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Population Cycles, Disease, and Networks of Ecological Knowledge

SUSAN D. JONES
Program in History of Science and Technology
University of Minnesota
100 Ecology, EEB, 1987 Upper Buford Circle
St. Paul, MN 55108
USA
E-mail: jone0996@umn.edu

Abstract. Wildlife populations in the northern reaches of the globe have long been observed to fluctuate or cycle periodically, with dramatic increases followed by catastrophic crashes. Focusing on the early work of Charles S. Elton, this article analyzes how investigations into population cycles shaped the development of Anglo-American animal ecology during the 1920s–1930s. Population cycling revealed patterns that challenged ideas about the "balance" of nature; stimulated efforts to quantify population data; and brought animal ecology into conversation with intellectual debates about natural selection. Elton used the problem of understanding wildlife population cycles to explore a central tension in ecological thought: the relative influences of local conditions (food supply, predation) and universal forces (such as climate change and natural selection) in regulating wild animal populations. He also sought patronage and built research practices and the influential Bureau of Animal Population around questions of population regulation during the 1930s. Focusing on disease as a local population regulator that could interact with global climatic influences, Elton facilitated an interdisciplinary and population-based approach in early animal ecology. Elton created a network of epidemiologists, conservationists, pathologists and mathematicians, who contributed to population cycle research. I argue that, although these people often remained peripheral to ecology, their ideas shaped the young discipline. Particularly important were the concepts of abundance, density, and disease; and the interactions between these factors and natural selection. However, Elton's reliance on density dependence unwittingly helped set up conditions conducive to the development of controversies in animal ecology in later years. While ecologists did not come to consensus on the ultimate causes of population cycles, this phenomenon was an important early catalyst for the development of theory and practice in animal ecology.

Keywords: Animal ecology – History, Elton, Charles Sutherland, Green, Robert Gladding, Population biology, Disease – wild animals, Scientific networks, Balance of nature concept

Introduction

Ecologists in the 1920s sought intellectual and institutional frameworks for their young discipline, and British zoologist Charles S. Elton offered an important framework to guide the early development of animal ecology. Elton, often called the "father of animal ecology," is best known for articulating concepts such as niche theory, the "pyramid of numbers," and relationships within food chains. Author of the classic text, *Animal Ecology* (1927), Elton also founded the *Journal of Animal Ecology* and Oxford University's Bureau of Animal Population (BAP) in 1932. Using Elton and his collaborators as a case study, this article analyzes a curious phenomenon observed in animal populations that I argue was a crucial early influence on animal ecology: the periodic, dramatic highs and lows ("population cycles") observed in populations of some species of insects, birds and mammals. Population cycling was an important early focus for animal ecologists because the phenomenon revealed patterns that challenged ideas about the "balance" of nature; stimulated efforts to quantify population data; and brought ecology into conversation with intellectual debates over natural selection. As we will see, explaining population cycles also led Elton to search fields such as climatology, epidemiology, and medical bacteriology for ideas, tools and expertise to bring into animal ecology. Focusing on disease as a local population regulator that could interact with global climatic influences, Elton facilitated an interdisciplinary approach in early animal ecology that revolved around the general problem of population regulation and the particular case of population cycles.

A well-known natural phenomenon, the boom-and-bust cycles of some wild animal populations would seem to portend severe consequences. As Robert Gladding Green, a professor at the University of Minnesota, wrote in 1936: "In the north country from Alaska to Labrador and from Hudson's Bay to Ohio a disastrous die-off of wild animals is under way that in another year will bring many species close to annihilation." But Green, who had grown up in the woods of northern Minnesota, had seen this happen before. He went on to describe the most likely sequel: rather than annihilation, the dwindling number of rabbits and foxes usually reversed itself dramatically in a predictable period of ensuing years, until the land fairly "teemed" with the animals. "I do not remember when I first heard of the 'seven year rabbit cycle' but it was very long ago," he wrote, recalling hunting expeditions that dated back to 1905.[1] Native peoples

[1] Robert Gladding Green, manuscript "Saturday Evening Post 1936," in folder "Popular Articles Manuscripts," Box 3, Robert Gladding Green Papers, Collection 349, University Archives, University of Minnesota (hereafter "RGG").

and backwoodsmen, long resident in these animals' northern environments, contended that these repetitive cycles occurred regardless of human activities. People suffered from the dearth of food and fur animals during the population nadir years but then counted on the historical pattern of steady increase and plenty for about 7–10 years before the next crash. Late nineteenth-century natural historians and, later, ecologists agreed that these population cycles were "natural" phenomena. Cycles occurred in areas not inhabited by humans, and in species not usually hunted; and they had been reported in northern species throughout the world (Allen, 1903; Collett, 1911; Duchesne, 1981; Lindstrom et al., 2001; Houston et al., 2003).

This odd phenomenon inspired many questions in the minds of contemporary observers. Why would wild populations of various species in places as diverse as North America, Scandinavia, and Russia – birds, hares, lynx, lemmings, voles, and foxes – experience die-offs only to become overcrowded in ensuing years? What caused these dramatic population fluctuations, and how did the animals avoid extinction? What purpose did these oscillations serve in relation to other populations? These questions intrigued Elton and other post-Darwinian scientists interested in the dynamic natural history approaches that characterized early animal ecology (McIntosh, 1986; Hagen, 1992; Ackert, 2012; Kingsland, 2005).

Elton (Figure 1) was a protégé of Julian Huxley in the early 1920s and later a Reader in Animal Ecology at Oxford.[2] The BAP that Elton founded in 1932 functioned as a central training ground for ecologists and other scientists who took the methods and concepts they learned there to the four corners of the world (Crowcroft, 1991). BAP scientists learned how to take animal censuses and conduct experiments, collect animals, and record and analyze the resultant data in ways that could illuminate regular patterns, a kind of invisible scaffolding that Elton suspected structured the fluctuations of animal populations. Elton's interest in populations was an enduring and important one that he returned to repeatedly throughout his professional life (even as he and other animal ecologists moved into community ecology approaches). Although he saw himself foremost as a practical scientist adept in the

[2] A recently discovered trove of Elton's field notebooks from the Oxford Museum of Natural History has been transcribed and digitized by Dr. Caroline Pond. *Notes on Wytham Area 1942–1965* and *Notes on Oxon, Berks, Bucks (excl. Wytham) 1942–1965* is available at http://ora.ox.ac.uk/objects/uuid:89c5e479-6003-45babd78-8a8a12858bf1. Elton's notes from the 1920 s expeditions to Svalbard are available on the website of the Norsk Polarinstittut, http://brage.bibsys.no/xmlui/handle/11250/226488. Accessed 15 April 2016.

