Contributions

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History of Ecological Sciences, Part 55: Animal Population Ecology

Frank N. Egerton
Department of History, University of Wisconsin-Parkside, Kenosha Wisconsin 53141
E-mail: egerton@uwp.edu

Modern population ecology began during the period 1860 to the 1920s, along with early formal development of animal ecology (Kingsland 1985:9–112, Price 2003:9–13, Egerton 2014*a*). Population ecology advanced on three fronts, sometimes linked: field studies, laboratory studies, and mathematical–theoretical studies (Cole 1954:106, 1958:6). It seems desirable to briefly treat here two special cases: invasive species and rare and extinct species, with bibliographic guides at these topics.

There is helpful literature on the history of population ecology; yet its authors were often unaware of each other's contributions. William Thompson wrote a 26-page historical introduction to his "Biological Control and the Theories of the Interactions of Populations" (1939:301–327). Thomas Park's "Some Observations on the History and Scope of Population Ecology" (1946) has such general comments it has limited current interest. LaMont Cole (1954:105–117, 1958:2–11) set an excellent example by surveying the history of human and animal demography, observational and mathematical. David Lack's *Natural Regulation of Animal Numbers* (1954) encompassed animals in general; although his *Population Studies of Birds* (1966) was narrower in scope, its appendix, "The Theoretical Controversies concerning Animal Populations," covers animals in general. Frank Egerton has written articles on animal demography from antiquity to Darwin (listed in McIntosh 1985:335, Egerton 2012:226). Kenneth Watt's "Use of Mathematics in Population Ecology" (1962) is a very insightful historical survey. Andy Andrewartha and Louis Birch's "The History of Insect Ecology" (1973) contains an important survey on the history of insect demography. (Although Lack, and Andrewartha and Birch, were participants in population controversies, they all attempted to present fair accounts.) J. P. Dempster (1975:121–128) provided a concise and lucid history of population theories. Evelyn Hutchinson's *Introduction to Population Ecology* (1978) began with a historical chapter and had historical comments and footnotes throughout the book, and five pages from it are reprinted in an anthology of his writings (Hutchinson 2010:10–14). In the same year as Hutchinson's population textbook, Robert Tamarin compiled a useful sourcebook, *Population Regulation* (1978) and Francesco Scudo and James Ziegler compiled *The Golden Age of*

Theoretical Ecology, 1923–1940 (1978). The last contained two papers by Lotka from 1923 and one by Volterra from 1927; all other papers were from the 1930s. Sharon Kingsland's *Modeling Nature: Episodes in Population Ecology* (1985) is a valuable guide, which cited Thompson (1939), Cole (1954), Lack (1966), Hutchinson (1978), Scudo and Ziegler (1978), but missed Watt (1962), Andrewartha and Birch (1973), and Tamarin (1978). The 50-page "Afterword" which she added to the second edition (1995) is more of a bibliographic guide to recent ecology history than a continuation of her original history. Robert ("Mac") McIntosh's *Background of Ecology: Concept and Theory* (1985) has a 47-page chapter, "Population Ecology." McIntosh provided a good bibliographic guide and arguments on both sides of issues, mostly without taking sides. Naomi Cappuccino (1995) and Peter Turchin (1995) wrote brief retrospective articles in the same volume, as background for taking population studies in new directions. Mark Hixon, Stephen Pacala, and Stuart Sandin (2002) utilized Egerton (1973), Kingsland (1985), Cappuccino (1995), and Turchin (1995), but neither Andrewartha and Birch (1973) nor Tamarin (1978) in their perceptive "Population Regulation: Historical Context and Contemporary Challenges" (2002). Giorgio Israel and Ana Millán Gasca compiled an important supplement to Scudo and Ziegler's *Golden Age* in *The Biology of Numbers: The Correspondence of Vito Volterra on Mathematical Biology* (2002), which includes a dozen of his correspondents who have significance for the history of ecology. Israel and Millán Casca also provided biographical sketches of each correspondent. Peter Price's chapter, "Historical Views on Distribution, Abundance, and Population Dynamics" (2003:9–47), is an important concise survey emphasizing insects, written using Thompson (1939), Tamarin (1978), Cappuccino (1995), Turchin (1995), but neither the article by Andrewartha and Birch (1973) nor by Hixon et al. (2002) nor Kingsland (1985). Daniel Botkin is a skeptic whose book, *The Moon in the Nautilus Shell: Discordant Harmonies Reconsidered* (2012), contains historical discussions and cited Hutchinson (1978), but not other above-named sources. Tim Birkhead, Jo Wimpenny, and Bob Montgomerie provide a valuable chapter (10) in their history of modern ornithology (2014:355–387) on population studies, emphasizing the controversy between David Lack and Vero Wynne-Edwards.

That controversy is also discussed below, as is the one in Australia between Nicholson and Andrewartha and Birch. Controversies highlight alternative explanations for phenomena, and their resolution advances science.

Before 1954

The history of population ecology from antiquity to Darwin is surveyed briefly by Cole (1954:105–117, 1958:2–11), in much greater detail by Egerton (1967, 2012), partly by Hutchinson (1978:1–46), and is beyond the scope of this essay. Various ecologists have seen the scope of population ecology in slightly different ways. As a practicality, I focus upon certain topics and neglect others, but without intentionally defining the scope of this subject, which is the prerogative of ecologists, not historians.

The existence of invasives was noted long before it became a scientific question. When Spanish conquistadores invaded Mexico and Peru in the early 1500s, they inadvertently transmitted European diseases to natives, which diseases quickly decimated the contacted populations (Crosby 1972:35–63, McNeill 1976, Bray 1996). When African slaves were imported into the Americas, they brought yellow fever and malaria. These catastrophes were also repeated in other parts of the world that Europeans penetrated, either as traders or conquerors. Additionally, Europeans noticed that local species on islands to which they brought livestock and (accidentally) rats tended to disappear. However, such early observations did not become the basis of scientific inquiry.

The Caribbean Islands, once taken from natives, became sites of slave plantations that raised highly profitable crops, especially sugar cane. Unfortunately, European ships also accidentally imported brown and black species of rats, which literally ate away at the profits. In 1816, "a Jamaican horticultural publication speculated that the mongoose might '…extirpate the whole race of the vermin'" (quoted in Laycock 1966:111). Only in 1872 did sugar-cane grower W. B. Espeut obtain from India and release four wild males and five wild females into his fields. Espeut was pleased with the effectiveness of his mongooses, and in 1877, Jamaican stock was introduced into Puerto Rico, with others soon sent to many other islands. A problem: mongooses are diurnal, rats are nocturnal; therefore, these predators varied their diet to include diurnal prey, especially as rats became scarce (Laycock 1966:114). Poultry was, for mongooses, a satisfactory alternative to rats, but not for poultry owners. Whenever poultry was protected, native island animals, which had evolved without predators, were an easy alternative.

A scientific context emerged in 1887 at the Fruit Growers Convention meeting at Riverside, California, where USDA entomologist Charles Riley (1843–95) was asked to address the crisis of a severe infestation of the cottony-cushion scale *Icerya purchase* in California citrus orchards (Egerton 2012:190–192, 2013:69–70). Riley told the convention that the pest was accidentally imported from Australia, and that if growers lobbied Congress for funds, he would send an investigator to discover and import enemies of this citrus pest. Funds became available, Riley sent Albert Koebele to Australia, and he succeeded in finding both a vedalia beetle that preys on this scale insect and a fly that parasitizes the scales. These enemies were imported and they controlled the scales. This was beginners luck; not only were later enemies of foreign pests often ineffective when imported, but sometimes the effort backfired (as mongooses eating poultry).

Agricultural pests were a problem that prompted some biologists to study insect population dynamics. In the year 1897, three significant publications by entomologists concerned insect populations. Most mathematically ambitious was a study on "Les plantations de pins dans la Marne et les parasites qui les attaquent," by Ad. Bellevoye, member of Société Entomologique de France, and J. Laurent, Professor at the Lycée and at l'Ecole de Médecine de Reims. Their monograph offered hypothetical calculations on the population dynamics of a bee and its parasite for a period of three years (1897:101–103, 1977). Appearing in a regional science journal, it would have attracted little attention of biologists elsewhere, unless publicized.

Professor of Entomology Paul-Alfred Marchal (1862–1942), Institut National d'Agronomie, Paris, was France's leading entomologist. Leland Howard reminisced (1930:240):

> *It is impossible for me adequately to express my admiration for Marchal. Following a correspondence beginning in 1894, I have known him personally since 1902, have often visited him in his laboratory and in his home, and spent the better part of three months with him traveling in the United States.*

Marchal published a brief note, "L'équilibre numérique des espèces et ses relations avec les parasites chez les insectes" (1897), arguing that oscillations in populations of crop pests—Hessian fly, oat midge,

Fig. 1 (a) Paul Marchal. Howard 1930: plate 19. (b). Leland Ossian Howard. Web.

army worm—was due to increase in their parasite population that followed increase in host population. When host populations crashed, parasite numbers also crashed, which then allowed hosts to increase again. Marchal called attention to Bellevoye and Laurent's paper to a broad audience by summarizing their mathematical argument in his longer "Utilization des insects auxiliaires entomophages dans la lutte contre les insects nuisibles à l'agriculture" (1907, English 1908:353–354, 1977).

Third, USDA entomologist Leland Howard wrote "Study in Insect Parasitism: A Consideration of the Parasites of the White-marked Tussock Moth" (1897, 1977). Illinoisan Howard (1857–1950) had B.S. and M.S. degrees from Cornell University (1877, 1883) and had become Chief, USDA's Bureau of Entomology in 1894 (Howard 1933, Graf and Graf 1959, Mallis 1971:79–86, Hatch 1972, Sawyer 1999, Egerton 2013:73–74). He undertook this study because in 1895, "Washington suffered from an extraordinary outbreak" of *Orgyia leucostigma* (Howard 1897:6). Previously, the tussock moth had mainly attacked fruit trees, but after the English Sparrow spread throughout American cities, it had rid city shade trees of cankerworms, and tussock moths seemingly filled the void. The Washington, D.C., outbreak motivated Howard to study the known and potential parasites of tussock moths. In 1896, however, Washington did not experience a repeat of the 1895 outbreak, and instead of crediting the English Sparrow, he credited all those parasites of tussock moths he had just studied. Alfred Lotka

(1925:90–91) quoted Howard 1897:40 and provided a graph that illustrated Howard's account.

Howard undertook another investigation, assisted by W. F. Fiske, head of the USDA's Gypsy Moth Parasite Laboratory, Melrose Highlands, Massachusetts (Howard 1933:114); that laboratory was combatting European gypsy moths and brown-tail moths. Their monograph (1911, 1977) was detailed, well written, with numerous photographs and drawing, and included a historical introduction. Their monograph, Thomas Park wrote (in Allee et al. 1949:331):

> *discuss[ed] the natural causes of mortality in insect populations. They divide this mortality into two large categories: "catastrophic" and "facultative." Catastrophic refers to factors that destroy a constant percentage irrespective of the abundance of the form. Facultative refers to factors that destroy a percentage increasing as the density increases.*

Their study attracted broad attention, and the earliest extract in Tamarin's sourcebook, *Population Regulation* (1978:31–35), is from Howard and Fisk (1911:105–109). Tamarin commented (1975:29): "They believed in the balance of nature, a view prevalent among those who believe in density-dependent population regulation."

USDA entomologist Dwight Pierce (1881–1967), stationed at Dallas, Texas, led a team of three who investigated enemies of the boll weevil; their report of 1912 was similar to Howard and Fiske's in describing many boll weevil parasites, but it went further in publishing a notable diagram, "The Boll Weevil Complex," which focused upon the cotton plant, indicating both parasites and hyperparasites (reproduced in Egerton 2007:54, 2014*a*:68; on Pierce and Hood, see Egerton 2014*a*:71).

Simultaneous with studies on insect pests were studies on human predation. About 1880, the population of a subspecies of willow grouse, the red grouse *Lagopus lagopus scoticus*, in Scotland, began to decline, and concern over this popular game species motivated Lord Lovat to establish a Committee of Inquiry on Grouse Disease, whose report (Lovat 1911) became "one of the first population studies of birds," (Birkhead et al. 2014:372).

Another practical human predation problem was annual fluctuations in commercial catch of fish. Norwegian fisheries zoologist Johan Hjort (1869–1948), whom we met in part 51 (Egerton 2014*b*:397–401), was head of the Norwegian government fisheries department, 1900–1916, and since annual fluctuations in fish populations were significant enough to affect the livelihood of commercial fishermen, he studied the problem (Schlee 1973:222–229, Smith 1994). Government catch statistics on cod began in Norway in 1860, when nearly 24 million were caught. A few years later the catch dropped to about 11 million, and in mid-1890s the catch shot up to about 40 million. Hjort investigated several environmental factors and found a decisive correlation with the abundance of phytoplankton, which surely pleased German zoologist Victor Hensen, whose rather different research led him to a similar conclusion (Egerton 2014*b*:236). Hjort (1914) suspected that year classes that began with abundant phytoplankton could be identified in the catch for several years, and his study of annual growth lines on fish scales verified that.

The enthusiastic American zoologist Raymond Pearl (1879–1940), from New Hampshire, and a

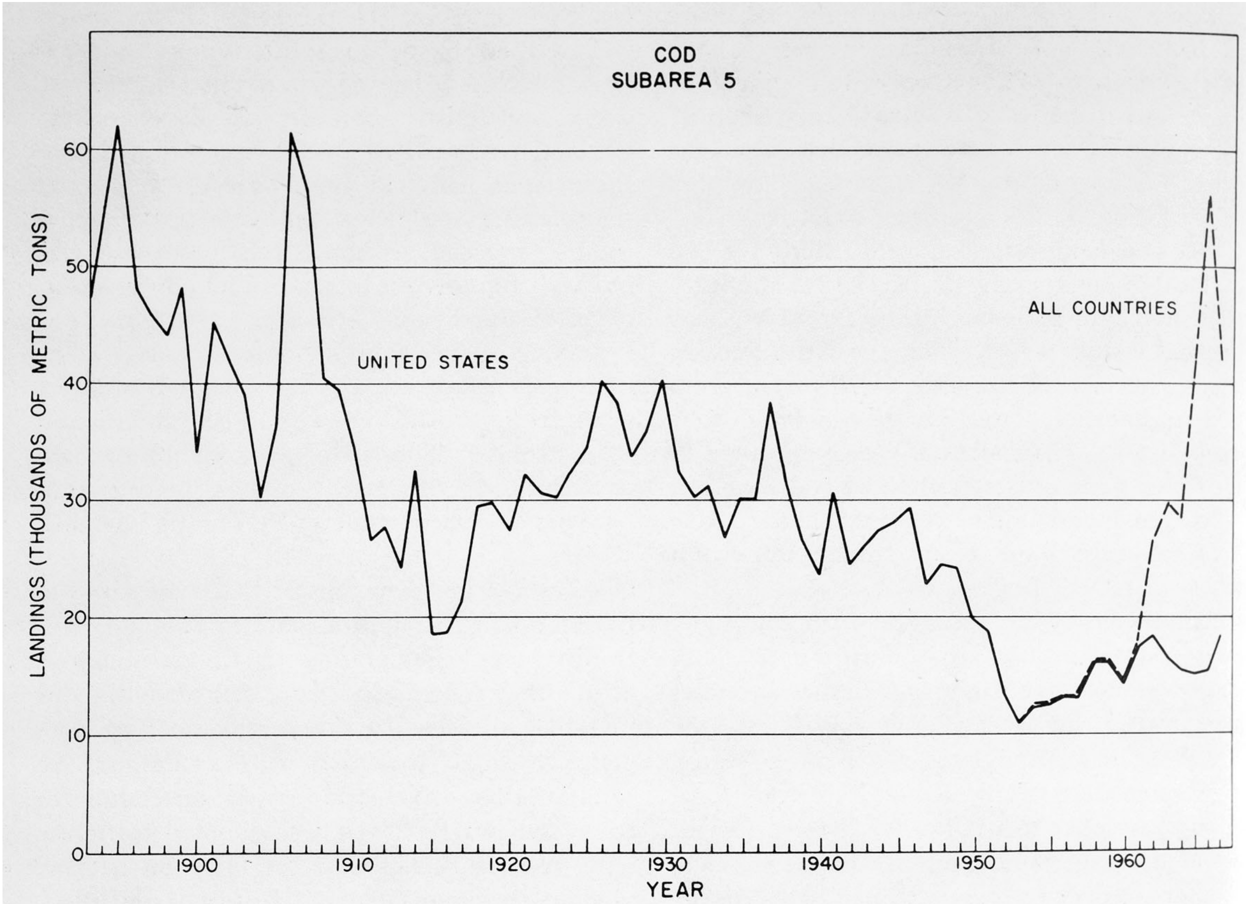


Fig. 2. Annual catch of cod from Georges Bank, 1883–1967. Graham 1970:250.

graduate of Dartmouth College (B.A., 1899) and the University of Michigan (Ph.D., 1902), gradually moved from the study of invertebrate physiology to genetics to human demography (Jennings 1943, Parker 1974, Kingsland 1985:56–76, Acker 1999). Pearl notably championed the logistic (sigmoid) curve as a mathematical tool to describe human population increase (Kingsland 1982). He developed this methodology unaware that the Belgian mathematician Pierre-François Verhulst (1804–1849) had achieved the same insight in three papers: 1838, 1845, 1847 (Kormondy 1965:64–69, Hutchinson 1978:16–20). The United States had taken a national census every decade since 1790, which provided data that Pearl and his mathematician colleague Lowell Reed used for their study, "On the Rate of Growth of the Population of the United States since 1790 and Its Mathematical Representation" (1920). However, their graph of population growth included a projection into the future to about the year 2000, which illustrated Pearl's tendency to think much beyond his data. Edwin Bidwell Wilson (1879–1964), a Harvard physicist, became a critic of Pearl's work (Kingsland 1985:87–95). The outcome of their controversy, and a lesser one between Pearl and Royal Chapman, was a more sophisticated appreciation of quantifying population questions (Kingsland 1985:96–97).

In the 1920s, animal ecologists were not highly trained in mathematics, and two science-oriented mathematicians, American Alfred Lotka (1880–1949), and Italian Vito Volterra (1860–1940), in mid-1920s and later, published explanations of how mathematics could be used to calculate animal population dynamics (Whittaker 1941, Scudo 1971, 1984, Gridgeman 1973, Volterra 1976, Scudo and Ziegler 1978, Kingsland 1982, 1985:25–49, 102–116, 1991:7–10, Fuchsman 1999). Pearl recruited Lotka to his Johns Hopkins laboratory for two years while Lotka wrote *Elements of Physical Biology* (1925). Volterra became interested in population dynamics by the influence of his soon-to-be son-in-law Umberto D'Ancona, who was studying Adriatic fishery statistics (Scudo 1971:2, 1984:23–26, Israel 1993:487–492). In 1926, the year after Lotka's book appeared, but without knowledge of it, Volterra published the first of his population studies in Italian, with summary in English (Volterra 1926*a*, *b*). The longer version is now also available in two English translations (Volterra 1931*a*, 1978). Kenneth Watt (1962:245–247) provided a critical discussion of strengths and weaknesses of Volterra's longer 1926 article, and found: "all the conclusions which Volterra draws out in a very thorough monograph are perfectly valid deductions from the assumptions he makes. However, the assumptions are not drawn from biological reality." Reality would involve more variables than could be conveniently added to the calculations.

