966). M. L. Roonwal, "Bibliographia Acrididiorum. A bibliography of the Orthopterous insects of the family Acrididae (comprising the short-horned grasshoppers and locusts) from the earliest times to the end of 1954 (with Some Additions for 1955-57)", *Records of the Indian Museum,* lvi (1961), 1-613. C. G. Johnson, *Migration and dispersal of insects by flight* (London, 1969), ch. 22. Stanley Baron, *The desert locust* (New York, 1972).
74. Charles J. Krebs and Judith H. Myers, "Population cycles in small mammals", *Advances in ecological research,* viii (1974), 267-399; see p. 389. Bodenheimer (ref. 61), 98-111. Bodenheimer (ref. 11), 217-46.
75. Egerton (refs 44 and 51).
76. Garrett Hardin, "The competitive exclusion principle", *Science,* cxxxi (1960), 1292-7; see p. 1296.
77. Y. M. Gall, "Experimental study of the struggle for existence as a factor of evolution (Works of Soviet botanists of 1920's)", *Iz Istorii Biologii,* v (1975), 26-46 (Russian with English summary). Gall, *The struggle for existence as a factor of evolution (historico-critical analysis of the Soviet botanical researches)* (Leningrad, 1976) (Russian with English summary).
78. Hardin (ref. 76), 1292, cites: [anon.], *Journal of animal ecology,* xiii (1944), 176.

79. Francisco J. Ayala, "Competition, coexistence, and evolution", in *Essays in evolution and genetics in honour of Theodosius Dobzhansky*, ed. Max K. Hecht and William C. Steere (New York, 1970), 121-58. Paul DeBach, "The competitive displacement and coexistence principles", *Annual review of entomology*, xi (1966), 183-212. Robert P. McIntosh, "Community, competition, and adaptation", *Quarterly review of biology*, xlv (1970), 259-80. Richard S. Miller, "Pattern and process in competition", *Advances in ecological research*, iv (1967), 1-74.

80. For the early history of the territory concept see Julian Huxley and James Fisher, "Foreword", in Henry Eliot Howard, *Territory in bird life* (New York, 1964), 7-26. For more recent studies, see Allen W. Stokes, ed., *Territory* (Straudsburg, Penn., 1974). Ayala (ref. 79), 122-4. Robert H. Whittaker and Simon A. Levin, eds, *Niche: Theory and application* (Stroudsburg, Penn., 1976).

81. Egerton, "Changing concepts of the balance of nature", *Iz Istorii Biologii*, vi (1977), in press (Russian with English summary).

82. Alexander of Aphrodisias, *Problemata* (Rome, 1475), bk 2, sec. 64, fol. 269v. Cited from Edward Topsell, *The fowles of heaven, or history of birdes*, ed. Thomas P. Harrison and F. David Hoeniger (Austin, 1972), 222 and n. 224 on p. 278. Topsell's reference came from Ulysse Aldrovandi, *Ornithologia, hoc est de auibus historiae* (3 vols, Bologna, 1599-1603), i, bk 12, ch. 2. I thank David Hoeniger for information on this citation.

83. Stephen A. Forbes, "On some interactions of organisms", *Illinois State Laboratory of Natural History bulletin*, 1 (1880), 3-17; see p. 6. Forbes, "The food of birds", *ibid.*, 80-148; see p. 85. Forbes, "The lake as a microcosm", 1887; reprinted in *ibid.*, xv (1925), 537-50. These papers are reprinted in Forbes, *Ecological investigations* (New York, 1977).

84. Frederic E. Clements and Victor E. Shelford, *Bio-ecology* (New York and London, 1939), 20-25. Robert P. McIntosh, "Natural order and communities", *Biologist*, xlii (1960), 55-62; see p. 57.

85. Den Boer (ref. 72). Emlen (ref. 70), 360-2. G. M. Woodwell and H. H. Smith, eds, *Diversity and stability in ecological systems* (Brookhaven National Laboratory Symposium in Biology, xxii, 1969). R. T. Paine has reviewed this last work in *Ecology*, lii (1971), 376-7. Daniel Goodman, "The theory of diversity-stability relationships in ecology", *Quarterly review of biology*, l (1975), 237-66.

86. Emlen (ref. 70), 38-42. M. J. Dunbar, "The ecosystem as unit of natural selection", *Connecticut Academy of Arts and Sciences transactions*, xliv (1972), 113-30.

87. Robert L. Trivers, "The evolution of reciprocal altruism", *Quarterly review of biology*, xlvi (1971), 35-57.

88. Michael T. Ghiselin, *The economy of nature and the evolution of sex* (Berkeley and Los Angeles, 1974), 22ff.

89. A. J. Jansen, "An analysis of 'Balance in nature' as an ecological concept", *Acta biotheoretica*, xxi (1972), 86-114. I thank James White for calling my attention to this article.