Figure 1. Charles S. Elton, collecting in Svalbard, 3 August 1923. Photo taken by E.R. Relf. From Elton's field notebook, Merton College Arctic Expedition Notes by C.S. Elton, p. 17. Courtesy of The Museum of Natural History, Oxford University, Oxford U.K. Digitized text available online at Norsk Polarinstittut, http://brage.bibsys.no/xmlui/handle/11250/226488

field, his genius lay with envisioning patterns and developing concepts in ecology's early years and being able to communicate his thinking clearly and concisely. His contemporaries later asserted that Elton's vision and methods kept the "natural history" in university-based zoology at a time when most had "turned their backs on nature" (Hardy, 1968; Topley, 1942; Editors, 1944).

Elton used the population cycles phenomenon to address three key conceptual and practical issues for the nascent discipline of animal ecology: (1) the interactions between local population conditions and universal abiotic forces in regulating natural systems; (2) stability, instability and the so-called balance of nature; and (3) the need to generate patronage and enlist allies through linkages to other disciplines. Elton created a network of epidemiologists, conservationists, pathologists, mathematicians, collectors and experimentalists who contributed to population cycle research. Although these people often remained peripheral to ecology, their ideas shaped the young discipline and linked local conditions with universal forces. Particularly important were their contributions to investigations of abundance and density; and the interactions between these factors and natural selection.

Natural selection has played an important role in historians' accounts of ecology's development, but the concepts of mass action, abundance and density have remained understudied in part because they have long been associated more with epidemiology and the study of disease. (Chapter Five of Sharon Kingsland's *Modeling Nature* is a notable exception; see also Connelly, 2010 and Murphy, 2013 for analyses of similar concepts.) Usually considered within the purview of the medical sciences, "disease" deserved an ecological analysis itself in Elton's view because it performed work for him in addressing each of the three conceptual and practical issues outlined above. Viewed ecologically, "disease" was not merely a medical problem but an effect of microbial–macrobial population interactions (and this is how Elton defined it). In multiple ways, ecological disease investigations illuminated the dynamics of local animal populations but also linked them with other populations and abiotic factors (such as climate). The concept of "disease" had an intellectual life of its own, but it was flexible enough to be useful in population studies.

Finally, the study of disease was a productive space in which to form a network of scientists. We will meet a few of them. Robert Green, the University of Minnesota professor quoted above, was a bacteriologist/virologist who contributed expertise and laboratory space for studies of microorganisms. Aldo Leopold, the famous conservationist, was an important American ally for Elton, particularly during the lean years of the 1930s. Ellsworth Huntington supplied data and ideas being debated in the climate sciences. While few of these scientists called themselves "ecologists," their ideas and practices influenced early Anglo-American animal ecology through Elton's study of population cycles.

As we will see, Elton focused on disease as a local population regulator that could interact with other influences to cause population cycles. For Elton, disease functioned as a special case of predation in which the population of hosts (hares, voles, lemmings) was coupled to that of the predators (microorganisms). Host populations thus cycled in relation to both their own density (intra-specific) and that of microorganisms (inter-specific). High host population density was more likely to result in high levels of microbes, leading to disease outbreaks, which then caused the periodic population crashes. This formulation cast disease as a negative density-dependent factor. During the 1920s and 1930s, Elton's persistent interest in disease helped to move ecologists away from simpler deterministic models (climatic cycles, such as sun-spots) of population regulation to the more complex and dynamic density-dependent ones.

In the end, Elton and his contemporaries during the interwar period could not come to consensus on the ultimate cause(s) of periodic population fluctuations. (The phenomenon is still an active area of study in population ecology.) However, their interest in this phenomenon provides a window into how early animal ecologists approached what historian Joel Hagen has called "creative tensions" inherited from the nineteenth century: stability versus instability of populations and communities; whether that in/stability could be best understood through organismic or mechanical analogies and metaphors; and whether Darwinian competition drove ecological patterns (Hagen, 1992, p. 3). In an approach that would remain characteristic of animal ecology, Elton framed invisible patterns underlying periodic population fluctuations and attempted to understand what these patterns told him about broad evolutionary and ecological questions.

Bridging the Local and Global: Climatic Determinism and Population Cycles

Population cycling had been observed almost exclusively in the northern reaches of the globe, and Elton owed many of his ideas to formative experiences above the Arctic Circle early in his career. In 1921–1924, at first while still a Huxley student, Elton participated in animal surveys during field expeditions to Svalbard Archipelago (a possession of Norway after 1920). Later in life, Elton remembered the adventures of shooting seals for food and almost drowning after falling through the ice. The island averaged only 40 degrees Fahrenheit in summer, and a bad-tempered population of polar bears made carrying a rifle mandatory. Svalbard was a rough place for tough men, and the expeditions were Elton's coming of age, personally and professionally. Elton later remembered that his experiences at Svalbard also "had a profound influence" on his ecological ideas (Elton, quoted in Southwood and Clarke, 1999, pp. 135–136). This influence began with his companions on the various expeditions, who (besides Huxley) included Alexander Carr-Saunders (a eugenicist and sociologist interested in population dynamics); the Arctic explorer George Binney; and Howard Florey, the Australian physician who later won a Nobel Prize for his role in penicillin production. Carr-Saunders impressed on the young Elton the importance of understanding the "sociology and economy" of animal populations – the very basis of ecological analysis (Anker, 2001, p. 101ff). Florey, who discussed physiology and disease with Elton, remained an important connection to biomedicine throughout Elton's career. Binney later helped Elton become a paid consultant to the Hudson's Bay Company (thus assuring Elton's access to longitudinal data on population cycles of Canadian wildlife).

Elton found the Arctic Northlands to be a valuable field site for investigators who could overlook the lack of "personal comforts": the plant and animal communities were simple, populations were easily counted, and population and community patterns could more easily be discerned. According to Elton's notes, the Svalbard expeditions planted the seeds of foundational ideas that he later included in his text *Animal Ecology* – food chains and the pyramid of numbers, for example (Southwood and Clarke, 1999). Elton also became enthralled by descriptions of population cycles in animals during the Norwegian expeditions. On his way back home in 1923, in Tromsø, he picked up a copy of Robert Collett's *Norges pattedyr* [Norwegian Mammals] (Collett, 1911). Collett detailed the dramatic population cycles and migration behavior of the Norwegian lemming. Elton later said this small book had changed his life (Southwood and Clarke, 1999). It provided him with the intellectual direction that would guide his work, and British animal ecology, for the next decade: investigating animal population regulation and interactions between populations.