Lotka saw Volterra's brief summary article (1926*b*) in *Nature* and immediately wrote a letter to *Nature* dated 29 October 1926 with a claim of priority, which the editor obviously sent (or a copy) to Volterra, since Lotka's letter and Volterra's reply both appeared in the first issue of 1927 (Lotka 1927, Volterra 1927). Both letters were reprinted by Israel (1993:496–497). But Lotka also wrote directly to Volterra. Between 2 November 1926 and 19 January 31, Lotka sent five letters to Volterra and Volterra sent three replies that are now also published (Israel and Millán Gasca 2002:280–288). Lotka wrote his first letter in French and later ones in English. Volterra wrote his replies in Italian. Their correspondence was entirely cordial, and the last letter was from Lotka thanking Volterra for sending him a copy of his *Lecons sur la théorie mathématique de la lutte pour vie* (1931). Egbert Leigh (1968) discussed at length the virtues of this treatise.

In 1926, Volterra was already a well-established leading mathematician, whose work attracted much more attention than did Lotka's. Scudo (1984:20) suggested that Lotka's book was too broad in scope: "Possibly by having thus overwhelmed most readers it was on the whole a flop, as Lotka bitterly lamented shortly after in letters to Volterra." Kingsland (1985:211), however, suggested that Lotka had published too early, and lacked a biological audience, though entomologists William Thompson, William C. Cook, and Royal Chapman would soon appreciate the utility of Lotka's work (see below).

A major concern for Volterra was reconciliation of mathematical calculations and theory with real biological data. He began with a real fisheries question, and he persisted in comparing mathematical calculations with biological data (Millán Gasca 1996:5–6, page numbers of reprint, 2002). Only three of the population ecologists with whom Volterra communicated were mathematically adept—Thompson, Gause, and Kostitzin--a Canadian and two Russians. The only theoretical biology Volterra knew was Darwin's theory of evolution by natural selection. The ecologist who wrote to Volterra wrote about real problems rather than theoretical problems.

Volterra's major collaborator on biological mathematics was Russian Vladimir Kostitzin (1882/1883–about 1963), who had been a revolutionary in early 1900s (Scudo and Ziegler 1976:396, Scudo 1984:31–

32). Kostitzin's wife Julie, a parasitologist, moved to Paris in mid-1920s, and he followed her by 1927. In 1931, Volterra refused to sign a loyalty oath imposed by Italy's Fascist government on professors, and he moved to Paris (Volterra 1976:86), where he lectured on animals struggling for existence, which attracted Kostitzin's interest. Kostitzin had already coauthored with his wife a mathematical analysis of a parasitic relationship between hermit crabs, *Eupagurus cuanensis*, and parasitic barnacles, *Chlorogasdter sulcatus* (Kostitzin and Kostitzin 1931). In 1934 Kositzin published *Symbiose, Parasitisme et Évolution*, followed by *Biologie mathématique* (1937, English, 1939). He wrote more papers than anyone else in Scudo and Ziegler's *Golden Age of Theoretical Ecology* (1978). The published Volterra–Kostitzin correspondence covers 42 pages (Israel and Millán Gasca 2002:225–266); however, Volterra died in 1940, and thereafter Kostitzin corresponded with Volterra's widow, Victoria (9 of those 42 pages), until 1962. Julie Kostitzin had died in 1950.

Italian mathematician Giorgio Israel contrasted Lotka and Volterra's contributions (1988:37):

> *Volterra's approach was strictly adherent to the classical physico-mathematical paradigm, while Lotka's point of view was more eclectic and open-minded as regards the new developments of physics, and somewhat skeptical about formal statements….while Volterra followed the 'mechanical analogy' Lotka had an inclination for the 'thermodynamic analogy' and had a great interest for the energetic problems in population dynamics.*

Israel quoted from two of Voltera's letters to Lotka, with English translations in footnotes, and quoted a long passage from Volterra's "Les mathématiques dans les sciences biologiques et sociales," also with English translation in a footnote. This paper showed Volterra's general interest in using quantitative methods in biological and social sciences before his future son-in-law interested him in population dynamics. Peter Wangersky's "Lotka–Volterra Population Models" (1978) is not an earlier paper on the same subject as Israel's; instead, Wangersky used their names as a general indication of his topic, which was really an explanation of mathematical population models.

Israel later published an excellent discussion of how Lotka and Volterra's contributions fit into the larger picture of population dynamics in the 1920s, including a discussion of their priority dispute (1993).

Russian zoologist Vladimir Alpatov, who first taught ecology in Moscow (Weiner 1988:66), gained access to several papers by Pearl and wrote to ask if he could come to Johns Hopkins University to study under him (Kingsland 1985:146–148). Pearl obtained a grant from the Rockefeller Foundation which enabled Alpatov to do so, 1927–1929. After returning to Moscow, Alpatov discussed Pearl's work with one of his students, Georgii Gause (or Gauze, 1910–1986), who had already conducted a survey of grasshoppers in the northern Caucasus Mountains and developed a mathematical formula to study the relationship between species abundance and environmental factors, which appeared in *Ecology* (Gause 1930).

Both Alpatov and Gause thought it would be very beneficial for Gause to spend a year at Pearl's laboratory, a move that Pearl encouraged (Kingsland 1985:149). Gause generalized from his grasshopper study to "Ecology of Populations," which appeared in Pearl's *Quarterly Review of Biology* (1932). However, despite Gause's publications, the Rockefeller Foundation turned down a travel fellowship, because Gause was only 22 years old in 1932. Gause began experiments on populations of microorganisms

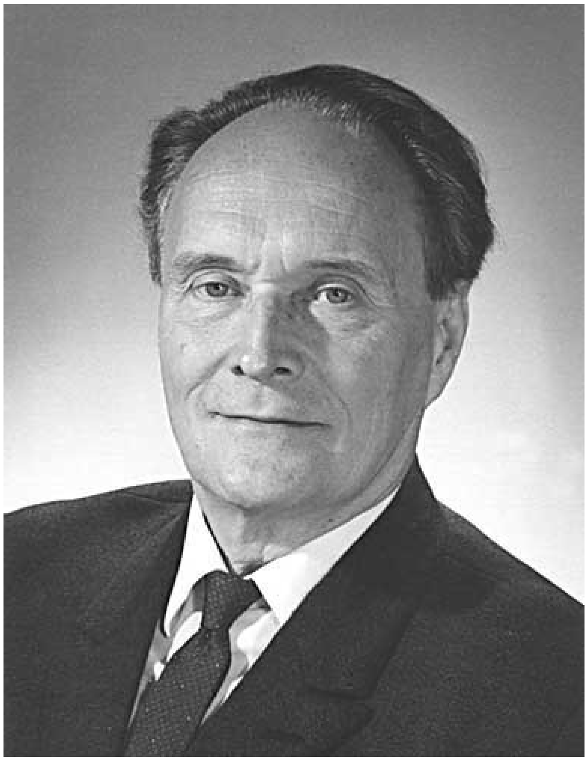
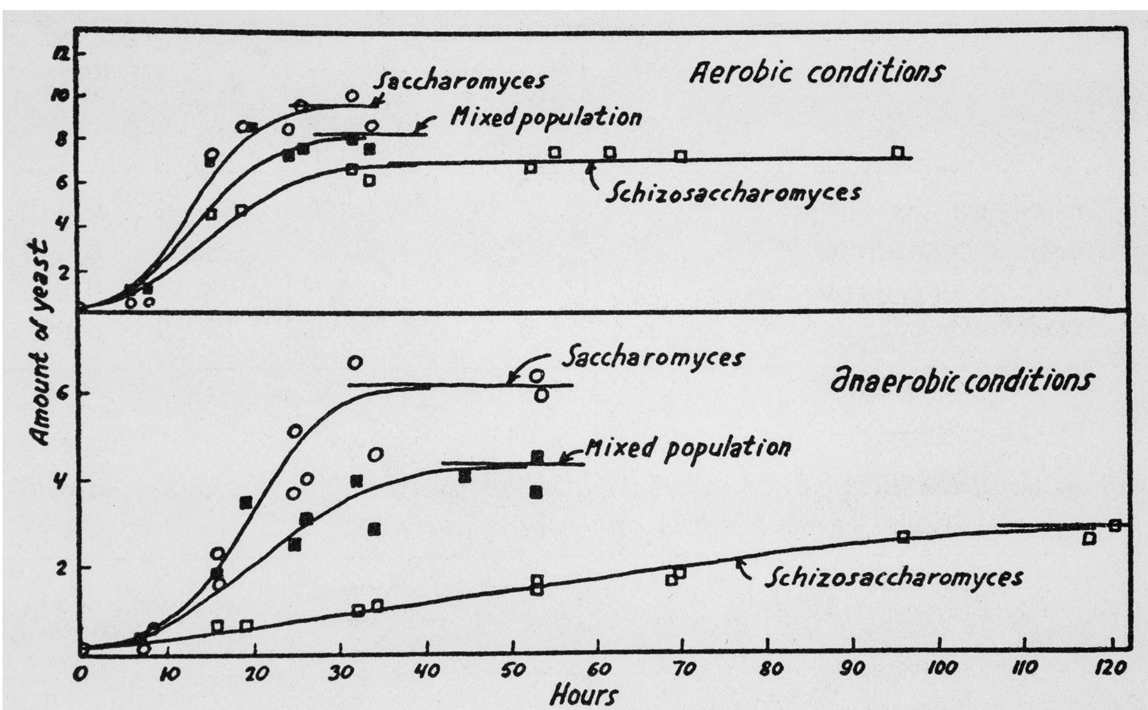


Fig. 3. (a) G. F. Gause. Web. (b) Growth in volume of *Saccharomyces cerevisiae, Schizosaccaromyces kephir* and mixed population, aerobic (above) and anaerobic (below). Gause 1934:85.



in a laboratory, and he hoped that if he wrote a book about his experimental population studies with microorganisms, the book could bolster his chances for a fellowship. Pearl was receptive, and so Gause conducted experiments on two basic phenomena concerning species relations: competition and predation. He also solicited assistance. On 12 November 1932 Gause wrote to Volterra, thanking him for a letter and a copy of a recent article and mentioning some current research (Israel and Millán Gasca 2002:212–213). He then acknowledged limits to his mathematical ability and invited a collaboration:

> *I am working in the field of experimental biology, and I am not qualified enough to analyze more closely the mathematical part of the problem and it would be very interesting if it will be possible for you to investigate these equations in the future, and to find their solution in the general form.*

Volterra responded in Italian in an undated letter. Volterra did collaborate with a few colleagues, but Gause seems not to have been one of them. In a letter of 12 October 1933, Gause wrote to Volterra telling of his pending book, *The Struggle for Existence*, and that he had confirmed experimentally some of Volterra's mathematical projections, and requesting any papers he had published since 1931 (Israel and Millán 2002:213–214). Gause had confirmed the results of competition between two similar species for the same resource, leading to the extinction of one species (Gause 1934*b*:89, 113), now called Gause's axiom, "the competitive exclusion principle."

Not mentioned in his letter was his finding on predation (1934*b*:140):

> *We expected at the beginning of this chapter to find "classical" oscillations in numbers arising in consequence of the continuous interactions between predators and prey as was assumed by Lotka and by Volterra. But it immediately became apparent that such fluctuations are impossible in the population studied, and that this holds true for more than our special case.*

Even before the book appeared, Gause published a preview note in *Science* (1934*a*:16) with the same mixed message: "Experiments on the competition between two species for a common place in the microcosm agreed completely with Volterra's theoretical equations, but as regards the processes of one species devouring another our results are not concordant with the forecasts of the mathematical theory."

His book became "a foundation stone of ecology" (Hutchinson 1978:120). It is fortunate that Gause had already made arrangements to publish in America, because in January 1934, at an Ecological Conference of the Academy of Sciences' Botanical Institute, a fanatical Stalinist ecologist, I. I. Prezent, denounced Alpatov and Gause for their use of mathematics in their "formalist, mechanist school" (quoted in Kingsland 1985:160–161, Weiner 1988:222). Subsequently, it might have been difficult for Gause to publish that book in the USSR. Gause continued for some years to publish papers in western journals, but he also decided it would be expedient for him to forget about going to America for a few years and instead do research in microbiology.

Two ecologically oriented entomologists, Canadian William Thompson and American Royal Chapman, were receptive to mathematical assistance from Lotka and Volterra (Graham 1941, Thorpe 1973, Kingsland 1985:123, 127–131). Thompson (1887–1972), from London, Ontario, earned his B.A.

degree at the University of Toronto (1909). In summer 1908, he worked at the USDA Gypsy Moth Parasite Laboratory (discussed above) and in 1909 the USDA sent him to Cornell University to study for a M.S. degree (1911) under Professor Comstock. In 1912, USDA sent him to Professor Filippo Silvestri's Instituto Superiore Agrario, Portici, Italy. In 1913 he resigned from USDA and went to Paris to study under Professor Maurice Caullery. In 1914, he went to the Zoology Department, Cambridge University, to study bacteriology and protozoology. During World War I, he joined the Royal Naval Medical Service and became an assistant in a clinical laboratory. In 1918, he returned to Paris and resumed studies of dipterous parasites, and earned a Ph.D. degree (1921). In 1919, he had married artist Mary Carmody, who became an insect illustrator and illustrated his papers. Leland Howard, at USDA, re-employed Thompson in 1919 and put him in charge of a European Parasite Laboratory, which he established at Hyères and ran for nine years. In 1929 Thompson returned to England to run the Farnham House Laboratory to study insect parasites and predators for the British Empire. During World War II, Farnham Laboratory closed and he returned to Canada as Director of the Imperial Parasite Service, Canadian Department of Agriculture. In 1948–1958 he established biological control laboratories in California, Trinidad, Uruguay, Switzerland, India, and Pakistan.

Thompson wrote seven letters, published posthumously, to Volterra, 29 July 1927–23 March 1931, but there is only one undated letter in response from Volterra (Israel and Millán Gasca 2002:368–373). Both wrote in French except for Thompson's last letter in English. With his first letter, Thompson sent a copy of several of his published papers and requested in return a copy of Volterra's longer 1926 paper, in Italian. Volterra responded, thanking him for sending his very interesting works and explained that his copies of that article were all gone, but that more copies were being printed and he would soon send one. On 23 August 1927, Thompson thanked him for a letter of August 16 and stated he hoped to publish in winter a small book on insect parasitology. On September 3, Thompson wrote to thank Volterra for sending him "votre grand travail publie par l'Academie dei Lincei." In a letter of 5 February 1931, Thompson thanked Volterra for sending him a copy of his *Leçons sur la théorie mathématique de la lute pour la vie* (1931) and lamented that his own mathematician collaborator, Soper, at the College of Tropical Medicine, had died, though they had a joint paper in press.

Culminating Thompson's researches was "Biological Control and the Theories of the Interactions of Populations" (1939), with a 27-page historical survey, beginning with Charles Darwin and including his own researches. He discussed Lotka and Volterra, but was wary of zoologists who substituted mathematical calculation for few field data (1939:381): "mathematical construction is so elegant and impressive that there is already a tendency to overestimate its value and to offer it as a description of what really happens in nature…." He had recently published a polemic, *Science and Common Sense: an Aristotelian Excursion* (1937), which made this point as well as attacking Darwin's theory of evolution by natural selection (Kingsland 1985:135–141).

Howard and Fiske's 1911 concepts of "catastrophic" and "facultative" causes of mortality for insects had been useful, but Thompson (1928) rejected their terms in favor of "general" and "individualized." Yet, Harry Smith (1935:889) decided that Thompson's terms were not much improvement, and he coined "density-independent" for weather causes and "density-dependent" for biotic causes of mortality. Smith's terms were accepted for some time, but Dempster (1998) suggested population *limitation* rather than *regulation*, and Berryman et al. (2002) urged a "requiem for density dependence," and Price et al. (2011:357) concluded that "population is regulated at some times, and not at others…"

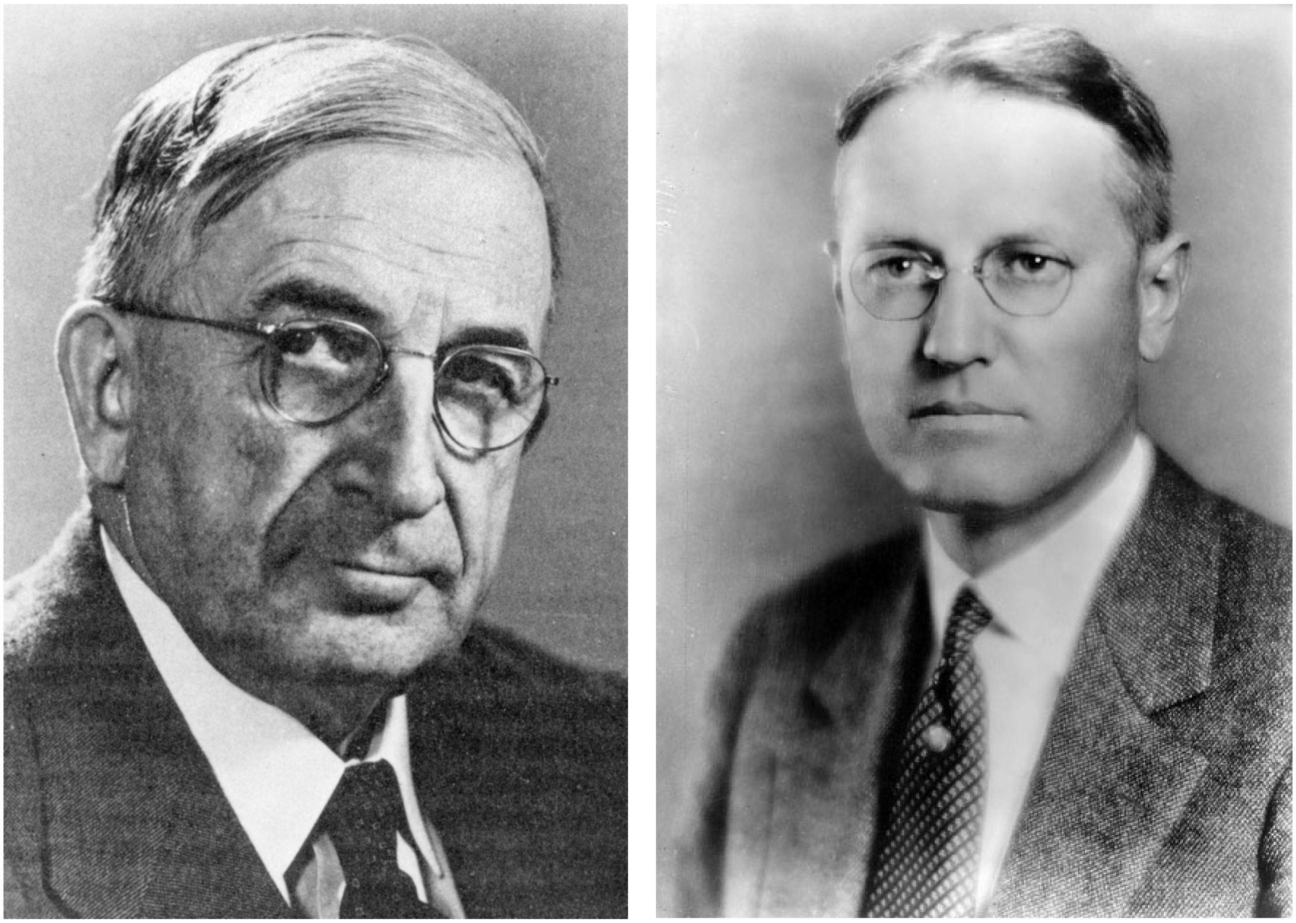


Fig. 4. (a) William Robin Thompson. Thorpe 1973. (b) Royal Norton Chapman. Web.

Minnesotan Royal Chapman (1889–1939) earned his B.A. and M.A. degrees (1914, 1915) at his state university and his Ph.D. (1917) at Cornell University. He returned to the University of Minnesota as a faculty member and developed an ecology course—the first at that university. His course emphasized "controlled experiment and quantitative field studies" (Graham 1941:522). In his *Ecology* paper, "The Quantitative Analysis of Environmental Factors" (April 1928), Chapman cited two of Volterra's papers, showing ecologists a worthwhile challenge which they would do well to master. However, he may not have seen them himself, for he wrote to Volterra on 9 August 1928 announcing he was sending him his own recent papers and requesting Volterra to send him his long 1926 paper (Israel and Millán Gasca 2002:123). In 1928 Volterra thanked Chapman for his interesting papers (Israel and Millán Gasca 2002:124); he was writing from Naples but would send him some reprints when he returned to Rome. On 26 September 1928 Chapman wrote and thanked him for reprints. Volterra wrote back asking for information on "qualitative and quantitative results of population fluctuations" (as Chapman paraphrased in English Volterra's request in his response of 28 January 29). Chapman sent him some reprints and also a manuscript not yet published. Chapman also wrote of a student, John Stanley, "who is taking work in mathematics and who is setting up a series of experiments in which we will have *Tribolium confusum* competing with a similar species, *Tribolium ferruginium*" and "we hope from this that we can get the substantiation of your calculations for the cases where two species compete for the same food" (Israel and Millán Gasca 2002:125). Chapman's textbook, *Animal Ecology with Especial Reference to Insects* (1931) had as an appendix an English version of a 40-page article by Vito Volterra, "Variations and fluctuations of the number of individuals in animal species living together." Chapman's own text never used Volterra's sophisticated mathematics, and Kingsland (1985:128) suggested that Chapman reprinted the article to add an aura of exactness to an insecure ecological science. The above-cited correspondence between Chapman and Volterra was unpublished when Kingsland wrote, and she seemed unaware of its existence.

A(lexander) J(ohn) Nicholson (1895–1969) was born in Ireland to English parents who soon moved to Birmingham, where he grew up and attended the city university, earning B.Sc. and M.Sc. degrees (1915, 1920 [Mackerras 1970]). Between earning those degrees, he served in the Royal Field Artillery during World War I as a second lieutenant, was promoted to first lieutenant, and received a King's Commendation for bravery. In late 1920 he received appointment as McCaughey Lecturer on Entomology at the University of Sydney and departed for Australia, via the United States, where he visited entomology laboratories for several months. In an entomology class he taught in Sydney, he itemized factors which limit the increase in insect populations, one of which was food (Egerton 2014*c*:59). A student challenged this claim, saying insect pests did not consume all available food. Nicholson realized that as a pest species became numerous, so did its predators and parasites (Kingsland 1996).

In 1930, Nicholson joined the Entomology Division of what later became the Commonwealth Scientific and Industrial Research Organization, where he had administrative duties and conducted research. Howard and Fisk (1911) had begun an informal "biotic school of population dynamics," and Nicholson (1933, Nicholson and Bailey 1935) became its chief defender. "Nicholson's 'Balance of Animal Populations' (1933) is probably the most important single paper published on population regulation, having sparked the many controversies in this field" (Tamarin 1978:29; Kimler 1986:223–227). What was so special about that paper? First, it was quite long, 47 pages, which enabled Nicholson

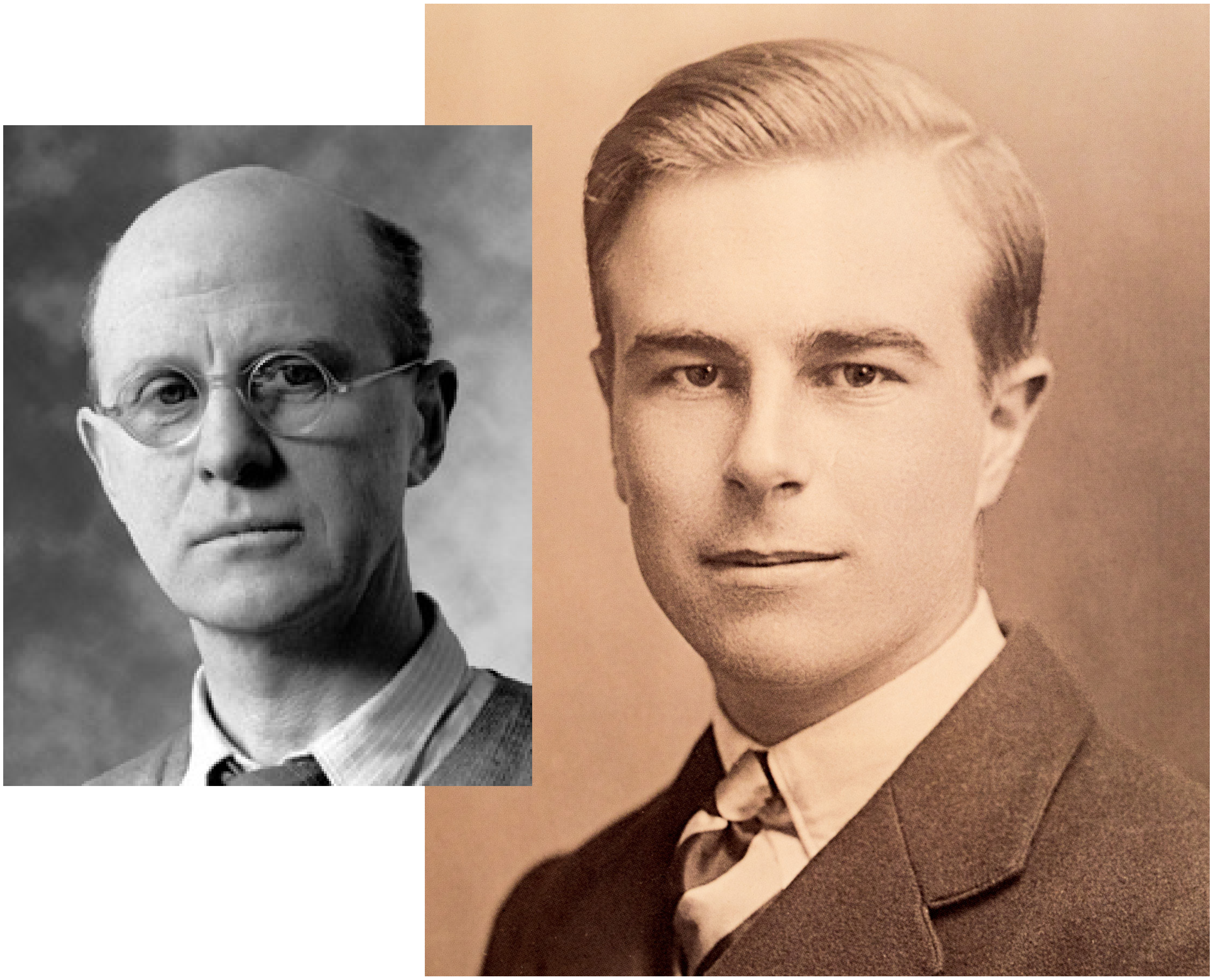


Fig. 5. (a) A. J. Nicholson. Australian Dictionary of Biography (online at Nicholson). (b) Frederick S. Bodenheimer. W. Junk brochure advertising five books by Bodenheimer.

to explore a new science of population dynamics, though he did not name it. Second, although this paper was not mathematical, his new science was quantitative, and this paper has 11 graphs based upon quantitative studies. Third, his science had both adequate data and theory based upon that data. His mathematical science was based upon cooperative research with University of Sydney physicist V. A. Bailey, and soon they published a paper with the same title, "The Balance of Animal Populations" (Nicholson and Bailey 1935, 48 pages) that covered the same terrain as the 1933 paper, but showing calculations upon which the study was based. Their paper also acknowledged the earlier quantitative works of Lotka, Volterra, and Thompson, initially unknown to them.

Nicholson assumed that a species fluctuated within certain limits: as its population increased, limiting factors gained intensity, and when its population declined, those factors became less intense. His 1933 paper defended his concept of the balance of nature against skeptics who dismissed the concept. He clearly had Elton (1930:17) in mind, as he listed that book in his bibliography. He explained his concept of such balance using the metaphor of a balloon floating in air; it rose in elevation when the air became warm and sank when air became cool, with air representing limiting factors that impinge upon a population (represented by the balloon). Not only did Nicholson defend his own hypothesis, he also cited and discussed papers published by an abiotic school of population dynamics, which he opposed, though he did not name either "school." However, he cited the work of Bodenheimer (1928) and of Uvarov (1931) as emphasizing climatic influences on populations (Nicholson 1933:134–137). Kenneth Watt (1962:247) had the same critique of Nicholson and Bailey's mathematical model (1935) as for Volterra's: "The specific conclusions follow correctly from the specific assumptions made. However, the conclusions do not relate to biological reality unless the assumptions relate to biological reality." Nicholson offered an inadequate number of assumptions.

Frederick Bodenheimer (1897–1959) had a background similar to Nicholson's: both were educated in their home country, served in World War I (Bodenheimer as a medic with the German army), and subsequently immigrated to their future home country, where each began learning native animal ecology. Bodenheimer had been born into a Zionist family of German Jews (Bodenheimer 1959). He immigrated to Israel in 1922, a year after Nicholson had immigrated to Australia. He was not a theoretician, and was content to conduct original investigations and then write two synthesis volumes, the first of which was *Problems of Animal Ecology* (1938). Boris Uvarov (1889–1970) graduated from St. Petersburg State University, Russia in 1910 and began research on grasshoppers and locusts, which became his life's work (Wigglesworth 1971, Waloff and Popov 1995). In 1920 the British government invited him to come to London to conduct research, and he remained there. Bodenheimer and Uvarov studied species that lived in arid regions, which species they saw as controlled by weather. Uvarov's most influential study was "Insects and Climate" (1931).

Bodenheimer (1925*a*, *b*, 1926, 1927, 1928) and Uvarov (1931) provided evidence for an "abiotic school on population dynamics," which Andrewartha and Birch (1954) further developed. Often when scientific controversies develop, each group has part of an answer, which it sees as the whole answer. Price (2003:17–18) argued that the biotic vs. abiotic schools was such a case.

Ecologist Charles Elton (1900–1991), son of an English literature professor at Manchester, and later at Liverpool, attended Oxford University and never left. He was the first leader of British animal ecology (Cox 1979, Paviour-Smith 2004). He participated in three Oxford zoology expeditions to Arctic islands of Spitsbergen (now Svalbard), 1921–1924, and he was junior author of two expedition reports with Oxford botanist Victor Summerhayes (1897–1974), the first of which contained a notable diagram of a food chain that must have been mainly or entirely by Elton, as it mostly involves animals (Summerhayes and Elton 1923, 1928, Cox 1979:17–28, Egerton 2007:58, Stolzenburg 2008:7–10). During those years Elton also published "Periodic Fluctuations in the Numbers of Animals: Their Causes and Effects," in which he attributed fluctuations to climatic fluctuations (1924:119). His first example was of lemming migrations in southern Norway; many attempted to swim across the ocean and drowned. Adult pairs had territories, and the migrants were young of the year searching for their own territories, after reproduction had been very successful. For the years 1862–1909, the "mean period [of fluctuation] between maxima is 3.6 years" (Elton 1924:127). Meteorological data from Kew showed no correlation with the 11-year sunspot cycle, and this was undoubtedly also true for Norway. Hudson Bay Company's trapping data from Canada indicated cycles in populations of Arctic foxes, which might correlate with lemming population cycles. However, field mouse plagues occurred on an eleven-year cycle which might correlate with sunspot minima (Elton 1924:141), since more storms occur during sunspot maxima. Elton's 1924 data was obviously suggestive, not definitive.

Elton published the second animal ecology textbook (first in Britain), which had two chapters on population ecology (1927:101–145), without any calculations. Liebold and Wootton (2001:xix) attributed the importance of Elton's book partly to its formulating basic questions that remain important, and partly to its "highly synthetic view of how to approach the field." Elton (1927:130) accepted an 11-year sunspot cycle as relevant for some species' population cycles, but he gave up on that correlation in his *Voles, Mice and Lemmings: Problems in Population Dynamics* (1942). Elton's field research in 1927 and later was on the population fluctuations of rodent species in the Bagley Wood near Oxford (Crowcroft 1991:1–12). In *Animal Ecology* Elton argued there were five important checks to population increase (listed by Cox 1979:51):

1) Food (food chains and food cycles)
2) Environmental instability (especially climatic variability)
3) Disease (including parasite-borne epidemics)
4) Hereditary powers of increase
5) Intrinsic or "automatic" means of control.

David Cox (1979:51–66) explained Elton's argument on each check. Two distinctive concepts that Elton publicized were niche and pyramid of numbers (Elton 1927:63–70). Neither concept was original with him (Cox 1980, Kingsland 1985:156–157, Egerton 2007), but Elton provided the ecological context in which both could be more fully appreciated than before. Three historians of ornithology (Birkhead et al. 2014:357-359), however, find some "muddled thinking" in Elton's discussion of population dynamics and suspected that his muddled thinking later led Wynne-Edwards astray (discussed below).

Publication of *Animal Ecology* brought notice beyond Oxford, and in 1929 he delivered three lectures at the University of London, an expansion of chapter 12 of *Animal Ecology* (1927:179–187), which he published as a 96-page book, *Animal Ecology and Evolution* (1930), since he found that animal ecologists tended to ignore evolution's significance. The first lecture-chapter was on "The Regulation of Numbers," in which he asserted that the balance of nature does not, and never has existed (Elton 1930:17, quoted in Egerton 1973:344). This claim was more controversial than his emphasis upon the concepts of niche and pyramid of numbers, and he failed to banish the balance of nature concept from ecology.

In 1931, after Elton had participated in the Matamek Conference on Biological Cycles in July, the president and the director of the New York Zoological Society, who was also present, awarded him a two-year grant that enabled him to establish a Bureau of Animal Population (BAP) at Oxford in 1932 (Cox 1979:158, Crowcroft 1991:11–12). Elton explained: “The main aim of the Bureau is to get further knowledge of fluctuations in numbers of wild animals, with special reference to disease and other factors causing them” (quoted in Crowcroft 1991:13). The Zoology Department at Oxford provided modest support, but Elton had to seek other grants to keep it going. The Agricultural Research Council in Britain judged his goal worthy of its support. Also in 1932, Elton persuaded the British Ecological Society to initiate its *Journal of Animal Ecology*, with him as editor.

“The Bureau of Animal Population was for thirty-five years one of the world’s foremost institutes for the study of animal ecology” (Cox 1979:164). In January 1932, BAP consisted of Elton, Doug Middleton, and graduate student D. H. S. Davis (Crowcroft 1991:13), but it grew, though not rapidly or to a large size (Kingsland 1985:132–133). In 1931 Volterra sent Elton a copy of his book on the struggle for existence, and in return, Elton sent him some reprints and wrote the first of seven letters, now published, to which Volterra replied in two published letters (Israel and Millán Gasca 2002:203–208). In 1935, mathematician Patrick L. Leslie (called “George”) came to BAP to do laboratory research and to advise others on mathematical questions (Kingsland 1985:133, Crowcroft 1991:21–22). Leslie could explain the mathematical reasoning in Lotka’s work, and Elton wrote to Lotka for a portrait which he hung in the BAP library. Lotka and Elton had a slight influence on each other (Scudo 1984:39). Leslie remained at BAP until it closed in 1967. Elton’s last four brief letters to Volterra (1936), lacked any mention of Leslie.

Elton’s 500-page *Voles, Mice and Lemmings: Problems in Population Dynamics* (1942) represented the work that he and his colleagues and students had accomplished during 16 years. It contains some statistical data and a few graphs, but little to challenge Leslie’s mathematical skills. This book is divided into four parts: (1) on historical records concerning vole and mouse plagues from around the world; (2) on fluctuations in populations of voles, mice, and lemmings in Britain and Scandinavia in modern times; and (3) and (4) on modern information concerning rodent fluctuations in Labrador and Hudson Bay. In a three-page review, Evelyn Hutchinson (1942) summarized Elton’s rather tentative conclusions, along with his own interpretations, for Elton seemed to invite readers to reach their own conclusions from his data.

David Lack (1910–1973) was a son of a prominent London physician and a former actress. At age 14, he went to Gresham School on England’s east coast, and became active in the school’s Natural History Society (Anderson 2013:8). That society sponsored field trips, which encouraged Lack’s growing interest in birds, and a few other boys shared that interest. In 1926, he won the society’s annual essay competition for original observations with “Three Birds of Kelling Heath,” on nesting nightjars, redshanks, and ringed plovers—all ground-nesting species (Lack 1973:423). Twice he also won the Silver Medal of the annual school contest sponsored by the Royal Society for the Protection of Birds, with essays on birds of Romney Marsh (1927) and nightjars of Kelling Heath (1928).