Through extensive reading during 1923–1924, Elton realized that population cycles were ubiquitous in the northern reaches of the globe, across widely divergent species and geographical areas. Gordon Hewitt's *Conservation of the Wild Life of Canada* described cycles in lynx and Arctic foxes for North America (Elton, 1924; Hewitt, 1921). N.G. Buxton, who conducted Siberian mammal surveys in 1901, told of lemming migrations and wildly fluctuating populations of small rodents in Russia and the Alaskan territory (Allen, 1903). Collett's book and Elton's own observations of Arctic foxes in Svalbard and lemmings in Lapland confirmed population cycles in Norway and the Scandinavian Arctic. All these sources depended on field observations and information from local people and all described a similar chain of events: periodic (even predictable) changes in population size. Elton pointed out that this phenomenon was "well known to practical men, like farmers, gamekeepers and foresters; but its importance has not been generally recognized by biologists until recently" (Elton, 1925, pp. 141–142). This statement was perhaps exaggerated; American natural historians had already taken note of periodic population fluctuations in small North American mammals (Howell, 1923). In his own publications, Elton cited two other early American ecologists, C.C. Adams and Victor Shelford, who had discussed population cycles. Northern population cycles defined the extremes of what Adams described as normal population oscillations that "swing from one side, then back, sometimes showing considerable amplitude in its swing" (Adams, 1913, p. 28). However, the Americans had made no programmatic effort to thoroughly explore and explain the underlying mechanisms regulating animal population numbers over time.

For Elton, the way forward was clear: organize and analyze data about local effects on animal populations, theorize about the underlying forces that caused fluctuations, and determine ''the regular laws governing the fluctuations of many small mammals'' (Elton, 1925, p. 142). After collecting multiple accounts of the phenomenon, Elton summarized the patterns of periodicity. Hare populations, for example, cycled every 10 years, while the cycle for Norwegian mice was as short as 4 years. With the exception of lemmings, observers recorded that most animals whose populations cycled had varying reproductive rates. The hares had, on average, eight to ten young in a brood and three broods per season in a good year; but in bad years, only three young in one brood. Populations of hares' predators, such as lynx, cycled in concert with the hare populations. Other species showed similar patterns. Shelford, the American zoologist, thought the population variations originated with the ''physiology of organisms'' – the capabilities of animals to alter their own feeding habits, metabolic rates and reproductive rates (Shelford, 1913, p. iv).

Elton, however, believed that the animals' physiology alone was not the ultimate explanation for a phenomenon observed across multiple species on multiple continents. Exogenous factors must also be involved (Elton, 1924 after Preble, 1908). He sought to identify a first principle or ultimate regulator that explained how population cycles seemed to run ''synchronously in widely separated countries'' (Elton, 1925, p. 160). First on Elton's list was the influence of what he called ''short-period pulsations of climate.'' Changes in climate would act broadly, influencing Canada, Svalbard, and Siberia all at once. Populations of many different species might be reacting accordingly. ''It is inconceivable that [physiology alone] could cause synchronized maxima…all over the Arctic regions. …The cause,'' he concluded, ''must be some periodic climatic change acting over wide areas'' (Elton, 1924, pp. 119, 132, 160). In trying to connect physical principles underlying the northern climate with the cycling animal populations, Elton's first causation model was an ecologically static one: the cycles functioned independently of populations' abundance or density. Bringing ideas from climatology into animal ecology thus tended to reinforce a more deterministic model – and this was initially very attractive to Elton.

The timing was propitious. During the first two decades of the twentieth century, the phenomenon of observed changes in the northern climate was a central question in climatology. As Elton described, climatologists' recognition of ''variations or pulsations in the climate'' had committed them to the position that ''climate never remains constant,'' a revision of earlier ideas of climatic equilibrium. By the 1920s, the climatological debate had moved from the existence of climatic variations to determining the phenomenon's underlying causes (Elton, 1924). For our purposes, the most important discussion arose from observations that the sun's energy output also seemed to have cycles, in contrast to older ideas of a "solar constant" (Hufbauer, 1991). Elton was interested in what climatologists could tell him about short cycles of climatic change, on the order of years and decades. He looked for correlations between the known cycles of animal populations (3–10 years) and similar-length climatic phenomena. Sun-spots, it turned out, had a measured periodicity of about 11 years (averaged over 150 years). Some climatologists postulated that sun-spot years caused decreased solar energy transmission and climatological perturbations that were especially pronounced near the poles of the Earth. Elton postulated that as climate cycled, so did animal populations in the Northlands. In this, he echoed the views of American climatologist Ellsworth Huntington, a global climatic determinist who found cycles in everything from sequoia growth to the development of human societies. Huntington's influence on ecology was at its peak around 1920: he had served as the second president of the Ecological Society of America and published several articles on this grand theory of cycles in the early to mid-1920s (Kingsland, 2005, pp. 138–141). Elton cited many of them in his work[3] (Elton, 1924).

Elton's early allegiance to the sun-spot theory represented a first step in understanding population cycles and in defining central questions for animal ecology. Elton first published his theory of sun-spot population regulation in 1924 in an article that sounded quite confident, despite the ongoing discussions among climatologists about the relationship between sun-spots and short-term climate "pulsations." His pursuit of this idea distinguished him from other zoologists, natural historians, and evolutionary thinkers. Shelford and Adams' earlier work had not discussed the climate theory. Alexander Carr-Saunders, with whom Elton had discussed measuring populations quantitatively while on expedition together at Spitsbergen, dismissed climatological determinism. In his influential 1922 treatise on human populations, *The Population Problem*, Carr-Saunders acknowledged some "influence of environment," especially the "external circumstances [such as] variations in temperature,

[3] Elton also cited the work of British climatologist C. E. P. Brooks (1921), who was a major competitor of Ellsworth Huntington. For a window into their debates, see Huntington (1922a, b). Huntington envisioned a more holistic role for cycles in climate, plant and animal populations and the development of human societies, and Huntington ended up being more influential on Elton than Brooks.

moisture and so on, when they pass a beyond a certain limit'' in increasing the death rates of animal (and primitive human) populations (Carr-Saunders, 1922, p. 58). But he dismissed Ellsworth Huntington's assertion that cyclical changes in moisture and temperature had been occurring within the period of interest in human (and animal) history: ''Doubt has been cast upon the 'pulsatory' nature of such changes as have taken place,'' he wrote (Carr-Saunders, 1922, p. 302). Of course, this disavowal of climate as a population regulator served Carr-Saunders' need to attribute human population increases and imperialistic migrations to anthropogenic causes such as advancements in agriculture and industrialization – the hallmarks of purportedly evolutionarily-advanced European societies (Carr-Saunders, 1922, p. 302). Nonetheless, Elton found the similarities between the periodicity of reported sun-spot cycling and wild-animal population cycling too tantalizing to resist. In the early 1920s, he viewed climatic cycles as the most determinative factor of population cycles' particular periodicities.

Reasoning by inference, Elton used climatological ideas in the early 1920s to try to bridge a gap common to many ecological questions: how local and global conditions interacted to cause observed effects. Elton surmised that global solar energy variations determined climate, affecting local weather conditions and thus regulating worldwide wildlife population cycles through local effects. ''There is certainly some widely-acting 10–11 year climatic factor at work,'' he wrote, ''and fluctuations in the numbers of many animals are correlated with it'' (Elton, 1925, p. 146). For Elton, ''local'' effects included the food supply and food chain, some physiological characteristics of the small mammal populations, and the outbreaks of disease (epizootics) that directly affected birth and death rates in wild animal populations. Increased birth rates followed by increased death rates created the population cycles. Climate determined the availability of plant life (and thus the food supply), Elton reasoned; the food supply then determined reproductive rates and other physiological factors; and disease functioned as a negative population regulator. The population grew until it increased ''to a density necessary for an epidemic, which kills off nearly all the animals'' (Elton, 1925, p. 146). The population did not increase dramatically until the climatic conditions became again favorable. In this way, local and global conditions interacted to create the observed population effects. From the periodicity of sun-spots and his developing data set, Elton inferred a causative relationship.

Elton's allegiance to the sun-spot theory in 1924 represented a first step in understanding population cycles, but it soon proved inadequate.

Although the sun-spot theory initially looked promising, Carr-Saunders' (1922) analysis proved correct over the next decade: climatologists could not come to consensus over exactly how the appearance of sunspots affected climate. This compromised the value of the sun-spot hypothesis for ecologists. Moreover, as Elton collected more animal population data in the mid-1920s, he acknowledged that the periodicities did not match neatly. Local inconsistencies in the data overpowered the effects of sun-spot cycles: microclimates varied, as did species in the periodicity of the cycles and in their responses to climatic effects. Elton's survey of the data increasingly showed that different species demonstrated population zeniths and nadirs at different times, regardless of recorded sun phenomena. This weakened the ability of the sun-spot theory to establish a global pattern that regulated local species' cycles. By the late 1920s, Elton realized that the first principle he sought was probably a *set* of principles, not attributable to a single cause (even so influential a factor as climate change) (Elton, 1933b). During the 1930s, Elton's associate Mary Nicholson made an exhaustive study of 200 years of longitudinal data from Canada (more on these data later), and she and Elton concluded that the shorter population cycles were actually out of phase with sun-spot cycles. Elton publicly disavowed the sun-spot theory completely by the early 1940s (Elton and Nicholson 1942).

In the meantime, however, Elton had committed himself to the study of populations, and the causes of their cycles, as a central problem in early British animal ecology. (This differed somewhat from the Americans, particularly Shelford, whose interest in population "oscillations" lay with their effects on the whole living community) (Shelford, 1913, p. 18). Periodic fluctuations were so important, Elton reasoned, because this phenomenon had profound implications for how ecological interactions affected evolutionary development. Elton's process of considering the sun-spot causation theory throughout the 1920s proceeded along with, and contributed greatly to, his assessment of the evolutionary implications of periodic population cycles.

Upsetting the Balance of Nature and Natural Selection in the Field

Elton noted that population cycles were important because they had such great magnitude and were predictably recurrent, yet the affected populations had not gone extinct within historical memory. This becomes a paradox only when considering natural historians' viewpoints on the role of population stability in maintaining some sort of larger equilibrium or ''balance of nature.'' Since at least the eighteenth century, natural theologians and historians had called attention to ''harmony'' and ''just proportions'' between groups of living creatures (Egerton, 1973). Many Anglo-American natural historians and philosophers traced the idea that wild populations strove toward ''balance'' in relation to climate back to the ''organism–environment interaction'' of evolutionary theorist Herbert Spencer (Pearce, 2010). After 1880, Americans Stephen A. Forbes and C.C. Adams argued that population oscillations occurred within a limited range and tended toward ''equilibrium'' in population numbers that ensured balance within the larger biotic community (McIntosh, 1986, p. 186). Forbes stated the basic principle most rigidly, describing populations that self-regulated like clockwork to achieve ''the greatest good'' for all (Forbes, 1887, p. 87). The whole mechanism worked because any built-in deviations were small. Reproductive rates adjusted themselves, in relation to the biotic and abiotic environment, to prevent overpopulation. Dramatic fluctuations in populations either did not occur, or simply could not continue indefinitely, according to this ''balance of nature'' tradition.

Obviously, observations of dramatic population fluctuations in northern animals problematized theories of nature's economy as a balanced and regulated meta-system. Nature's ''balance'' had been attractive to natural historians for several reasons: it explained observations; was aesthetically appealing; and dovetailed with ways of knowing in other disciplines (such as the concept of homeostasis in physiology) (Mitman, 2005; Kricher, 2009). However, for those seeking to make natural history ''scientific,'' such as Elton, there were precedents that needed to be delicately dissected and either reconfigured or abandoned. For the post-Darwinian generations of the early 1900s, the ''balance of nature'' idea was potentially problematic due to its implications of stasis and teleology and the potential to favor internal over external causative factors (Plutynski, 2008). Elton worked to think through the evolutionary implications of population cycles in the mid-1920s.

Elton wrote in 1924 that periodic fluctuations revealed complexities within the theory of evolution through natural selection, and indeed functioned as a powerful influence on evolutionary outcomes. Put simply, different factors would be selective depending on the state of the population: periodic fluctuations were themselves an evolutionary force. As Elton put it, ''There will be different types of selection at the maximum and the minimum in numbers…the degree to which a species does remain uniform in characters will depend therefore not only on the factors usually quoted, such as natural selection and crossing, but also on the extent of its periodic fluctuations'' (Elton, 1924, p. 156). Years of high numbers, Elton argued, tended to encourage new mutations and to allow for the persistence of ''indifferent mutations,'' or those variations in a species that did not contribute to fitness under natural selection. Thus ''the struggle for existence, and therefore natural selection, tend to cease temporarily during the rapid expansion in numbers from a minimum'' (Elton, 1924, p. 161). Years of scarcity were even more intriguing. Elton theorized that nadir years could explain the persistence of variations that were neutral according the natural selection (neither increasing or decreasing fitness). ''The great problem,'' he wrote, ''has always been to explain how such indifferent characters could become established in a population at all often'' (Elton, 1924, p. 161). Although he acknowledged that his thinking was in its early stages, and that the implications for evolutionary theory might be ''problematical,'' Elton was very certain that these periodical fluctuations had ''profound implications'' for selection (Elton, 1924, p. 161).

These statements from Elton's (1924) article could be viewed as anticipatory of important concepts in nascent population genetics; but Elton was no geneticist. Ultimately deciding not to delve more deeply into evolutionary theory, he instead highlighted the implications of cycles for the ''balance of nature'' concept in his book *Animal Ecology and Evolution* (1930).

> It is assumed that an undisturbed natural community lives in a certain harmony, referred to as the ''balance of nature,'' and that although rhythmical changes may take place in this balance, yet that these are regular and essentially predictable…and…nicely fitted into the environmental stresses without. …The picture I have given you is, I think, a very fair representation of the ideas most prevalent on this subject among biologists up to recent times. The picture has the advantage of being an intelligible and apparently logical result of natural selection in producing the best possible world for each species. It has the disadvantage of being untrue. (1930, p. 16).