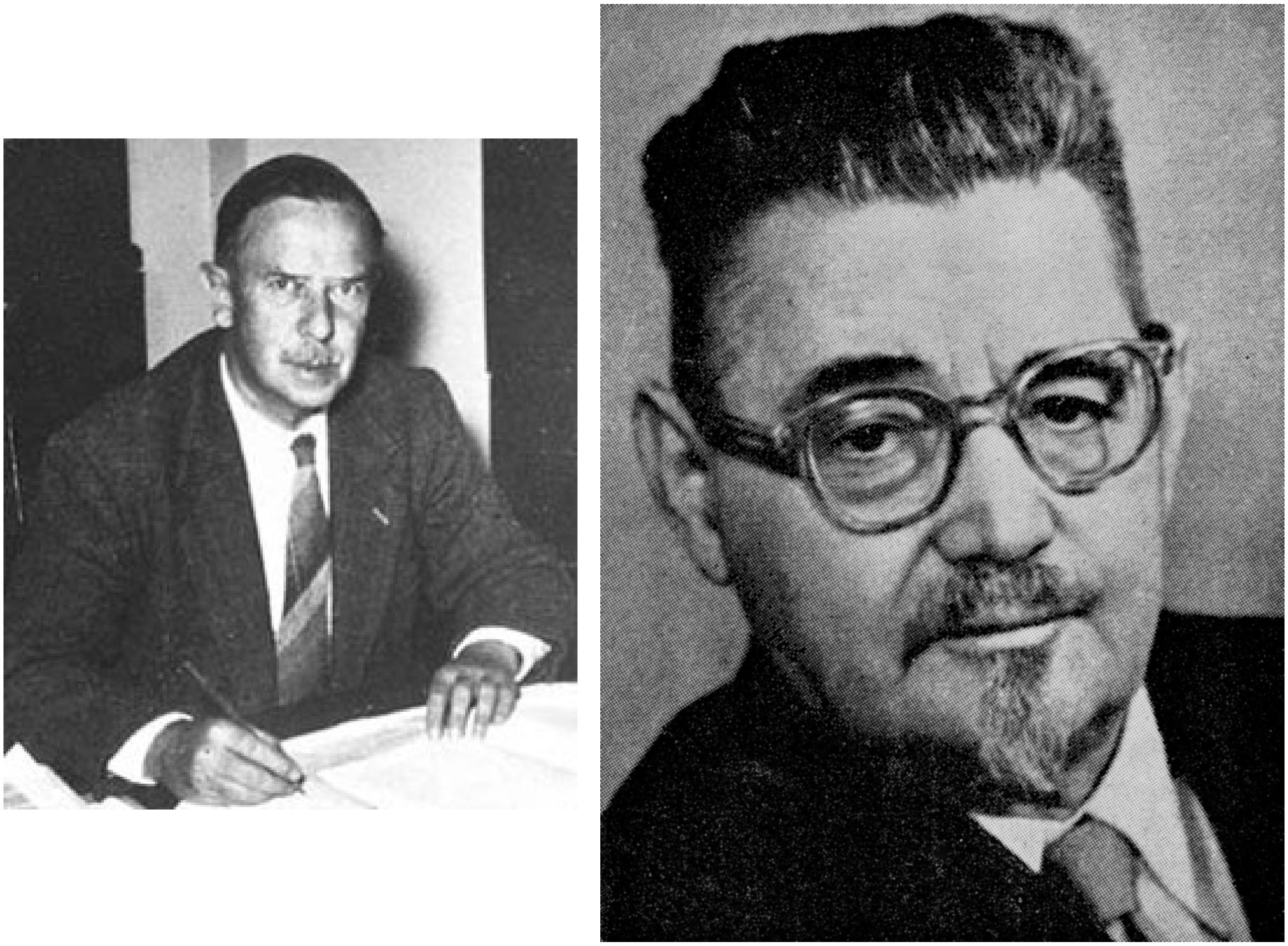


Fig. 6. (a) Charles S. Elton. Web. (b) David L. Lack. Anderson 2013:cover.

David declined his father's wish that he study medicine, and studied zoology. However, at Cambridge University he was excited by neither comparative morphology nor invertebrate embryology (Anderson 2013:14–15). He became president of the Cambridge Ornithological Club, and he participated in Cambridge expeditions during the summers of 1931–1933, coauthoring two articles on Bear Island. He earned a B.A. degree (1933) and paid a fee for a M.A. degree (1935). In 1934 he published *The Birds of Cambridgeshire*. In 1933, Julian Huxley helped Lack obtain a position as science teacher at Dartington Hall School, five miles from England's southeast coast. Much later, one of his former students, Eva Wiesner Ibbotson (1925–2010), who gained prominence as an author, remembered Lack as her best teacher (Ibbotson 2006, quoted in Anderson 2013:35): "He helped me to see biology as a fascinating, rich subject."

Because Lack continued publishing on ornithology while at Dartington (Bircham 2007:375–376), Huxley was able to obtain research funds for him to lead a research expedition to the Galapagos Islands in 1938 (Anderson 2013:51–65). Living conditions there were uncomfortable, but the outcome was a well-remembered book, *Darwin's Finches* (1947*a*). During World War II, Lack became a civilian advisor to the army, and while working with radar discovered he could detect migrating birds with it (Thorpe 1974:275). In 1945, he was a prominent enough ornithologist to be appointed the second head of the Edward Grey Institute of Field Ornithology (EGI) at Oxford University. It was named for a former chancellor of Oxford University and had an endowment that saved it from the precarious financial predicament that haunted Elton's BAP. Since BAP emphasized mammals and EGI birds, they did not compete in subject matter, but they were campus neighbors, which enabled Elton to see a younger colleague manage a more secure operation that did not disappear when Lack's directorship ended, as BAP did upon Elton's retirement. They never became friends. In 1949, Cambridge University conferred on Lack a Sci.D. degree for his book on the 14 species of Galapagos ("Darwin's") finches.

The foundation of both Elton and Lack's ecological thinking was Darwin's *Origin of Species* (1859). Lack's biographer, Ted Anderson, called Lack "father of evolutionary ecology" (2013). Animal ecologist James Collins discussed Lack (1986:268) but not Elton in his "Evolutionary ecology and the use of natural selection in ecological theory," though without claiming Lack as "father of evolutionary ecology." Anderson's claim may depend upon the fact that Lack's *The Natural Regulation of Animal Numbers* (1954) was more influential than Elton's *Ecology and Evolution* (Bircham 2007:see index, Birkhead 2008:see index, Birkhead et al. 2014:see index) Daniel Botkin, wrote two books (1990, 2013) based largely upon the premise that ecologists did not take evolution seriously in their thinking. Neither Botkin nor Anderson cited Collins' article (1986) nor Price's more recent (2003:25–42) accounts of "Evolutionary ecology" and "Evolutionary perspective on population dynamics." Collins and Price provided a range of citations that Anderson and Botkin should have explored.

Tamarin (1978:92–93) suggested that Thompson was the first of a "compromise school of population regulation." This school saw some truth in both the biotic and abiotic schools of population regulation. Thompson (1939:319–321) also responded to Nicholson and Bailey's criticisms of his earlier work.

Edward Deevey (1914–1988) graduated summa cum laude (1934) from Yale University, and became a doctoral student under Evelyn Hutchinson, with a dissertation on paleolimnology—having little, if any, relevance for population ecology. Yet he shared Hutchinson's interest in quantitative ecological studies, and he explained to ecologists the utility of "Life tables for natural populations of animals" (1947) and how to construct them. There was no stampede to follow his example, because few ecologists in 1947 had a requisite mathematical training. Peter Price (2003:19) praised R. F. Morris and C. A. Miller for "The development of life tables for the spruce budworm" (1954), but they explained that they were adapting Deevey's methods to insects. Deevey's life tables were derived from examples of human life tables compiled for actuarial purposes to set insurance rates. Life tables are a valuable tool for animal population studies, if available.

Illinoisan ecologist brothers Orlando (1901–1969) and Thomas Park (1908–1992) earned their B.S. and Ph.D. degrees under W. C. Allee, University of Chicago (Burgess 1996:85), and they later became coauthors of Allee et al., *Principles of Animal Ecology* (1949). Both brothers researched insect ecology. Orlando Park studied species in natural environments, especially nocturnal species; after brief appointments at two other universities, he settled at Northwestern University. Thomas Park conducted laboratory experiments; he taught at Johns Hopkins University, 1933–1937, then joined the faculty of the University of Chicago. His publications provided influential patterns for other experimental ecologists. Allee's experiments had focused upon cooperation, Thomas Park's upon competition. Thomas Park taught the first course in population ecology and first used that term. Jane Lubchenco and Leslie Real (1991) reprinted Park's "Experimental studies of interspecies competition: I. competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst" (1948) because it foreshadowed many later studies of competition.

1954

In retrospect, London-born Northern Arizona University entomologist–ecologist Peter W. Price (b. 1938) detected "a tremendous wave of activity in population ecology building in the 1950s and cresting in the 1960s" (Price 2003:19) but he viewed these studies as mostly descriptive. He singled out three as important: Lack (1954), Andrewartha and Birch (1954), and Morris and Miller (1954), to which list I add two by Cole (1954*a*, *b*) and two by Nicholson (1954*a*, *b*). Since all these studies appeared about the same time, we may assume that none influenced the others' 1954 publications. What new understanding emerged from all this simultaneous research?

Lack studied controls of bird populations in a series of papers (1946, 1947, 1947–1948, 1948*a*, *b*, *c*, *d*, 1949, 1950, 1951, 1952) leading up to his *Natural Regulation of Animal Numbers* (1954). He noted that "some parts of the population problem have been studied intensively, others rather little, and some scarcely at all" (1954:275). For example, by banding nestling Song Sparrows (called "ringing" in Britain), a daughter of an Amherst College professor, Margaret Morse Nice (1883–1974), had discovered that first-year mortality was extremely high (Nice 1937, 1979, Trautman 1977, Burkhardt 1980, Birkhead et al. 2014:see index). For Song Sparrows, she found that mortality was 79% during the first year and 45% for individuals older than a year. Lack and others obtained similar mortality rates in Europe (Lack 1954:85). His main conclusion was that "The reproductive rate of each species, evolved through natural selection, is that which normally results in the greatest number of young surviving to independence." That claim was not controversial, but his further claim, "that in most animals density–dependent variations affect the reproductive rate much less than the death-rate," was somewhat controversial. He did agree that too many deer in an area could consume all the food and then starve, and that in some insect species, if their

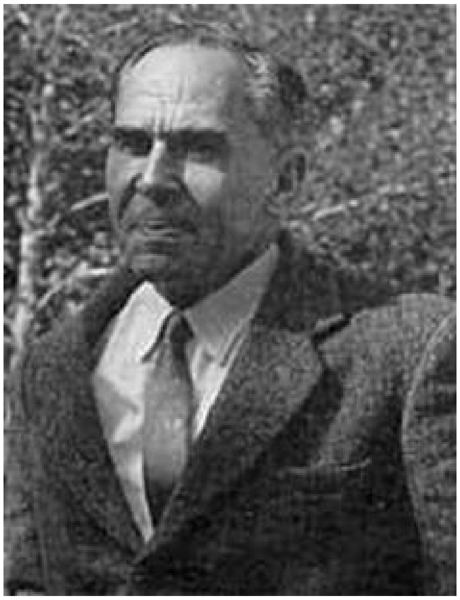


Fig. 7. (a) H(erbert) G(eorge) Andrewartha. Web. (b) L(ouis) C(harles) Birch. Web.

density is high in a region, some will go elsewhere to breed. Lack summarized that entire book in his *Population Studies of Birds* (1966:281–287), as part of an appendix on "The Theoretical Controversies concerning Animal Populations." He acknowledged an influence on his thinking of Nicholson (Nicholson 1933, Nicholson and Bailey 1935).

Nicholson (1950) conducted experiments, consulted Gause's *Struggle for Existence* (1934), and concluded (1950):

> *populations do not conform to any single pattern, such as the logistic curve; but there is a single dominant controlling mechanism, namely, density-dependent reaction. This governs the general levels of populations, usually in some relation to the availability of food; and it produces stability or oscillation mainly according to the degree of delay between the initiation of reaction and its effective operation.*

Next, Nicholson published "Experimental Demonstrations of Balance in Populations" (1954*a*), on sheep blowflies *Lucilia cuprina*;"Compensatory Reactions of Populations to Stress, and Their Evolutionary Significance" (1954*b*); and "An Outline of the Dynamics of Animal Populations" (1954*c*). The third article was a lengthy new synthesis updating his 1930s papers. He showed that significant work by himself and others supported his earlier interpretations and conclusions, and he responded to criticisms by Thompson and others of his 1930s papers.

Australian H(erbert) G(eorge) Andrewartha (called "Andy," 1907–1992) collaborated with a former student, L(ouis) C(harles) Birch (1918–2009), in writing *The Distribution and Abundance of Animals* (1954), which P. W. Price (*personal communication*) regards as "a very important and highly regarded treatise, which emphasized weather effects and a shortage of time favorable to reproduction." Their book was encyclopedic, having xv + 782 pages, compared to Lack's viii + 343 pages. Andrewartha and Birch's population data and theory were largely contained in chapters 13 (91 pages) and 14 (18 pages). In chapter 14, they argue that "generalizations about 'density-dependent factors' and competition in so far as they refer to natural populations are neither theory nor hypothesis but dogma" (Andrewartha and Birch 1954:649). They cited Nicholson as a perpetrator of this dogma (1954:19–20).

Indianan animal ecologist LaMont Cole (1916–1998), who had earned his B.S. (1938) and Ph.D. (1944) at the University of Chicago under Allee, was at the Department of Zoology, Cornell University, when he published "The Population Consequences of Life History Phenomena" (1954*a*). He did not cite Lack, but Lack cited Cole's "Population Cycles and Random Oscillations," (1951), and Cole cited Charles Birch's "The Intrinsic Rate of Natural Increase of an Insect Population" (1948). Since Birch's paper appeared in the British *Journal of Animal Ecology*, Lack would have seen it, but since Lack confined his book to bird populations, Birch's paper was irrelevant. Cole "regarded as axiomatic that the reproductive potential of existing species are related to their requirements for survival; that any life history features affecting reproductive potential are subject to natural selection" (Cole 1954*a*:239). These comments placed him and Lack in the same ballpark, but since Cole was not just discussing birds, he saw some utility in species that invested much less in each offspring than birds did, having a high degree of fecundity to aid in dispersing the species, as seen in ground pine *Lycopodium*, "whose light wind-borne spores may be scattered literally over the whole face of the earth and so make it likely that all favorable habitats will come to be occupied" (Cole 1954*a*:239). Cole's article explained "how to think in 'strategic' terms, that is, to see the entire life history of an animal as a strategy designed to maximize fitness" (Kingsland 1985:174). Cole's other 1954 article focused narrowly upon whether small-mammal cycles were random or regular. He noted that cycles of three or four years were "essentially identical with those obtained from a long series of tree rings" (1954*b*:3). Years that favored tree growth also favored small-mammal reproduction, presumably because climate was favorable for both groups of species. We now know that small mammals are successful in raising many offspring in masting years, when oaks produce abundant acorns, and small mammals are less successful in reproducing during years of acorn scarcity (McShea 2000).

What Cole meant by the population life history phenomena was primarily demographics: birth and death rates, longevity, and the presence or absence of overlapping generations. Cole was comfortable handling demographic calculations, and devoted 7.5 pages to "Computational Methods." He had absorbed the lessons of Lotka and Volterra and obviously expected other population ecologists to do likewise.

R(obert) F(ranklin) Morris (b. 1916) and C. A. Miller wrote "The Development of Life Tables for the Spruce Budworm" (1954) to show the utility of such tables for insect forest pests. They cited Edward Deevey's "Life Tables for Natural Populations" (1947), so their task was to adapt what he did for vertebrates to insects. That is not a great step conceptually, but in practice it required much research, and Peter Price (2003:19–23) attested to the important influence of their paper on forest entomology: "The reason why Morris and Miller's methodology became so widely adopted rested on the apparent rigor of the approach, and its conceptual simplicity, even though laborious field sampling was inevitable" (Price 2003:23).

The impact of all these 1954 studies? They displayed the breadth of population ecology, without resolving controversies.

1957–1958

Ray(mond) Beverton (1922–1995) and Sidney Holt (b. 1926), from Britain's Fisheries Laboratory, Lowestoft, on the East Anglia coast (Cushing and Edwards 1996, Ramster 1996), published the first great synthesis of mathematical studies on fish populations, *Dynamics of Exploited Fish Populations* (Beverton and Holt 1957, 533 pages, 2004). Their sources included a number of their own earlier studies, but by 1954 (when they completed this study) there was already a substantial literature from other fishery biologists as well. They were familiar with Lotka and Volterra's work, but cutting-edge computation was not their goal: "Well known standard statistical methods have been used in interpretation and treatment of the basic data; beyond that little more is asked of the reader than an acquaintance with the elementary techniques of the differential calculus" (Beverton and Holt 1957:21). Their monograph was encyclopedic, and they emphasized North Sea fisheries, which a number of European countries exploited. It was important for all of those countries to share data and computational methods, so they could all agree on harvesting limits. Unfortunately, that is not what happened (Clover 2006:106–110; see below).

Since 1933, the Biological Laboratory, Cold Spring Harbor, Long Island, New York, has hosted Cold Spring Harbor Symposia on Quantitative Biology. On 3–12 June 1957, a symposium on Population Studies: Animal Ecology and Demography, hosted about 150 scientists; it was funded by three federal agencies and three philanthropic foundations. The goal was to discover what animal population ecologists and human demographers might learn from each other. (Answer: not much.) Cole's opening talk, "Sketches of General and Comparative Demography" (1958), has a history of both demography and animal population studies down to Darwin's *Origin of Species*, and mentions Lotka and Volterra's work, followed by discussion of comparative life histories, population regulation, fluctuations, and age structure.

At this symposium, a dispute between Andrewartha and Nicholson became "highly charged and personal," to the dismay of Americans. Andrewartha spoke on "The Use of Conceptual Models in Population Ecology" (1958), Birch spoke on "The Role of Weather in Determining the Distribution and Abundance of Animals" (1958), and Nicholson spoke on "The Self-Adjustment of Populations to Change" (1958). Discussions that followed talks were published following the talks. Neither Andrewartha nor Birch commented on Nicholson's talk, but he commented on both of theirs.

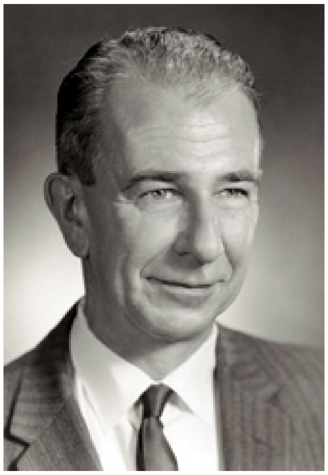
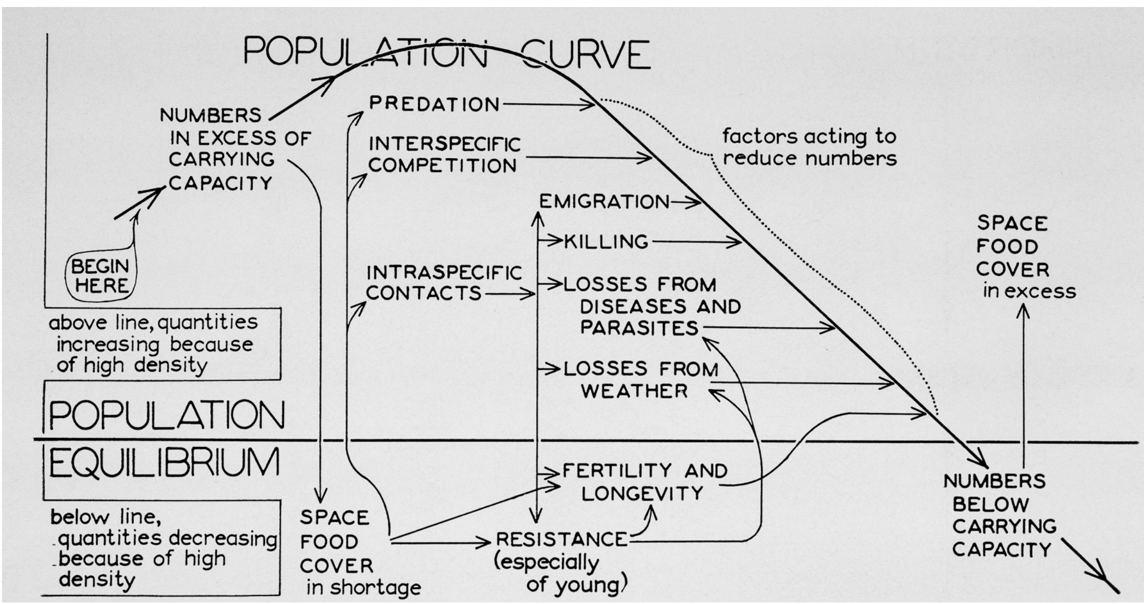


Fig. 8. (a) LaMont Cole. Web. (b) Regulation of numbers in natural populations, when the population is in excess of carrying capacity. Chitty 1952. From Pitelka 1958:248.