Thus, between 1924 and 1930, Elton decided that population cycles were reflecting underlying natural systems far more complex than he, or anyone else, had realized existed. In thinking through the impact of cycles on the balance of nature concept, Elton began to envision the phenomenon as a dynamic one, dependent on the abundance of various organisms in an animal's local area. Far from being regular and predictable, ''each variation in the numbers of one species causes direct and indirect repercussions on the numbers of the others, and since many of the latter are independently varying in numbers the resultant confusion is very remarkable.'' Populations migrated, crashed, and sometimes crashed together; the one constant, it seemed, was inconstancy. For Elton, ''the balance of nature does not exist, and, perhaps never has existed'' (Elton, 1930, p. 17).

Elton claimed later in his life that he had been ''the first academic'' to challenge the concept and that ''until 1924 academic zoology considered nature to be steady and balanced…as a normal thing.''[4] In reality, moving away from the various components of the ''balance of nature'' was as difficult for him as for many other biologists in the 1920s. In their introduction to the most recent re-printing of *Animal Ecology* (2001), ecologists Matthew A. Liebold and J. Timothy Wooton argued that Elton's ''conviction of tight regulatory processes in nature'' was challenged by the evidence of these high-magnitude population fluctuations (Liebold and Wooton, 2001, p. xl). From his early years with Huxley in Svalbard, the North had been an important intellectual laboratory for Elton and for animal ecology. There, in the sparest of ecological systems, Elton could search for the patterns and underlying principles that regulated the animal world, or so he thought. By 1930, he had conceded that it would not be so simple to explain the causative principles of population regulation and the consequences of population cycles.

Networks of Allies and Patterns of Thinking: Abundance and Disease

In searching for dynamic causes of population cycling, Elton had chosen to follow an a priori method of reasoning from causal assumption to mechanism to confirmation through field observations. He began with a short list of causes that he thought most likely to trigger the ''great die-offs'': cyclical climatic changes, food availability, and increases in predation (of which disease was a special case) (Elton, 1924). Elton decided to investigate disease after reading a translation of Collett's *Norges Pattedyr* (*Norwegian Mammals*). Collett had been developing his multifaceted explanation for lemming population fluctuations in Norway since the early 1890s. While he acknowledged that climatic conditions were probably ''conducive'' to lemming population increases, he wrote in 1895 that ''It is probable that the abnormal increase…will prove to be due to the activity of certain bacteria whose characteristics we do not know,'' which he footnoted with this observation:

[4] Charles Elton to James E. Schindler, 3 March 1980, folder E-69, Charles Elton papers Ms. Eng. C. 3335, Bodleian Library, Oxford University (hereafter CSE).

> Provided one could assume that all life was dependent on the mutual relations of certain bacteria, of which those destructive to existence are, under normal conditions, kept in the balance by those that support vitality, it is likewise presumable that, under conditions which are unknown to us, the latter group might temporarily gain an ascendency, which would result in an excess of population.[5]

Collett's vision of dynamic population interactions greatly influenced Elton's concept of the "optimum density of numbers," discussed in the chapter on "Variations in the numbers of animals" from *Animal Ecology*. This "optimum" represented a positive interaction between a population's abundance and its environment. According to Elton, predation and the "food-cycle" were the most important factors regulating the optimum. In practice, populations seldom reached the limits of the food supply, even during dramatic increases. Elton cited the case of lemmings when he asserted that "alarming" increases in some animal populations would lead to irruptions "which are terminated by disease or some other factors, or else are relieved by migration during which the animals mostly perish." If animal population numbers rose too high, "the over-eating of the food supply…is always the ultimate check on numbers, but in practice other factors usually come in before that condition is reached." For Elton, disease was the most intriguing of these "other factors" and he lamented the fact that data were lacking to illuminate this process (Elton, 2001 [1927], pp. 101, 110, 117).

Elton viewed disease as a kind of "ecological explosion" of microorganisms that interacted with the abundance and density of host populations (Elton, 1958). By the late 1920s, he linked disease explicitly to the phenomenon of population cycles.

> Disease…forms one of the commonest periodic checks upon the numbers of wild animals, especially in the case of mammals. …Epidemic diseases are usually associated with overcrowding in the population…there is usually a rather well-marked fluctuation in the numbers of the population, great density being followed by great scarcity, and this by a gradual increase up to another maximum, which is in turn followed by another epidemic. (Elton, 1931, p. 436)

This conception of disease dominated Elton's thinking about the ultimate causes of population cycles through the decade of the 1930s. Population numbers got regulated by climate, other populations,

[5] Collett (1895, p. 19, note 1). Collett drew on the rapid increase in bacteriological knowledge in the late nineteenth century.

microorganisms, and their own rates of increase. A dynamic pattern of population interactions depended on the local abundance of microorganisms, hares, voles, and their predators (such as lynx); the question at hand for Elton and his BAP colleagues was how to gain access to abundance data.

In the early 1920s, much of the observational data on animal populations were anecdotal or incomplete. Elton needed two distinct types of data sets: first, population censuses of *longue durée* that would allow for generalizations about cycle periodicity over time; and second, detailed field surveys of particular species over divergent geographical areas. Surveys needed to include information on age structure of the population; availability of food; predators; reproductive rates; and outbreaks of disease. Analyses of the disease required a unique combination of methods: the epizootiological data (in essence, animal epidemiology) and bacteriological and pathological examinations by experts. Elton found the former in the records of the Hudson's Bay Company; and he found the latter in the person of Robert Gladding Green, with whose observations I began this essay. I will discuss each in turn.

The Hudson's Bay Company was incorporated in Britain in the seventeenth century to mine the Canadian wilderness for furs. For our purposes, the Company became another example of British colonial capitalism's linkages to scientific development (Worboys, 1981). Almost from the beginning, Company employees were sent across the ocean to make contacts with remote hunters and trappers (many of them Native American) and to assess the species of animals available for exploitation. Over time, the Company also collected diaries, journals, and other records from fur traders and missionaries. The Company men kept good records, and some (such as Peter Fidler in the 1790s) were dedicated natural historians. Company men moved into Canada and began keeping fur catch statistics in table form (from 1752) along with more informal written observations (Houston et al., 2003; Binnema, 2014).

By 1900, the Company records contained the only known long-term data on fur catches, which could be extrapolated to note the magnitude of fluctuations of several populations of wild fur-bearing animals in the globe's northern reaches. These data would themselves be mined by a succession of investigators, among them Roderick Ross MacFarlane (1905), Seton (1911), and D.A. MacLulich (Houston et al., 2003, p. 177). Elton had discovered the records by reading Hewitt's book, *The Conservation of the Wild Life of Canada* (Hewitt, 1921).[6] In the mid-

[6] Hewitt died of pneumonia at a young age and this book was published posthumously; his death was a great loss for Canadian ecology and conservation biology.

1920s, George Binney (who had accompanied Elton on all three expeditions to Svalbard) worked for the Company. He recommended Elton to his employers as a consulting biologist, and Elton successfully cultivated an ongoing relationship with the Company beginning in 1925. Elton and his colleagues thus gained access to the Company's extraordinary fur return records that he and his associates at the BAP used through the 1940s.