A. Milne, Agriculture Research Council Unit of Insect Physiology, Durham University, England, thought that terminology and concepts in population ecology lacked precision: "Today the student of animal population dynamics is confronted with an ever-growing literature which is a disheartening jumble of insufficient facts, alleged facts, ill-defined terminology, and conflicting theories" (Milne 1958:254). He acknowledged that ecologists study very complex phenomena and so cannot achieve the precision of some other sciences. He cautioned that "Theories of natural control of mammal and bird populations are not likely to be very useful for insects," since warm-blooded animals have "more efficient water-conserving mechanisms, are far less affected by the irregular vagaries of weather, and they may also exhibit 'territorial' behaviour which is important in limiting density." Dempster commented (1975:123):

> In many respects, Milne's ideas form a halfway house between the views of Nicholson and of Andrewartha and Birch (Milne 1957*a*, *b* [=1957, 1958], 1962). He believes that the latter underestimate the part played by density-related processes in the determination of animal numbers, but thinks that Nicholson overestimates the frequency with which intra-specific competition occurs in nature.

Hutchinson had the last word at the symposium, but he devoted little more than a page to the previous papers in his "Concluding Remarks" (1958) before explaining "The Formalization of the Niche," probably the most cited part of the symposium volume.

Elton, Lack, and Bodenheimer were absent from the symposium; perhaps they were invited and declined. Both Elton and Bodenheimer published relevant books in 1958.

Bodenheimer went to Australia in 1956, where a conversation with Nicholson helped shift his perspective from skeptic to acceptance of much of Nicholson's arguments (Bodenheimer 1959:164–165, 167). Nicholson was one of four animal ecologists to whom Bodenheimer dedicated his *Animal Ecology To-day* (Bodenheimer 1958), which contained two long chapters on population ecology. In it, Bodenheimer only devoted one brief paragraph to the arguments of Andrewartha and Birch, then devoted seven pages to explaining the progress Nicholson had made in mathematical representation of animal populations (Bodenheimer 1958:118, 120–126).

Elton's *The Ecology of Invasions by Animals and Plants* (Elton 1958, 181 pages) broke new ground (Chew 2006:209–286). Its relevance for population ecology lay in the fact that local increase in numbers enabled species to invade new territory. However, this book had no statistics or mathematical calculations, and most of its illustrations were maps plotting the ranges of invasive species. The claim that it initiated a new line of ecological research was challenged by Daniel Simberloff (2011), who claimed that distinction for his 1981 paper.

Robert H. MacArthur (1930–1972) was to become one of the most brilliant leaders of American ecology by emphasizing the hypothetico-deductive method and more (Cody and Diamond 1975:vii–ix, Fretwell 1975, Kingsland 1985:180–205, Wilson and Hutchinson 1989, Burgess 1996:69–70, Brown 1999, Pianka and Horn 2005, Kaspari 2008, Birkhead et al. 2014:see index). Natural history was a dominant interest as he grew up, but he majored in mathematics at Marlboro College (B.A., 1951) and Brown University (M.S., 1953) before switching to ecology at Yale, where he studied under Evelyn Hutchinson (Ph.D., 1958). His first three publications were on population dynamics: "Fluctuations of Animal Populations, and a Measure of Community Stability" (MacArthur 1955), "On the Relative Abundance of Bird Species" (1957), and "Population Ecology of Some Warblers of Northeastern Coniferous Forests" (1958). The last of these was his doctoral dissertation of 1957, for which he studied five species of wood warblers in the genus *Dendroica*: *tigrina, coronata, virens, fusca*, and *castanea*, which had overlapping territories, and therefore apparently challenged Gause's law that two closely related species cannot occupy the same niche. MacArthur discovered that they all did inhabit the same forest, but they partitioned their environment in subtle ways that did not violate Gause's law. This last

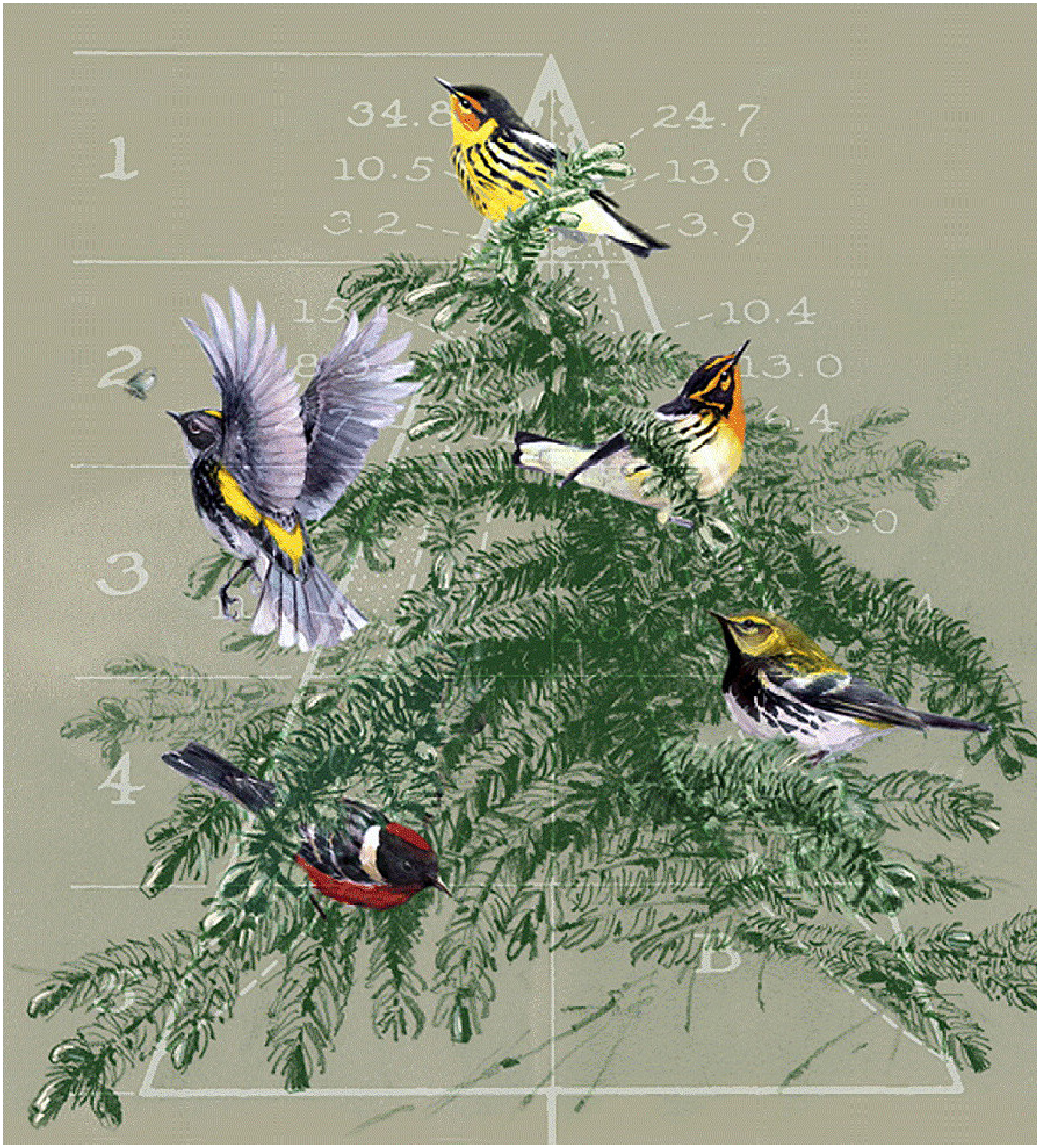


Fig. 9. Five closely related wood warbler species MacArthur studied in boreal forests on Mt. Desert Island, Maine (1958): clockwise from bottom: Bay-Breasted (*Dendroica castanea*), Myrtle (*D.* coronate), Cape May (*D. tigrina*), Blackburnian (*D. fusca*), and Black-throated Green (*D. virens*). Painting by Debby Kaspari. Kaspari 2008:451.

paper won the ESA Mercer Award. MacArthur's warbler research was original, but the idea that related species could partition an environment where their distributions overlapped had previously been noted by Charles Kendeigh (1945:433): "warblers are so prominent in the mixed evergreen–deciduous forest because they fill so many diverse niches."

MacArthur, like Darwin, was a theoretician who also synthesized his own field observations and those of others to support his theoretical arguments. His best remembered concept was the *r*- and *K*-selection model of reproductive strategies. Mark Boyce (1984) traced aspects of its history back to 1958, but its first explicit use in print was by MacArthur's student Martin Cody (1966), who acknowledged MacArthur's formulation of it. It gained widespread recognition in MacArthur and Wilson's *The Theory of Island Biogeography* (1967:149). As other ecologists adopted the concept in their own work, different understandings of it emerged, which Boyce evaluated.

Since 1958

After Andrewartha and Birch's *Distribution and Abundance of Animals* (1954) appeared, an enhanced reputation enabled Andrewartha to move from the Waite Agricultural Research Institute to the Department of Zoology, University of Adelaide, where he taught a course in population ecology based upon their book. That book, however, was a lengthy monograph, not a textbook, and he "felt the need for a compact text that the students may use" (Andrewartha 1961:xv), entitled *Introduction to the Study of Animal Populations* (xvii + 281 pages). It appeared about simultaneously with Slobodkin's textbook (see below); these seem to be the first two texts on population ecology. Andrewartha wrote his after four decades of his career, and Slobodkin wrote his after one decade into his career, and not surprisingly, Andrewartha's was about 100 pages longer than Slobodkin's. Gordon Orians (1962*b*) reviewed Andrewartha's book in *Ecology*, stating that it is a briefer version of the 1954 book, which could be used to supplement a general ecology textbook in courses. He explained the non-evolutionary thinking in this book and the previous one as reflecting the present-mindedness among practical ecologists focused upon eliminating insect pests of agriculture.

The second part of Lack's appendix (1966:290–299) argued against Andrewartha and Birch's theory (1954). Lack did not consider in this appendix Andrewartha's textbook (1961), though Lack's appendix cited other Andrewartha publications since 1954. Lack's 1966 arguments against them were too involved to be easily summarized, but perhaps equally important was his list of other ecologists who disagreed with them (1966:296–297). The Australians' books used mathematics to describe populations, Andrewartha's text more so than the coauthored treatise.

Lawrence Slobodkin (1928–2009), from New York City, at age nine had a menagerie of a canary, rabbit, tortoise, horned toad, baby turtles, newts, and tropical fish. He earned a B.S. degree from Bethany College, West Virginia (1947), then went to Yale and earned a Ph.D. (1951) under Hutchinson (Slobodkin 2009). His doctoral dissertation was experimental: "a detailed study of the role of age structure in the growth of experimental populations of the microcrustacean *Daphina* epitomized his approach—a quantitative experimental test of a mathematical theory that was intended to apply broadly" (Colwell and Futuyma 2011:19). He began working for the U.S. Fish and Wildlife Service in Florida and solved the "mystery of the red tide." In 1953 he moved to the Zoology Department at the University of Michigan and became third author of a well-known theoretical paper, "Community Structure, Population Control, and Competition" (1960), with the first two authors Nelson Hairston and Frederick Smith.

Slobodkin's first book, *Growth and Regulation of Animal Populations* (1961, viii + 184 pages), as mentioned above, was one of the first two textbooks on population dynamics along with Andrewartha's. Kingsland commented (1985:180):

> *His book covered problems in niche theory, demography, logistic theory, competition, and predator-prey relations; and ended with a projection of a unified ecological theory which would provide answers to practical problems as well as unite both ecology and genetics into a predictive evolutionary theory. It did a great deal to spread the mathematical message of the Hutchinson school, even though Slobodkin himself later became more skeptical of mathematics.*

Another Hutchinson student, MacArthur, reviewed it in *Ecology* (summer 1962) and stated that ecologists are either observers or theoreticians, and that Slobodkin's textbook was the best yet by a theoretician. MacArthur might not yet have seen Andrewartha's, which was reviewed in the fall 1962 issue of *Ecology*.

A. Milne, Durham University School of Agriculture, Newcastle, England, continued his earlier discussion (Milne 1962:19):

> *The mechanism of natural control of population is undoubtedly the most controversial problem in animal ecology today. In 1956 at Montreal, I pointed out the shortcomings (as they seem to me) of previous theories of the mechanism and then proposed a new theory for insects (Milne 1957a, b). The time has come to consider the inevitable criticism which my theory has aroused.*

He criticized the theories of both Nicholson (1933, 1954, 1958) and of Andrewartha and Birch (1954) and they responded without being convinced that they were wrong and he was right. Milne argued that the old density-dependent vs. density-independent controversy was "inadequate." His alternative was to subdivide the density-dependent category into imperfectly density-dependent and perfectly density-dependent factors (Milne 1962:21). The imperfectly density-dependent category included a mix of dependent and independent factors, so Milne was solidly intermediate between the previous two schools of thought. Lack (1966:296) agreed with Milne that "even the best field studies of the problem suffer from ecological deficiencies and statistical inadequacies," but whereas Milne thought a remedy of these inadequacies would resolve controversies, Lack saw differences in theories as due to "difference in basic assumptions concerning the extent to which competition is held to be important or unimportant in natural populations." Lack did not comment more directly upon Milne's ideas.

Milwaukeean Gordon Orians (b. 1932) earned his B.S. degree (1954) at his state's university, then earned his Ph.D. in animal ecology at the University of California, Berkeley (1960). He joined the Zoology Department at University of Washington, Seattle, where he remained (Orians 2010, Birkhead et al. 2014:see index). He wrote a critique of population theory, "Natural Selection and Ecological Theory" (1962*a*) that contrasted Andrewartha and Birch's *Distribution and Abundance of Animals* (1954) and Lack's *Natural Regulation of Animal Numbers* (1954), in hopes of ending a controversy. Andrewartha and Birch dismissed evolutionary aspects of the species studied as beyond the scope of ecology, while Lack investigated evolutionary aspects of the species being studied to understand its ecology. Lack,

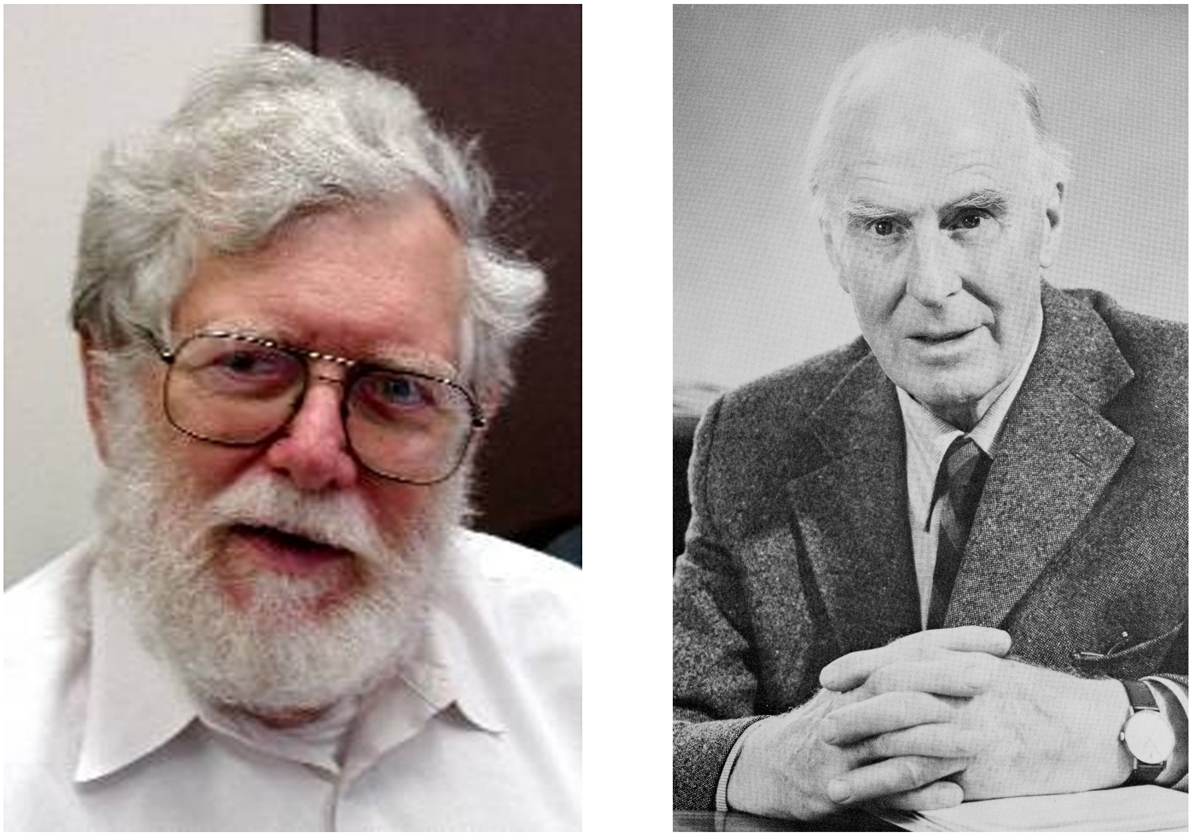


Fig. 10. (a) Lawrence B. Slobodkin. Wikipedia. (b) Vero Wynne-Edwards. Wynne-Edwards 1985: facing 487.

in turn, dismissed climate as unimportant to population dynamics, while Andrewartha and Birch saw climate as crucial. The two perspectives come from different agendas. Andrewartha and Birch wanted to control insect pests of crops, which emphasized correlations between weather and insect activity. Lack was interested in how species were adapted to their environment. Orians commented that ecology has descriptive generalizations, such as the principle of competitive exclusion, but ecology's only theory is natural selection.

Orians' attempted end to controversies over population dynamics was a worthy goal, but the morass seemed broad enough for more than one mopping up operation, and Milne had added to the complexity without resolving issues. K. Bakker, Zoölogisch Laboratorium, Leiden, wrote "Backgrounds of Controversies about Population Theories and Their Terminologies," praising much in Orian's paper (1964:193), but faulting him for only picking up the argument in the works of Lack (1954) vs. Andrewartha and Birch (1954), whereas Bakker thought a better understanding came from starting with Nicholson (1933) vs. Thompson (1929, 1939). If Orians had done so, he would not have found "such a clear difference between the two authors as regards an 'evolutionary' versus a 'functional' point of view." Bakker explained the distinctions in details, and their significance.