Several fur-bearing species experienced the nadir of their "natural cycles" in the late 1920s, causing what Elton called "a good deal of unnecessary alarm and foreboding" among Company functionaries (who stood to lose a good deal of money). Elton presented himself at London headquarters, offering to apply scientific principles to the investigation.[7] By 1928, he was able to travel to Canada under Company sponsorship. There he acquired more Company records and, more importantly, secured the cooperation of the Company men in the field who would supervise local data collection for him for the next couple of decades. "They were glad to have the cycle idea explained to them personally by the individual who was working at it…they would be much better able to cooperate in obtaining the necessary data," he later remembered. The Company's district officers compiled the data in questionnaires Elton had designed and sent them to him on a regular basis (dubbed "mail-order zoology" at the BAP) (Bocking, 2008). Elton assured the Company men that "cycles were regular and predictable," and when he met conservation officers that "it should be possible to apply this knowledge to the game laws."[8] (Predictability remained an important selling point for Elton with potential funders of this research.) Thus Elton secured a critical tool: his most important source of data for his early work; while simultaneously converting the vernacular knowledge of local hunters, amateur naturalists, conservation officers, and Company men into ecological knowledge.[9]

Albeit unintentionally, the Company and its Canadian agents also played a key role in confirming the link between population cycles and disease, and in creating a transnational network of investigators interested in population cycles. While in Canada in 1928, Elton learned from game wardens that rabbits suffered major "epidemics" once they be-

[7] Elton, "Report of Research Work in Canada," November 28, 1928, p. 3, Folder C.21, Ms. Eng. C. 3329, CSE.

[8] Elton, "Report of Research Work," CSE, pp. 1 and 4.

[9] Archivist Anne Morton has made a similar point: Elton, she wrote, "grafted history onto ecology…making the old fur traders, missionaries" and Company men "into posthumous contributors to ecological knowledge." Quoted in Houston et al. (2003, pp. 181–182).

came "too crowded;" these epidemics, he wrote, not only regulated the populations of rabbits but also of the lynx that preyed on the rabbits.[10] Two years later in London, Company officials sent American businessman and philanthropist Copley Amory up to Oxford to consult with Elton. Amory was concerned about the disappearance of fish and animals in communities near his summer property on the upper Gulf of St. Lawrence in Quebec. Elton related his theories about population cycles, and Copley was fascinated. Copley had found an entrée into the scientific world, and Elton had found a crucial source of networking, funding, and organizational assistance. The immediate result was the 1931 Matamek Conference on Biological Cycles (1933a), at which Copley hosted ecologists, climatologists, a bacteriologist, wildlife and conservation officials, fur trappers, First Nations representatives and even the captain of an ice-breaking ship. (Elton famously joked that he could use an "ice-breaker" with his Oxford colleagues.)[11] The next year, with advice and funding he had cultivated at Matamek, Elton was able to establish the BAP at Oxford (Bocking, 2008; Crowcroft, 1991, pp. 11–12; Houston et al., 2003, p. 182).

At Matamek, Elton first met Robert Gladding Green (Figure 2). For Elton and Green, Matamek was the start of a lifelong friendship and professional collaboration. During the conference, Green lectured on "Tularemia: a disease of wild life"; Elton was next on the program with "Cycles in the fur-trade of Canada." Elton was delighted to find that Green not only conducted disease investigations but also participated in ecological surveying in northern Minnesota.

On the surface, Green seemed an unlikely collaborator. A faculty member at the University of Minnesota, he taught bacteriology and eventually became head of the Department of Bacteriology and Immunology in the University's medical school. Green is best known to posterity as a virologist, for theorizing the evolutionary origins of viruses and carrying out numerous studies of viral diseases common to humans and animals.[12] However, Green's first love was ecology, and from the late 1920s through World War II he carried on what can best

[10] Elton, "Report of Research Work," CSE, p. 7.

[11] Elton wrote up the proceedings of the conference, published in 1933. Elton's copy is in folder A.58, Ms. Eng c. 3327, CSE. This meeting, which deserves more attention from historians, stimulated interest in biological and climatological cycles as metaphors for political and social events such as global economic cycles. The work of economist Edward R. Dewey and the establishment of the extant Foundation for the Study of Cycles can be traced directly to Matamek.

[12] Green published mainly in *Science* and medical journals; but also in journals such as the *Journal of Range Management* (see Evans, 1948).

Figure 2. Robert Gladding Green at his research microscope, December 1939. Robert Gladding Green Papers, Collection 349, Box 9. Courtesy University of Minnesota Archives and Special Collections

be described as a double professional life as a top-flight biomedical scientist and active ecologist.[13] Green established a small research station at Lake Alexander, Minnesota and helped gather what Elton called the most comprehensive data set on the lives and population cycles of snowshoe hares: taking censuses, noting food habits and weather, and conducting sampling studies. He supported his ecological research in part by serving as consultant virologist to large mink farms in the Upper Midwest – a position that required the outfitting of a laboratory to study the diseases of fur-bearing animals. Over the next two decades, Green and his co-workers contributed to ecological knowledge of several species. But more importantly for our purposes, Green and his laboratory became crucial collaborators on the question of population cycles, particularly on the effects of diseases.

Elton needed to bring microbiology to bear on the problem of population cycles – to bring the microbial world into animal ecology –

[13] Elton put it well when he told Green in a letter that he believed that Green's "natural habitat" was "in the northern woods." Elton to Green, 16 February 1940, folder "E miscellaneous, 1938–1944," Box 1, RGG.

and he depended in part on Robert Green to accomplish this. From 1930 to the early 1940s, Green was the principal investigator in the ''Minnesota Wildlife Disease Project,'' a cooperative venture between the University's Bacteriology Department, the Minnesota Department of Conservation, and the USDA's Bureau of Biological Survey.[14] The Project investigated diseases in animal populations ''with special reference to the relation of disease to wild animal cycles.''[15] Green hypothesized that tularemia (''rabbit fever''), a disease newly found in rabbits and wildlife in the 1920s, could be an ultimate cause of population cycles. Caused by the bacterium Green knew as *Pasteurella tularensis* (later re-named *Francisella tularensis*), tularemia afflicts over 100 species of mammals, many insects, and also humans (usually by direct contact, such as hunters' dressing of infected game). It causes sepsis, organ damage, and death, although an animal can harbor it without showing any signs of illness. Green set up his University of Minnesota laboratory to test blood samples (from humans as well as animals), develop therapeutic anti-sera, and to do experiments on several species of small animals. He actively corresponded and visited with Elton, continuing to pursue the relationship between disease and population cycles up until his death in 1947.

Along with Robert Green, Charles Elton met Aldo Leopold at Matamek. Elton's ideas about the ''pyramid of numbers'' greatly influenced Leopold's own ''land pyramid,'' an important foundational concept for Leopold's famous ''land ethic'' (Leopold, 1949). Although much has been written about Leopold, his interests in disease as a cause of population fluctuations remain largely unexplored by historians. But it was Leopold who so well summarized the relationship between disease and population cycles that was proposed at Matamek in 1931. Leopold felt that Green's most important contribution to the overall discussion at the conference was his theory of cyclical virulence on the part of pathogenic bacteria (such as the causative agent of tularemia, *P. tularensis*). After the conference, Leopold characterized Green's theory this way:

> It explains how virulence in a bacterial disease, such as tularemia, might fluctuate rhythmically without the intervention of any cosmic forces. …the pathological evidence favors bacterial or virus disease, rather than parasites, as the primary lethal agent in grouse

[14] Green to J.E. Shillinger of the BBS, May 5, 1933; ''Cooperative Agreement for the Conduct of Studies on Diseases of Wild Life''; and Shillinger to Green, May 9, 1933, folder BBS April–June 1933, RGG.

[15] Green, ''Report of Research Studies in Manitoba – Hudson Bay – 1933,'' pp. 1–2, Folder 8 Hudson's Bay Report, box 6, RGG.

> and rabbit, and varying virulence, rather than varying resistance, as the determinant of mortality.[16]

Leopold's understanding appears to be evolutionary as well as ecological (implying a change in the microorganisms that could explain increased and decreased virulence). In response to Green's insistence that virulence was a function of bacterial *populations*, Leopold made it clear to Green that he understood virulence to be a function of microbial communities that included properties of both ecological interactions and inheritance. In 1935, he told Green that he saw ecological analogies in Green's theory, comparing it to "a cycle in the effectiveness of nitrogen-fixing bacteria in the process of passage through successive host plants" as "coming very near the Matamek hypothesis of cyclic virulence in pathogenic bacteria."[17] Leopold continued to correspond with Green for the next 15 years and was an ardent defender of Green's ideas and work (to the point of intervening successfully when a Congressional committee threatened to abolish Green's Bureau of Biological Survey funding in 1934).[18]

Leopold's synthesis of Green's ideas about bacterial populations and Elton's report of cyclical outbreaks linked the worlds of microorganisms and their hosts through a theory of population abundance, which Elton imported into animal ecology. As all three investigators agreed, disease was an effect of the interactions between varying populations of microorganisms and their mammalian hosts. Disease occurred when microorganism populations were high, but also usually when the host populations were at high density. Microorganisms experienced cycles of virulence and abundance, both of which were keys to their effects on the mammalian host populations. Host populations demonstrated the observed phenomenon of periodic fluctuations due to microorganism predation; but the extreme intensity of the effect was due to the *initial abundance* of the host population. In other words, this was a dynamic system depending on abundance and competition within and between at least two populations of organisms. Ecologists would call this relationship "density-dependence": the effect depended on the initial abundance of the populations (as we will see, the definition and appli-

[16] Aldo Leopold, "Writings: Game Management Book, Correspondence," date unknown, p. 102. Aldo Leopold Papers online, University Wisconsin, http://digital.library.wisc.edu/1711.dl/AldoLeopold.

[17] Leopold to Green, January 30, 1935, in folder "Leopold, Aldo 1934–1938," box 2, RGG.

[18] Leopold to Hon. Frederick C. Walcott (Congressional Committee on Wild Life Resources), 20 January 1934, folder "Leopold, Aldo, 1934–1938," Box 2, RGG.

cations of this concept proved controversial later).

Along with ideas, Green supplied Leopold and Elton with some essential credentials: bacteriological and medical knowledge and a laboratory in which to analyze microorganisms and their presence in insect and animal bodies. As Leopold wrote to the 1934 Congressional committee: "The study of diseases which cause the game cycle…is done by Dr. Green at the University of Minnesota. He is covering what might be called the laboratory end, and has made brilliant progress." Leopold believed that the relationship between the "laboratory end" and the field studies was crucial: "Obviously each would be crippled without the other."[19] The tools of the field (biological surveys) and the laboratory (especially serology) together provided essential information to follow the disease and assess its ability to cause population fluctuations in the wild.

Green brought another important tool to the partnership. An ongoing problem for ecologists was how to manage the reams of data generated by field surveys. In his dual capacity as a medical school professor and principal investigator of the Minnesota Wildlife Disease Investigation, Green had a concrete plan for data management that he had borrowed from the University of Minnesota hospital's medical statistics department. The brainchild of H.L. Dunn, medical statistics were kept centrally using a punch-card system and archived permanently. Green began using this system to catalogue field and laboratory data in early 1930. In a letter to Green, Leopold did not hide his enthusiasm: "Your logic in urging a central repository for game data so that it can be handled on punch cards, is irrefutable." Leopold cited food habits records and disease records from the field as the "two kinds of data that need it worst."[20] Overall, Leopold felt, "Dr. Green has built up an approach to wild life disease questions which is entirely novel and which seems by far the most promising of any attempts so far made to explore disease phenomena in wild populations." With his "scientific knowledge of bacteriological methods," and his adaptation of data management tools from the University of Minnesota hospital, Green was an essential part of the population cycles investigation in the 1930s.[21]

[19] Leopold to Walcott, 20 January 1934, folder "Leopold, Aldo 1934–1938," Box 2, RGG.

[20] Green to Leopold, 3 March 1934; Leopold to Green, 5 March 1934, folder "Leopold, Aldo 1934–1938," Box 2, RGG.

[21] Leopold to Jay N. Darling (Chief, BBS), 3 December 1934, folder "Leopold, Aldo 1934–1938," Box 2, RGG.

Green, Leopold and Elton also kept each other informed about developments in mathematical studies of population and disease. It was not lost on Green that his punch-card method of data storage would convert qualitative knowledge (natural history observations) into quantitative knowledge that could be analyzed using mathematical models and statistics. "We are collecting a large mass of data which must of necessity go on punch cards, and Dr. Dunn is available with all of his ideas and statistical machinery. …Getting our data into 'machinery' analysis is a rather acute situation for us," Green wrote to Leopold in 1934.[22] None of the three was an able mathematician; Elton later referred to himself simply as "bad at maths" and hired Patrick H. "George" Leslie in 1935 to conduct the statistical and mathematical analyses at the BAP.[23] Nonetheless, Elton, Green and Leopold were all convinced of the value of quantitatively understanding the interactions between populations of microorganisms and animals, even if they did not engage directly in the theoretical and computational details.