English zoologist Vero Wynne-Edwards (called "Wynne," 1906–1997) had broad ecological interests, which helped make him a good teacher and administrator (Wynne-Edwards 1985, Kimler 1986:227–231, Newton 1998*a*, Bircham 2007:378–380, Birkhead 2008:257–260, Birkhead et. al. 2014:356–366). His father, who taught mathematics and studied the British flora, was headmaster of the Leeds Grammar School. At age 13, Wynne was sent to Rugby boarding school, where he flourished. In 1924, he entered Oxford University and studied under Huxley and Elton. He became active in the Oxford Ornithological Society and Oxford Bird Census. He spent part of three summers at the Port Erin Marine Biological Station, Isle of Man. In 1930 he married and accepted an assistant professorship at McGill University. On the voyage to Canada, he kept records on seabirds he observed and "discovered the basic pattern of inshore (coastal), offshore (to the edge of the continental shelf), and pelagic (deep-water) marine zones, with different species in each zone" (Wynne-Edwards 1930, Newton 1998:476). His insight applied to seabirds worldwide and ornithologists accepted it (Saunders 1973:10).

On an expedition to North Labrador, he studied fulmars and saw that some birds of reproductive age did not breed, "which he thought was a form of population control" (Wynne-Edwards 1939, Newton 1998:477). During World War II, he taught radar mechanics to members of the Canadian Air Force. In 1946 he became Professor of Zoology at the University of Aberdeen, where he remained and became very active in academic and professional affairs.

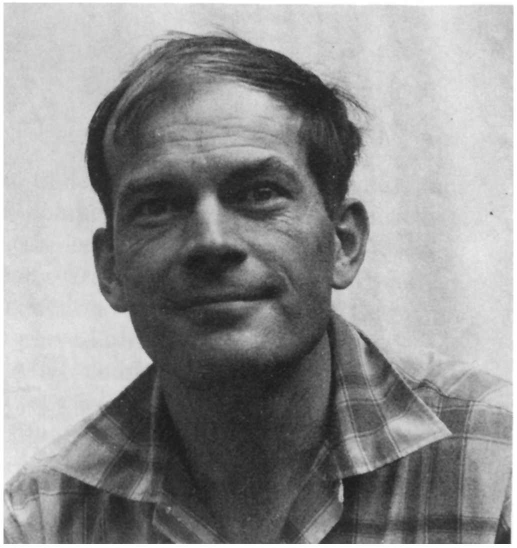
Wynne-Edwards' landmark achievement was his *Animal Dispersion in Relation to Social Behaviour* (1962, x + 653 pages), summarized in *Scientific American* and in *Science* (Wynne-Edwards 1964*a*, 1965). A noncontroversial feature of his population theory was the existence of breeding territories in many species of birds (Wynne-Edwards 1962:145–164). Various naturalists since John Ray in 1678 had commented on bird territoriality, but its significance was only generally appreciated after Eliot Howard published *Territory in Bird Life* in 1920 (Klopfer 1969:77–91). However, Wynne-Edwards' book was immediately controversial. John Maynard Smith (1964) was willing to acknowledge that territorial breeding behavior in many kinds of birds would tend to limit the number of nesting pairs in a given region, but he argued that that behavior could have evolved by natural selection at the individual level, without the need to postulate group selection. Wynne-Edwards' response (1964*b*) was that it was difficult for a field naturalist like himself to have a meeting of minds with a laboratory zoologist like Maynard Smith. That was a mischaracterization: Maynard Smith was a theoretician.

Tim Birkhead, Jo Wimpenny, and Bob Montgomerie (2014:357–359) wondered if Elton's *Animal Ecology* (1927) had misled Wynne-Edwards. Lack became a prominent opponent who devoted the third part of his "Theoretical Controversies concerning Animal Populations" (1966:299–312) to refuting Wynne-Edwards' hypothesis. George Williams (1966:243–246) also rejected Wynne-Edwards' theory. The big stumbling block was Wynne-Edwards discounting the importance of natural selection with respect to social behavior in comparison to his own theory of group selection (Birkhead 2008:357–360, Birkhead et al. 2014:see index), which earned an unfavorable book review from Elton (1963). Ed Wilson (1973) defended kin selection with natural selection as sufficient for explaining the origin of social behavior.

Ed Wilson's blockbuster monograph, *Sociobiology* (1975:63–129) had one chapter on population (4) and one on group selection and altruism (5). His conclusion to the latter chapter was (1975:129): "… although the theory of group selection is still rudimentary, it already has provided insights into some of the least understood and most disturbing qualities of social behavior." Group selection remained a controversial concept (Wilson 1983, Leigh 2010), but it could not be dismissed as simply a quirk of Wynne-Edwards' imagination.

Perhaps more accumulation of evidence would help Wynne-Edwards; he published additional evidence in *Evolution through Group Selection* (1986), which did not win any more acceptance, but rather, "universal criticism" (Montgomerie 2015, personal communication). His swan song was "A Rationale for Group Selection" (1993). Wynne-Edwards was generally well liked, and his theory, which some considered heretical, did not detract from his popularity. Furthermore, Newton (1998:482) thought his natural history observations were a valuable contribution to behavioral ecology or ethology; Bob Montogomerie doubts this (*personal communication*). Wynne-Edwards' general idea that social behavior can influence population density was not abandoned; in 1978 a conference was held at the State University of New York, Plattsburg on crowding, density-dependence, and population regulation, and Yale University Press published the conference volume of 16 chapters (Cohen et al. 1980). Lack's followers continued to dismiss group selection as an unnecessary hypothesis, but others continued defending group selection (D. Wilson 1983, Werfel and Bar-Yam 2004, Leigh 2010). In 2010, however, Edward Wilson changed his mind about group selection and endorsed it (Nowak et al. 2010, Gibson 2013). Wynne-Edwards had died and so could not appreciate that shift in judgment.

If Slobodkin's text was one of the first on animal populations, another Hutchinson student, Robert MacArthur, coauthored probably the third such text, *The Biology of Populations* (1966). Were these authors dissatisfied with Slobodkin's book? If so, they did not admit it in their text (nor did they cite Slobodkin [1961], though they cited a paper by him). However, they made it clear that their text had been planned in 1960 as the third of three texts, the first two being on the biology of cells and the biology of organisms (MacArthur and Connell 1966:v). What did they say about Milne's theory? Nothing; they did not even cite him. MacArthur was on the faculty of the University of Pennsylvania, 1958–1965, then at Princeton University, 1965–1972. He became one of the most influential ecologists of his time.



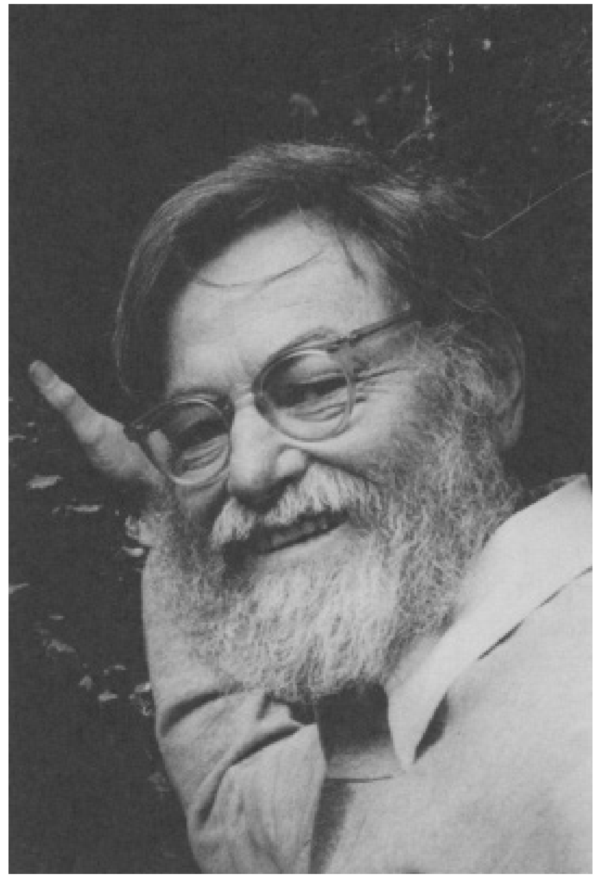


Fig. 11. (a) Robert H. MacArthur. Wikipedia. (b) Joseph Connell. ESA Bulletin 67 (1986) 38.

Joseph Connell (born 1923), from Gary, Indiana, earned his B.S. degree (1946) at the University of Chicago, his M.A. degree (1953) from the University of California, and his Ph.D. (1956) from Glasgow University. He joined the zoology faculty at the University of California, Santa Barbara in 1956, and received ESA's Mercer Award in 1963 and Eminent Ecologist Award in 1985.

MacArthur and Ed Wilson's famous *Theory of Island Biogeography* (1967) is, in a sense, a study on population dynamics: species' populations expand to new islands as populations increase (or for other reasons); local extinctions occur when island populations cannot maintain their numbers (for various reasons). This dynamic MacArthur absorbed into his last book, *Geographical Ecology: Patterns in the Distribution of Species* (1972:84–126), which book was itself a noteworthy achievement. Arthur Boughey published a concise, attractive *Ecology of Populations* (1968, edition 2, 1973).

English fisheries biologist D(avid) H(enry) Cushing (1920–2008) served in the British Army during World War II, graduated from Oxford University, and eventually joined the same Lowestoft Fisheries

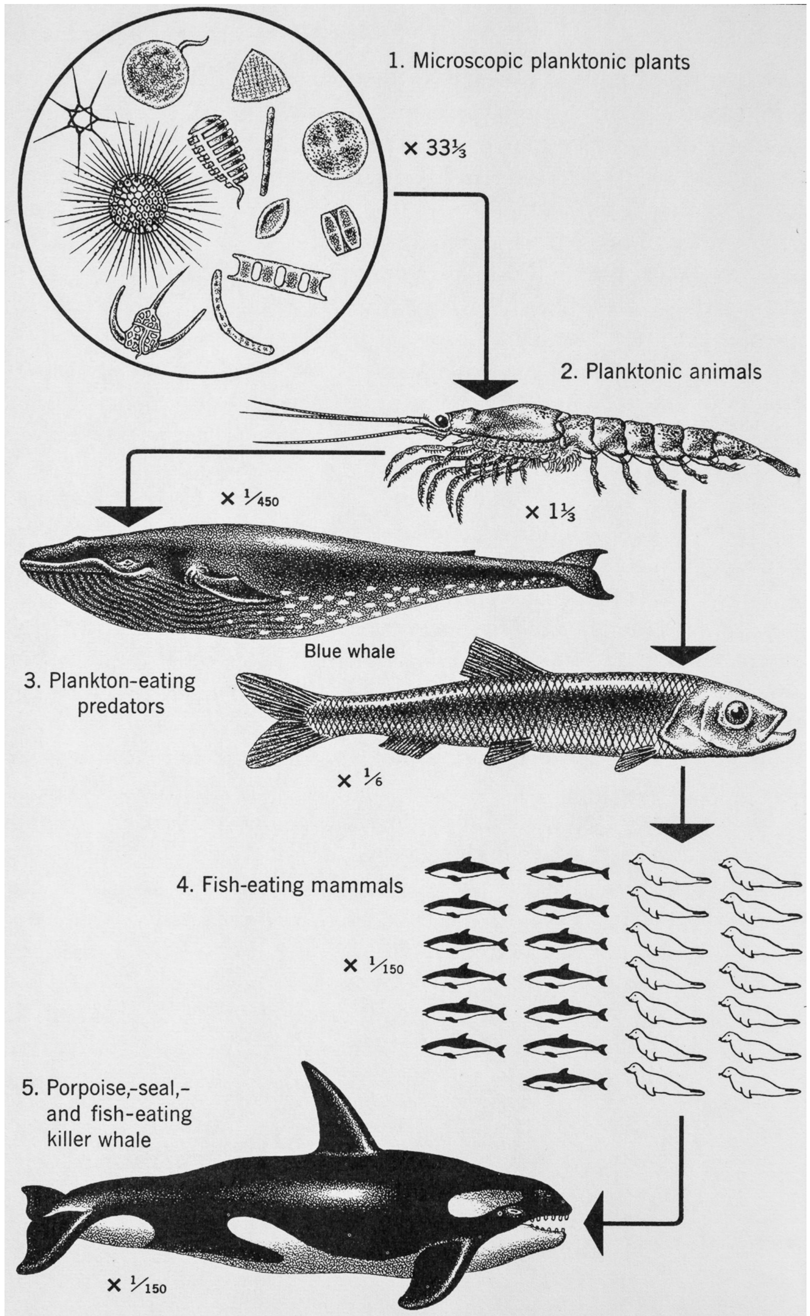


Fig. 12. Two food chains of different lengths. One killer whale's stomach contained 13 porpoises and 14 seals. MacArthur and Connell 1966:180.

Laboratory as Beverton and Holt, and he continued their fisheries population studies. In 1963, Professor Arthur Hasler arranged for him to go to the University of Wisconsin to deliver a series of lectures, which became the basis of Cushing's advanced textbook, *Fisheries Biology: A Study of Population Dynamics* (1968, xii + 200 pages). He judged fish stocks individually (Cushing 1968:3):

> *In the last ten years, the world's catch of fish (about 50 million tons in 1965) in freshwater and in the sea has doubled. Some stocks, such as the sardine-like fishes off African coasts, are underexploited. Others, like the bottom-living fish stocks in the northeastern and northwestern Atlantic, are exploited at about the right rate. Other stocks are overfished. For example, Antarctic blue whales have been fished nearly to extinction.*

A large conference volume appeared about simultaneously: *The Future of the Fishing Industry of the United States* (Gilbert 1968, 346 pages). This volume includes far more than population dynamics, but that was a crucial part of the conference concerns.

Meanwhile, in England a volume appeared (Southwood 1968), containing 13 papers presented at a symposium of the Royal Entomological Society of London (1967) on insect abundance. Three speakers were from London, with the others from elsewhere in Europe, North America, Africa, and Australia. In their introduction to the volume, O. W. Richards and T. R. E. Southwood summarized the history of insect population studies from 1888 to 1967. Symposium participants discussed both population theories and methods of investigation.

Only slightly less comprehensive and less hefty was Kenneth Johnstone's *The Aquatic Explorers: A History of the Fisheries Research Board of Canada* (1977, xv +342 pages), which celebrated the first 75 years of that great organization.

In the same year, 15 fishery biologists contributed chapters to *Fishery Population Dynamics* (Gulland 1977, xi + 372 pages). W. E. Ricker's chapter, "The Historical Development," emphasized methods of assessing the size of particular populations of commercial species. The earliest determination of wild fish ages that Ricker knew (1977:2–3) was by Swedish clergyman H. Hederström, published in 1759. Hederström counted rings on fish vertebrae, but at the time there was no one interested in exploiting this discovery. The same lack of interest had been true when Antoni van Leeuwenhoek (1632–1723) studied fish scales in 1684 and decided the ridges on them represented annual growth (Egerton 1968:8–9, 2006:55–56, 2012:65–66). His discovery was unknown to Ricker, since others independently rediscovered that technique later.

University of Toronto professor Henry A. Regier (b. 1930) explained in his chapter (1977) that there were four major types of population problems that fishery biologists encountered, and each type should be handled differently: (A) large stable resource species; (B) large fluctuating resource species; (C) stable systems of small resources; and (D) systems of interacting resources that fluctuate erratically. He explained how to identify each type and how to calculate their populations.

Under the guidance of three references cited above, one might have expected all oceanic nations to maintain prudent controls on their fisheries to avoid depleting these wonderful resources. However, ecologist Robert May and four associates explored the "Management of Multispecies Fisheries" (May et al. 1979) and found that the common goal of maximum sustained yield (MSY) was an interesting academic exercise, which only worked when fishermen were the only factor impacting prey species. In the real world, complex factors and interactions meant that MSY calculations were invariably too optimistic, and MSY was never achieved.

A large multiple-authored *The Management of Marine Regions: North Pacific* (Miles et al. 1982, xxxiv + 656 pages) was organized at the Institute for Marine Studies, University of Washington, Seattle, in September 1976 and funded by the Rockefeller Foundation. Like Beverton and Holt's treatise, this report attempted to achieve an understanding and consensus among several nations having commercial fisheries in the north Pacific.

Two decades after Cushing reported a mixed bag in fish stocks (quoted above), he reported that "a method was devised in 1965 from which annual catch quotas (total allowable catches, TACs) could be readily estimated" (Cushing 1988:259). So, did responsible management solve all problems? "Many pelagic stocks collapsed….A particular difficulty is the effect of fishing when poor year classes succeed each other due to a persistence of environmental factors. The anchoveta stock failed off Peru because three poor year classes (two associated with El Niño) succeeded each other when fishing was intense…" Tim D. Smith (1994:1) complained that fishery science had been driven by economics and politics and admitted: "The ecological effects of fishing can be significant, reducing the number of fish in the sea and changing marine ecosystems in ways that we are unable to anticipate even after more than a century of study." He wrote that two years after the spectacular collapse of the western Atlantic cod fishery (Kurlansky 1997, Clover 2006:121–130). Anne Platt McGinn made clear in *Rocking the Boat: Conserving Fisheries and Protecting Jobs* (1998) that, in practice, for both fishery enterprises and for countries, short-term advantages trumped long-term sustainability. Carl Safina, *Song for the Blue Ocean* (1997:437), agreed with these diagnoses but chose to find some hope in the rise of many organizations during the 1990s dedicated to preserving the oceans' living resources. Those organizations have their virtues, but have not reversed the degradation of the Earth's oceans. Political commentary magazine *Mother Jones* published three articles that document both overfishing and pollution (Franklin 2006, Robbins 2006, Whitty 2006). Jennifer Hubbard explored the difficulties of monitoring fish populations in *A Science of Scales: the Rise of Canadian Atlantic Fisheries Biology, 1898–1939* (2006).

Other publications from the 1960s and early 1970s indicate a rising interest in population ecology, including: Lloyd Keith, *Wildlife's Ten-Year Cycle* (1963); William Hazen compiled a large volume of *Readings in Population and Community Ecology* (Hazen 1964, x + 388 pages, edition 2, 1970, x + 421 pages); Maurice Solomon wrote a concise *Population Dynamics* (Solomon 1969, iii + 60 pages); Lowell Adams compiled a small collection, *Population Ecology* (Adams 1970, x + 160 pages); Anthony Alison edited 12 original articles, *Population Control* (Alison 1970, 240 pages) on both animal and human demography; Ian McLaren compiled 10 reprinted articles, *Natural Regulation of Animal Populations* (McLaren 1971, v + 195 pages); P. J. den Boer and G. R. Gradwell edited the first of two symposia volumes, *Dynamics of Populations* (den Boer and Gradwell 1971, 611 pages) from the 1970 proceedings at the Advanced Study Institution on Dynamics of Numbers in Populations, at Oosterbeek, Netherlands, which included 37 invited papers, an opening address, and 3 conclusions; and M. S. Bartlett and R. W. Hiorns edited nineteen original chapters from a 1972 conference sponsored by an Institute of Mathematics and Its Applications and an Institute of Biology, at Oxford, UK., *The Mathematical Theory* *of the Dynamics of Biological Populations* (Bartlett and Hiorns 1973, xii + 347 pages).

Rather oddly, Hutchinson, in retirement, wrote his only textbook, *An Introduction to Population Ecology* (1978), after two of his former students had published textbooks on that subject. His preface recommended Slobodkin's book as being more concise than his own, and he warmly acknowledged the influence of his deceased former student, MacArthur. Hutchinson could also have recommended English ecologist J. P. Dempster's *Animal Population Ecology* (1975) as being as concise as Slobodkin's textbook and more recent, but Dempster was not one of his former students. Hutchinson's *Introduction* contained many historical discussions and footnotes, which may make it entertaining reading for population ecologists, but possibly distracting to students. It also contained numerous drawings, graphs, and mathematical equations. He was then among the foremost ecologists in the world, and so his textbook presumably had a wide audience and influence.

By outliving Nicholson, Andrewartha and Birch apparently had the last word in their dispute, in *The Ecological Web* (1984, xiv + 506 pages), which updated their arguments after 30 years. They hoped "this book will be accepted as a new contribution to population ecology—not merely a revision of our previous work" (1984:xiii). In support of their claim of newness, they explained:

> *In* The Distribution and Abundance of Animals *the chapter on general theory follows the chapter that summarizes fourteen empirical studies of populations. In this book the order is reversed: theory precedes practice. To put theory last would imply that theory is little more than a summary of empirical knowledge, which is to approach perilously close to the philosophy of induction by simple enumeration (sec. 9.02). We did not intend to give this impression in 1954 and we wish to avoid it now, because we hold that good theory depends not only on knowledge but also on objective judgment, supported by insight and imagination.*

Reviewer Charles Krebs praised their first book, but not this one (Krebs 1985:873):

> *Their 1954 book had a salutary effect on ecology because they preached rugged empiricism as a philosophy, the importance of weather to population dynamics as a mechanism, and the significance of local populations, their genetics and dispersal, as a new outlook….Andrewartha and Birch are not happy with the present state of population ecology, and many population ecologists will not be happy with the message of this book.*

Krebs complained that "Population ecology is exciting now because it is rigorous, quantitative, and experimental, all the virtues espoused by Andrewartha and Birch in 1954 but curiously lacking in this book." Krebs thought that they had not kept up with a movement they had initiated, and so their critique was outdated.

Gone but not forgotten; in 1995, the centennial of Nicholson's birth, the Division of Entomology, Commonwealth Scientific and Industrial Research Organization (CSIRO) organized an impressive celebration conference in Canberra of over 200 ecologists from a dozen countries. By then, Andrewartha was also dead, but not Birch, who did not contribute a published paper. The centennial volume is impressive: *Frontiers of Population Ecology* (Floyd, Sheppard and De Barra, editors, 1996, xii + 639 pages). Paul Wellings, who wrote the preface, claimed (1996:xi):

Fig. 13. Ian Newton. Birkhead et al. 2014:383.

John Nicholson is recognized as one of the leading ecologists of this century and is familiar to ecologists throughout the world because of his research on the factors causing population limitation and the concept of regulation through density dependence. Debate about his research on populations dominated ecology during the middle third of this century and these debates reached their zenith at the Cold Spring Harbor Symposium on Quantitative Biology in 1957. Robert MacArthur reviewed the Proceedings of this meeting for the Quarterly Review of Biology *(MacArthur 1960)*.

MacArthur had predicted that the heated debate at the symposium would soon be forgotten. Not so, but Wellings stated that the debate "did change markedly after 1957 as the focus shifted to the development of a methodology of density dependence (e.g. Varley and Gradwell 1960) and the consequences of nonlinear relationships on population dynamics (e.g., Cook 1965)."

English ethologist Jane Goodall (b. 1934) based her research upon wild chimpanzees studied in Africa (Peterson 2006). She set a record for longevity of a close monitoring of a wild animal species, which began in 1960. In 1983, she published "Population dynamics during a 15-year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania," using data from 1965 to 1980. This was an unusual study in that she was able to collect data on individuals in a community, which in some cases extended from birth to maturity, and including their own offspring, and year of death of some community members. However, she published in an animal psychology journal, and few population ecologists may have seen her results.

Ornithologist Ian Newton (b. 1940), from the UK Midlands, became interested in birds as a child (Newton 2014). He was first in his family to attend a university; at Bristol University he studied zoology. An important influence on him was his attendance (for 40 years) at Lack's annual Edward Grey Institute undergraduate conferences on ornithology. At his first one, as a freshman, he spoke on Bullfinch *Pyrrula pyrrula* feeding, and afterwards he accepted Lack's offer to help him modify it for publication (appearing in *Bird Study*). He spoke at later conferences on other finches, and Lack accepted him as a D.Phil. student, with a dissertation on finches. On a postdoc he studied factors influencing Bullfinch populations.

After six years at Lack's Institute, Newton joined the Nature Conservancy (UK), a government agency, and studied waterfowl, which he had not previously researched. During the pesticide crisis of the 1950s and 1960s, populations of raptors declined drastically, and his research shifted to them, leading to his *Population Ecology of Raptors* (1979), which attracted much attention because of the crisis. Initially, his research was species specific, but over time he focused on ideas and did more calculations and less field work. The volume he edited on *Lifetime Reproduction of Birds* (1989) has 26 chapters written by 37 ornithologists from all over the world. By then, he was located at Monks Wood Experimental Station, Cambridgeshire, UK. He synthesized much of his lifetime of research and reading in *Population Limitation in Birds* (1998*b*) and much of his other research and reading in *The Migration Ecology of Birds* (2008) and *Bird Migration* (2010). His online bibliography lists (my count): 13 books, which he wrote, coauthored, or edited; 61 book chapters; and 167 articles, which he wrote or coauthored.

Predator–prey interacting populations have been discussed in theory ever since Lotka and Volterra during the 1920s (Kingsland 1985:104–105, 109–111). What about real populations? Gause (1934) had described predator–prey laboratory experiments, which had become equally well known. What about in nature? More of a challenge, but nature conveniently ran an experiment as neat as those of Gause at the U.S. Isle Royale National Park, in northern Lake Superior, closer to Canadian than U.S. shores. There is no archeological evidence of moose on Isle Royale before they swam there shortly before 1904 (Peterson 1995:22). They flourished, without predators. National Park Service biologist Adolph Murie (1899–1974) visited Isle Royale in 1929–1930 and estimated that there were 1000–3000 moose on its 210 square miles (544 km^2), and that their browsing was degrading the environment (Murie 1934). A population crash occurred in 1935 that reduced the population to 500–600 moose, and a fire in 1936 burned 20% of the island's vegetation (Peterson 1995:22–23). Isle Royale became a national park in 1940. Wolf tracks were reported there in 1948, but since coyote were also present, there was uncertainty. However, in 1951 a park ranger made a plaster cast of a wolf footprint, which left no doubt.

Durward Allen (1910–1997) was a biologist in the Washington office of the U.S. Fish and Wildlife Service and immediately realized that a natural experiment was about to unfold. He applied for funds to study that development, but a new Eisenhower Administration was uninterested, so Allen resigned and joined the faculty at Purdue University, where he could establish a study group with graduate students in wildlife management (Allen 1979:xviii–xx). Between 1958 and 1976, he had four doctoral students and two post-doctorates who conducted research there under his supervision.

His first student was David Mech (b. 1937), who subsequently studied wolves in Minnesota and in the Arctic Circle (Mech 1970, 1988, 1991, 2000, Mech et al. 2015). The last of Allen's students, Rolf Peterson (b. 1949), earned his Ph.D. in wildlife ecology at Purdue in 1974, remained there as a research associate, 1974–1975, then joined the faculty at Michigan Technological University in Houghton and assumed supervision of Isle Royale research when Allen retired in 1975. Books by Allen (1979) and Peterson (1995) tell of their researches.

One of Peterson's students, John Vucetich, joined him on the MTU faculty. Vucetich earned a B.S. degree in biology (1995) and a Ph.D. in wildlife ecology (1999), with a dissertation on "Demographic and Genetic Components of Extinction Risk." They coauthored recent updating articles: "The Influence of Top-Down, Bottom-Up and Abiotic Factors on the Moose (*Alces alces*) Population of Isle Royale" and "The Influence of Prey Consumption and Demographic Stochasticity on Population Growth Rate of Isle Royale Wolves (*Canis lupus*)" (Vucetich and Peterson 2004*a*, *b*). For moose, top-down influence is the wolf, bottom-up influence is vegetation, and abiotic factors are environmental. They found that "wolf predation, the dominant cause of death for Isle Royale moose (Peterson 1977), appears to be a dominant predictor of the moose equilibrium, but has much less influence on variation around that equilibrium" (Vucetich and Peterson 2004*a*:188). Furthermore, "abiotic factors are an important and complex influencer of the dynamics of terrestrial populations."

For wolves, "ratio-dependent kill rate (i.e. kill rate depends on the ratio of prey to predator) may be the important stabilizing force of the predator–prey dynamics on Isle Royale" (Vucetich and Peterson 2004b:318). Also, "Per capita growth rate of the Isle Royale wolf population appears to increase with the rate at which wolves kill moose."

Long-term studies can reveal things not noticed in the short term. Peterson and Vucetich were part of a team who reported (Nelson et al. 2011:32):

> *In the early 1980s wolves declined dramatically (about 80%) due to an outbreak of canine parvovirus. Shortly after this decline, moose increased to an incredibly high abundance, only to themselves crash (also about 80%) due to the combined effects of a severe winter, a tick outbreak, and a catastrophic food shortage. Most recently, it was learned that of all the factors affecting short-term fluctuations in moose abundance, wolves are the least important; whereas climatic factors, such as summer heat and winter severity, are far more significant.*

Fig. 14. (a) Rolf Peterson. Peterson 1995:dust jacket. (b) John Vucetich. Web.

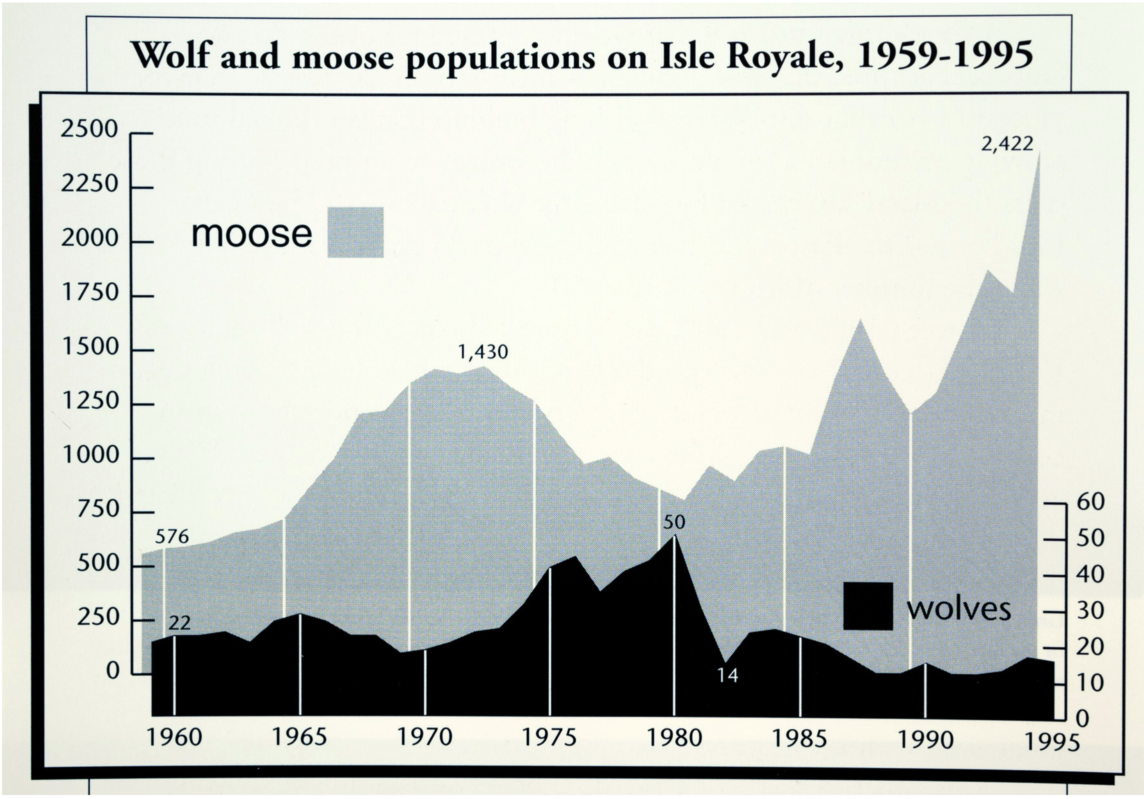


Fig. 15. Wolf and moose populations on Isle Royale, 1959–1995. Peterson 1995:30.

The greatest biotic threat to moose was not wolves, who kill a few, but ticks, that can be as numerous as 100,000 per moose, on all moose. The greatest threat to wolves was probably inbreeding. A dark-colored wolf did make it out to Isle Royale at a later time than the original pack, but it died without reproducing. In 2012, when the wolf pact had dwindled to nine, the park administration debated whether to bring in new wolves (Marcotty 2012). Sometimes new wolves are accepted, sometimes not. A spring 2014 assessment showed only 8 or 9 wolves and about 1100 moose (Bergquist 2014). By April 2015, there were only three wolves in the park.

Mark Hixon, Stephen Pacala, and Stuart Sandin (2002) found that previous population theorists assumed closed populations even when not stated, and that the possibility of metapopulations providing recruits for declining populations of a species had been little considered.

Price, whose comment on the rise of population ecology during the 1950s and '60s is quoted above, believed that during the 1970s (2003:25):

> *…two factors resulted in a radical decline of interest. One was the seemingly insoluble debate in those times on density-dependent versus density-independent factors in population regulation, accompanied by an aging population of combatants (cf. Murdoch 1994). The other was the rise of evolutionary ecology in the 1960s with the diverse range of topics that we can now see impinging directly on the population dynamics of organisms.*

However, after new perspectives were absorbed, a population dynamics revival occurred (Price 2003:39):

> *The decade of the 1980s, I regard as a reawakening of much interest in population dynamics, much of the activity focusing on life history traits correlated to outbreak dynamics. At this time we began to see sufficient activity so that researchers were directly and rapidly influencing each other's approaches.*

With what results? William Murdoch (b. 1939), University of California, Santa Barbara, in a MacArthur Award Lecture, "Population Regulation in Theory and Practice" (1994), thought density-dependent regulatory processes were clear in theory, but verification in practice was elusive. He and colleagues studied red-scale insects *Aonidiella aurantii* and its controlling parasitoid *Aphytis melinus* to identify the specific cause of stability. They tested eight hypotheses, including spatial heterogeneity in attack rates, a refuge, and metapopulation dynamics. They failed to find evidence for a density-dependent mechanism, but remained open to that possibility. Recent laboratory and modeling studies suggested other possibilities to investigate.

Another insect ecologist, Naomi Cappuccino, Carleton University, Ottawa, briefly highlighted aspects of the history of population ecology and then commented that earlier proponents of population regulation by density-dependent versus density-independent factors often argued at cross-purposes, since these factors are not mutually exclusive: "One of the most refreshing aspects of the renaissance of population dynamics is the absence of polarizing debate," replaced by a "new pluralist synthesis" (Cappuccino 1995:12). Yet, immediately following her article in the same volume, Peter Turchin (1995:19) claimed

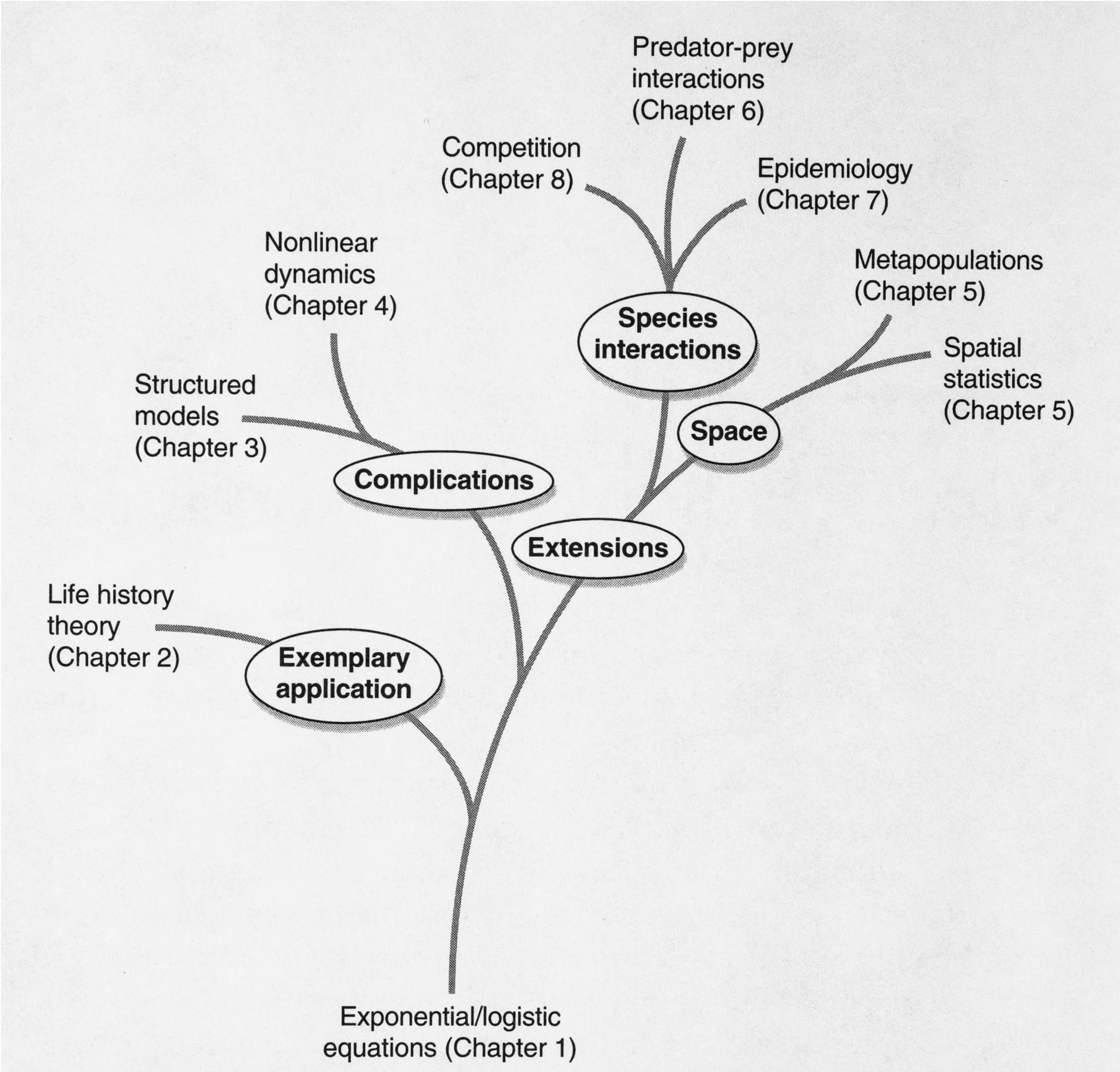


Fig. 16. Diagrammatic representation of population ecology. Vandermeer and Goldberg 2003:256.

that the debate over density-dependent vs. density-independent regulation "continues to this very day." Since Cappuccino was senior editor of that volume, she had a chance to attempt to reconcile hers and Turchin's assessments, but let both stand. When Turchin published his *Complex Population Dynamics: A Theoretical Empirical Synthesis* (2003), he thought that population ecology was a mature science that had outgrown some long-standing debates.

English parasitologist Peter Hudson (b. 1953), now an endowed professor at Penn State University, earned his Phil.D. at the Edward Grey Institute, Oxford University, and later studied red grouse populations for the British Game Conservancy Trust (Hudson 2014). Grouse in North Yorkshire experienced population cycles which did not seem caused by territory spacing. In 1978, Roy Anderson and Robert May had published a model of population cycles caused by parasites. Hudson thought their model fit grouse cycles. That conclusion was controversial, but he proved it by inventing a "medicated grit" that rid the grouse of parasites and population cycles (Hudson 1986). This reminds us of Marchal's explanation (1897) of host–parasite population oscillations among insect pests, though Hudson might never have known of Marchal's French paper on insects.

Competent textbooks have the virtue of explaining the scope and achievements of a discipline. One can argue that population ecology is not as well delimited as many other disciplines, and perhaps has included more controversies than many disciplines. Peter Price devoted three chapters of *Insect Ecology* (Price 1997:431–549) to population dynamics. A dozen years after John Vandermeer and Deborah Goldberg published *Population Ecology: First Principles* (2003) their book might still be considered "recent." In a summary final chapter, these University of Michigan ecologists present a diagram that provides a visual explanation of the scope of this (highly mathematical) field as they see it. Two other books that appeared in 2003 were Peter Turchin, *Complex Population Dynamics* and Peter Price, *Macroevolutionary Theory on Macroecological Patterns*. Turchin's is an advanced-level synthesis, in greater detail than the Vandermeer-Goldberg text that announced maturity of population ecology. The publisher's blurb on the back of Price's book stated: "For the first time in book form, the study of distribution, abundance, and population dynamics in animals is cast in an evolutionary framework." Vandermeer and Goldberg's assertion that population ecology had achieved maturity by 2003 is challenged by Price's simultaneous conclusion (Price 2003:231):

> *...the overriding impression received is that an emphasis on ecological factors in population dynamics yields the full panoply of possible influences. Almost anything ecological can impinge on a species' dynamics.*

Invasives

Intentional introductions of alien predators to control accidentally imported alien species during the later 1800s and early 1900s have already been discussed above. These efforts were scientific in the sense that problems were studied scientifically and proposed solutions were assessed scientifically after implementation. No significant theory emerged from these empirical studies. However, the practical significance of the problem ensured its study and remediation. Charles Elton's *The Ecology of Invasions by Animals and Plants* (1958) was the first synthesis, including numerous illustrations and maps, and

Fig. 17. Jeff Fobb holding a Burmese python in Florida swamp. By Karine Aigner and Ken Geiger. From Reimers 2014:cover.

had a broad readership. Ecologist Mark Davis' textbook, *Invasion Biology* (2009), a half-century later, synthesized recent knowledge on invasion problems and avenues of research. Subsequently, he decided that "Buckthorn, Garlic Mustard and Many Other Invasive Species Do Not Pose as Big a Threat as Some Scientists Think" (quoted in Borrell 2011). Three earlier popular books on invasives reflect still-current concerns: wildlife manager George Laycock's *The Alien Animals* (1966) discussed Barbary sheep, ring-necked pheasants, brown trout, striped bass, Russian wild hogs, starlings, English Sparrows, gray squirrels in England, muskrats, nutria, mongoose, myna birds in Hawaii, African snails, pigs in New Zealand, camel, burro, pigeons, carp, rabbits in Australia, and *Coturnix* quail; biologist Alvin Silverstein and coauthor Virginia Silverstein's *Animal Invaders: the Story of Imported Wildlife* (1974) discussed Ring-necked Pheasants, English Sparrows, starlings, pigeons, muskrats, nutria, mongoose, rabbits in Australia, horses, catfish, African snail, and insect friends and foes; naturalist Kim Todd's *Tinkering with Eden: a Natural History of Exotics in America* (2001) discussed pigeons, honey bees, Hessian flies, mosquitoes in Hawaii, lamprey in the Great Lakes, European gypsy moth, Ring-necked Pheasants, brown trout, scale insect *Icerya purchase*, English Sparrow, Starling, reindeer, mountain goats in the Olympic Mountains, rhesus monkeys in Florida, nutria, South American parakeet *Myiopsitta monachus* in New York, insects eating knapweed in Montana, and kangaroos in the Midwest and West.

Besides popular books, particular articles address specific cases. Burmese pythons are only one example of exotics let loose in southern Florida. Frederick Reimers' "Python Patrol" (2014) tells of a collaborative project by Florida Fish and Wildlife Conservation Commission and the Nature Conservancy to train Florida citizens to capture these snakes, which threaten Florida's native wildlife. Perhaps such stories helped inspire *Time*'s cover story, July 28, 2014, by Brian Walsh, "Invasive Species," which also includes a photo of him subduing a feral python in Florida (p. 3). Unsurprisingly, PBS' *Nature* has a film, "Invasion: Giant Pythons." Maddie Oatman tells of an "Attack of the Killer Beetles" (2015), on pine-bark beetles that sweep across North America's western forests: they became invasives because of global warming. It is a native species with previous limited damage because kept in check by winter weather. That beetle dilemma is an aspect of J. B. Heffernan et al., "Understanding Ecological Patterns and Processes at Continental Scales" (Heffernan et al. 2014).

The five Great Lakes along the Canadian–U.S. border hold some 20 percent of the Earth's freshwater, and they became the location of profitable commercial fisheries in the 1800s, to which very popular sport fishing was added during the later 1900s, after salmon were introduced to eat accidentally introduced alewife. Unfortunately, this is not a "happily ever after" story. Not only was commercial over-fishing a persistent problem, but efforts promoting Great Lakes shipping for ocean-going ships became an avenue for accidental introduction of destructive alien species. Most devastating have been the sea lamprey and zebra and quagga mussels, but others are also very important. Wayne Grady tells this sad story in *The Great Lakes: the Natural History of a Changing Region* (Grady 2007:273–301). Not only do previous threats persist, but others appear rather regularly, such as a threat of Asian carp in the Chicago River, which currently empties into Lake Michigan (originally it flowed west). Asian carp in the Great Lakes would be a disaster, but prevention is still possible, with an effective plan.

Rare and extinct species

Rare and extinct mammal, bird, and fish species have attracted much attention and resulted in a substantial literature, including, for the world: Caras (1966), Fisher et al. (1969), Reader's Digest Editors (1975), Regenstein (1975), Ehrlich and Ehrlich (1981), Day (1989), and Ceballos et al. (2015). Broad geographical surveys include: Laycock (1969), McClung (1969), Allen (1974), Stewart (1978), Howell (2013), and Ehrlich et al. (1992) on North America; Walsh with Gannon (1967) on South America; Moorehead (1959) and Grzimek and Grzimek (1960) on Africa; Serventy (1966) on Australia; Badger et al. (2008) on China; Seshadri (1969) on India; Mowat (1984) on the North Atlantic; and Durrell (1983) on Madagascar and Mascarene Islands. Implicit or explicit in these studies is the population dynamics of species whose numbers decline until extinction or until much human effort revives their numbers to a safe, stable level. An early famous example was the dodo from the island of Mauritius (one of the Mascarenes), discovered in 1507 and extinct by 1681 (Greenway 1967:120-122, Halliday 1978:56-67, Day 1989:26—28, Cheke and Hume 2008:see index, Barrow 2009:50-56). Dodo extinction illustrates a common hazard for island species that evolved without predators: later, humans arrived, accompanied by human-invasive predators—some brought intentionally, others unintentionally—which found endogenous species easy prey.

Paul and Anne Ehrlich addressed the general significance of *Extinction: the Causes and Consequences of the Disappearance of Species* (1981). Do we care about the loss of dinosaurs? (Not caused by humans.) Snail darter? (Which would be blamed on humans?) How to save species we value. Errol Fuller (2014*a*) documented some modern extinctions in *Lost Animals: Extinction and the Photographic Record*.

The passenger pigeon of North America during the later 1800s was decimated by market hunters, going from being the most numerous species on the continent to virtually none, with actual extinction when the last individual died at the Cincinnati Zoo in 1914 (Schorger 1955, Greenway 1967:see index, Halliday 1978:87–95, Day 1989:32–37, Barrow 2009:see index, Fuller 2014*b*, Greenberg 2014, Yeoman 2014). American wildlife was often seen as too numerous to worry about their numbers, and in the early 1800s there were still doubts that species became extinct. That skepticism was laid to rest by French zoologist–paleontologist Georges Cuvier (1769–1832) in studies on living and fossil elephants (Coleman 1964, Bourdier 1971, Barrow 2009:39–42, Egerton 2010:23–25). Even after extinction became accepted as real, there was a long struggle to persuade federal and state legislatures to enact restrictive hunting laws and enforce them (Trefethen 1975, Dunlap 1988, Line 1999).

Less famous than the pigeon is the extinct Carolina Parakeet *Cornuropsis carolinensis* (Greenway 1967:see index, Halliday 1978:96–100, Day 1989:66–68, Snyder 2004, Barrow 2009:127–130), the extremely rare or extinct Ivory-billed Woodpecker *Campephilus principalis* (Halliday 1978:108–109, Fitzpatrick et al. 2005, Steinberg 2008), and California Condor *Gymnogypus californianus*, saved from extinction by captive breeding (Halliday 1978:106–109, Snyder and Snyder 2000, Nielsen 2006). European aurochs *Bos primigenius* became extinct about 1627 and the Caucasian wisent *Bison bonasus caucasius* about 1925 (Day 1989:186–189). Saved at the brink of extinction was the American bison (buffalo). The latter story has received many tellings (including Haines 1970, Roe 1970, Lott 2002, Barrow 2009:130–133, Bechtel 2012, Dehler 2013), with some emphasis upon crusader William T. Hornaday (1854–1937).

Also saved were Whooping Cranes *Grus americana*; there were less than 30 in the world in 1945; they wintered at the Aransas National Wildlife Refuge, on San Antonio Bay, but their breeding grounds in Canada had not then been located (McCoy 1966, McNulty 1966, Doughty 1989). Canadian Wildlife

Fig. 18 (a) David Wingate making his rounds on a Bermuda government motor boat. Gehrman 2012:cover. (b) *Pterodroma cahow*. Cahow web site.

Service, U.S. Fish and Wildlife Service, and National Audubon Society collaborated to increase their numbers. In early 1970s, two Ph.D. students at Cornell University, both studying cranes, Ron Sauey and George Archibald, decided to establish the International Crane Foundation. Sauey's father, who had a farm close to Baraboo, Wisconsin, provided space for them to begin in 1973. After obtaining grant support, they acquired their own property nearby—225 acres--where they established facilities to raise all fifteen crane species, with the goal of returning offspring to the wild in native habitats. This Foundation now flourishes (Schoff 1991, Conover 1998, ICF web site), though Sauey is deceased.

World-wide use of DDT insecticide after World War II was highly effective in killing insects, but unknowingly had catastrophic impacts on vertebrates and other non-target species. Rachel Carson marshalled evidence on animal impacts in *Silent Spring* (1962). Conspicuous casualties were Bald Eagles (Halliday 1978:111, Savage 1987, Breining 1994) and Peregrine Falcons (Hickey 1969, Ratcliffe 1980:81–85, Enderson 2005:see index, MacDonald 2006:116–122, Stirling-Aird 2012:114–116), whose egg shells were too thin to protect chicks until hatching. It took a decade for scientists and environmentalists to overcome the agriculture lobby's influence in Congress and get DDT banned from use in the United States (Dunlap 1981). David Kinkela (2011:188–189) stated that the World Health Organization approves of indoor use of DDT in countries burdened with malaria.

Bermuda native, David B. Wingate (b. 1935), was teased while young because he preferred watching birds to playing sports (Gerhan 2012:4–5). When 15, he joined American ornithologist Robert C. Murphy and Bermudan naturalist Louis S. Mowbray in seeking the cahow, or Bermuda petrel *Pterodroma cahow*, which had disappeared in the 1620s due to predation by humans and domesticated animals (Gerhan 2012:8). Their 1951 search was successful, for Murphy pulled one out of a nesting burrow. It had escaped notice for three centuries because it was rare and nocturnal. When Wingate graduated from high school, he enrolled at Cornell University to study ornithology and conservation. He realized that if cahows were to be saved from extinction while new homes were being built each year in Bermuda, they required active protection. His successful half-century effort is the subject of Elizabeth Gehrman's fascinating dual biography of Wingate and cahows (2012).

Robert McFarlane's *A Stillness in the Pines: the Ecology of the Red-cockaded Woodpeckers* (1992) is notable for discussing and evaluating all potential factors that could affect the population of this rare species in southeastern USA's coastal pine forests.

At the First World Congress of Herpetology (1989), it became clear that there were world-wide declines of many amphibian species (Lannoo 2005:xix). A decade later, with more details, Australian herpetologists Ross Alford and Stephen Richards, James Cook University, wrote an outstanding "Global Amphibian Declines" (1999). It is unlikely that they had seen McFarlane's study of a rare American woodpecker, but they saw the same need to evaluate all factors affecting populations: ultraviolet radiation, predation, habitat modification, environmental acidity and toxicants, diseases, changes in climate, and interactions among these factors. They called for more metapopulation studies. With continuing declines, 114 herpetologists contributed to a collective *Amphibian Declines: the Conservation Status of United States Species* (xxi + 1094 pages [Lannoo 2005]). What comes out of their stupendous effort? It contains the first detailed treatment of all 289 amphibian taxa of the United States, and this information is used to "make informed management decisions so that we may indeed conserve the amphibians of the United States" (Lannoo 2005:926). Subsequently, that effort was enhanced by a magnificent *North American*

Amphibians: Distribution and Diversity (Green et al. 2013), with color photos of all species.

Similar tragedies affect American honey bees and bats. The bee problem was discovered in 2006 and is complex, with pesticides and mites being among causes. The bat crisis is caused by a previously unknown fungal parasite, *Geomyces destructans*, which causes a highly contagious and mostly fatal white-nose syndrome (WNS).

Journalist Jim Sterba's well-informed *Nature Wars: The Incredible Story of How Wildlife Comebacks Turned Backyards into Battlegrounds* (2012) focused mainly on northeastern states. During the 1800s, many farmers from the region migrated to the Midwest, which had more fertile soils than the farms they deserted. Most abandoned farms reverted to forests similar to what had existed before lands were cleared for farming. Into these forests came white-tail deer, black bear, and wild turkeys, which had been practically hunted out of the region by the early 1900s. Since Americans do not hunt game in suburbs, Sterba argues that these species lately have worn out their welcome. Beaver had been trapped out of New England by 1750 (Sterba 2012:60). By the 1890s, only about 100,000 remained in North America, mostly in Canada (Sterba 2012:73). Environmentalists supported beaver reintroduction into former habitat to recreate ponds and wetlands that had existed before Europeans arrived. Beaver were assets in national, state, and county parks, but their dams in suburbs created floods.

While there is evidence supporting Sterba's claims about wildlife in U.S. suburbs, species overabundance is not the main problem worldwide. Elizabeth Kolbert is another well-informed journalist who has written two pessimistic books on humankind during the Anthropocene: *Field Notes from a Catastrophe: Man, Nature, and Climate Change* (2007) was one of numerous warnings on global warming; *The Sixth Extinction: an Unnatural History* (2014) is an even more pointed warning about the consequences of human depreciation of the world's environment. Little in her books is new to ecologists, but public opinion on these matters is important to ecologists, and her books can be recommended. Two ecologists recently warned of global warming as a likely cause of significant extinctions (Lambers 2015, Urban 2015). Yet, Anne Charmantier and five coauthors (2014) used 47 years of data on the great tit *Parus major* to argue that this species had enough "adaptive phenotypic plasticity" to respond successfully to climate change. Some zoologists have dreamed of a "science of de-extinction" (Shapiro 2015).

Conclusions

Animal population ecology had as long a development as any branch of ecology—extending back into antiquity—yet it had a more contentious history than most branches. Its modern history began with Darwin's theory of evolution by natural selection, and there is a substantial historical literature documenting its development. New perspectives and developments began in the 1890s, and the first modern landmark was Howard and Fiske's 1911 monograph on the population dynamics of two invasive moths from Europe, studied in Massachusetts. They distinguished between biotic and abiotic factors which limit population growth, though their terminology was unsatisfactory. In the 1920s, Pearl and Lotka in America and Volterra in Italy began to explore mathematical means of quantifying theoretical population changes. Scudo and Ziegler (1978) pronounced a golden age of theoretical (mathematical) ecology, 1923–1940. Nicholson in Australia published a landmark empirical study (1933), based like Howard and Fiske's study upon insects, and emphasizing competition. Independently of Pearl, Lotka, and Volterra, whose publications were unknown to him, Nicholson obtained assistance from mathematical physicist Bailey in quantifying his findings. Their mathematics resembled that of their predecessors. Nicholson and Bailey's critics were fellow Australians, Andrewartha and Birch, who in a landmark monograph (1954) defended the importance of environmental control of insect populations and dismissed biotic controls as unproven. Population ecology flourished in 1954, with other important studies by Nicholson, by Lack, by Cole, by Morris and Miller, and by Beverton and Holt, though this last study did not appear until 1957. No consensus emerged from this diverse literature. In hopes of encouraging a consensus, a Cold Spring Harbor Quantitative Biology Symposium (1957) was held on animal and human demography, which resulted in a substantial volume of papers (1958), but no consensus. Subsequently, publication of textbooks by Andrewartha (1961), Slobodkin (1961), MacArthur and Connell (1966), Cushing (1968), and Hutchinson (1978) provided some coherence. Price (2003) identified the heyday of insect population ecology as during the 1950s and 1960s. By the 1970s a substantial tradition of anthologies and symposia reports were being published, and by the 1980s there was a substantial history literature, with some books and numerous articles. Further achievements by population ecologists are indicated in three books that appeared in 2003, by Price, by Turchin, and by Vandermeer and Goldberg.

Botkin's complaint (2012) that ecologists were not thinking in an evolutionary context had limited validity, in that he could cite supportive evidence, but there were counter-examples that he ignored. Animal population ecology consists of field and laboratory studies on the reproductive cycle of species and theoretical interpretations of collected data.

Invasive species and rare species are important practical demographic problems that often attract attention from population ecologists, who help solve some of the problems.

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