Disease continued to be an important focus in population studies at Oxford in the late 1930s. Elton hired a medically-trained pathologist, A.Q. Wells, who joined the BAP in 1936. Wells, along with Green, provided crucial bacteriological and pathological expertise. Elton's data collection methods also reflected this focus on disease. The BAP's 1935 and 1936 questionnaires to the Hudson's Bay Company men asked only about "the year-to-year comparisons of abundance" and outbreaks of disease (nothing about climatic factors or the availability of food resources).[24] The high point of Elton, Green and Leopold's collaboration came in 1937–1938, when Green visited Europe and Elton visited Canada and the United States. Elton and Green had been corresponding about tularemia, with Elton speculating that this might have been the cause of a synchronous 1887 beaver and snowshoe hare die-off he found in the Hudson Bay Company records. Elton was still keen to investigate disease outbreaks. Green spent several days at the BAP and enjoyed dinners at the Eltons' home. Discussions were intense, and the denizens of the BAP were impressed with Green. His trip cut short by an emergency at home, Green later particularly asked to be remembered to

[22] Green to Leopold, 3 March 1934, folder "Leopold, Aldo 1934–1938," Box 2, RGG.

[23] Elton to James E. Schindler, 3 March 1980, p. 1, folder E-69, Ms. Eng. C 3335, CSE.

[24] Bureau of Animal Population, "Snow-shoe Rabbit Inquiry, 12 June 1935"; Elton to Green, 7 September 1936; Elton to Green 18 March 1937; Green to Elton, 6 September 1937, folder "E misc, 1936 and 1937," Box 1, RGG.

George Leslie and A.Q. Wells, with whom he had had such fruitful discussions.[25]

Elton reciprocated the next year, visiting his Hudson's Bay Company contacts in Canada then continuing into Minnesota and Wisconsin to visit Green and Leopold (he spent a night in Leopold's famous ''shack'' at his farm). Moving on to Washington, Elton met with J.E. Shillinger, Stanley P. Young, and other Bureau of Biological Survey officials to urge their continuing support of Green, Leopold and the Minnesota Wildlife Disease Investigation Project. Elton thus played several roles in these travels: consultant on the practical problems of natural history surveys; collaborator on questions of disease and cycles; and advisor to the USDA's wildlife bureaucrats.[26] Records from these North American collaborations appeared prominently in Elton's book *Voles, Mice and Lemmings* (1942a), in which reams of data from a variety of species definitively demonstrated the existence of population cycles (or so Elton hoped) (Elton, 1942a).

Charles Elton and his contemporaries considered many hypotheses to explain the periodic cycling of animal populations. Explaining cycles was a daunting task, especially when Elton began his investigation in the 1920s. His data spanned two centuries, and the animals under study lived all over the northern reaches of the Earth, from Canada to Norway to Siberia. Understandably, Elton sought a model that could bring both temporal and spatial order to this mass of data. Young and ambitious for his ecological ideas, Elton adopted an a priori deterministic model in which he investigated one chosen factor at a time, seeking an ultimate cause for population cycles. Elton first sought a unifying principle in the climatology of the early 1920s, focusing on studies that showed sun-spots to appear with similar frequencies to population cycles among hares, lemmings, fox, lynx, and other animals. This model had the advantage of potentially connecting local population patterns to global climate patterns. Such a model situated the causation of cycles in external variables that were independent of the animal populations themselves. This hypothesis not only de-coupled any feedback from population cycles to causes, it was also rather deterministic. Elton's own publications problematized this climatic determinism model almost immediately because it failed to sufficiently explain the observed phenomena in his data. When sun-spot cycles

[25] Green to Elton, 23 April 1938; Elton to Green 8 April 1938, folder ''E misc, 1936 and 1937,'' Box 1, RGG.

[26] Elton, untitled diary of 1938 trip to North America, folder C.24, Ms. Eng. C 3329, CSE.

turned out to be only randomly associated with animal population cycles, Elton considered various other factors: competition, food supply, predation, and disease. His 1925 article, ‘‘Plague and the Regulation of Numbers in Wild Animals,’’ and his 1927 book *Animal Ecology* moved away from static models of population regulation and toward more interactive population dynamics, while preserving a clear distinction between density-dependent and density-independent factors regulating populations – some of the major questions that BAP ecologists worked on during the 1930s and into the early 1940s.

The period after the end of World War II brought many changes for the BAP and the inquiry into population cycles. Elton, who had begun conducting population-cycle surveys on rodents in the nearby Wytham Woods (acquired by Oxford in 1942), had become more interested in detailed empirical studies of delimited spatial areas rather than broadly-based phenomena (Bocking 2008). The partnership between Elton, Green and Leopold ended with Green’s death in 1947 and Leopold’s in 1948. Moreover, younger ecologists had turned to increasingly complex mathematical methods to explore questions about cycles and other population phenomena (Kingsland, 1985), a move with which Elton often felt uncomfortable despite the fact that some of the BAP’s activities furthered it. Research and theory about population cycling continued to develop, but in the 1950s some of the tensions that had been present since the 1920s surfaced and threatened to fragment the field of animal ecology.

Whose Nature? Controversies in Population Cycle Studies

Charles Elton’s method of defining the magnitude of a population’s cycle depended on the ‘‘abundance’’ of the population: the intensity of the change in numbers was related to how large the population was at the start of the change. This was a way of disciplining the variation in population size between species and locations, and differentiating true ‘‘cycles’’ from ordinary non-periodic population variations. It also pointed away from autologous physiological variables (such as reproductive efficiency) and toward exogenous interactive variables – competition for food, predation, and disease – as causative factors. In this way of thinking, physiological changes were responses conditioned by exogenous causative factors and the initial abundance of the population. For Elton, understanding ‘‘nature’’ and ‘‘natural’’ phenomena depended on basic shoe-leather ecological surveys by observers on the ground, many of whom were hunters, fur-traders, and agents resident near wild animal populations (Kohler, 2011). Working from a priori assumptions about the possible causes of cycles, Elton and his colleagues at the BAP pursued the agenda of finding patterns in the observations they made as field naturalists.

This model of population change, important in animal ecology from the 1930s onward, depended on another type of ecology: the network of scientists and ideas that coalesced around it. Far from *sui generis*, Elton's early interest in disease as a regulator of animal populations owed much to his discussions with his Svalbard mentors (Huxley, Carr-Saunders, and Florey); the data collected by observers around the world; and to his reading in the medical literature. Early ventures into studying disease as an interaction between measured populations included the work of Ronald Ross, the well-known malariologist (Ross, 1915, 1916; Ross and Hudson, 1917). In his 1924 "Plague and Regulation of Numbers in Wild Animals," Elton cited articles from the British medical journal *Lancet*; the epidemiologists and physicians Wu Lien-Teh, Major Greenwood, and W.G. Liston; and the tropical medicine specialist Patrick Manson-Bahr. After meeting Green and Aldo Leopold at the 1931 Matamek conference on population cycles, Elton found other scientists who were also convinced that disease played an important causative role in observed mammalian population cycles. Finally, focusing on disease reinforced his use of the a priori density/abundance model used by epidemiologists interested in complex disease models (such as vector-borne diseases).

However, Elton's reliance on density-dependence and the a priori model, in the service of identifying causes of regular population fluctuations, unwittingly set up conditions conducive to the development of major controversies in animal ecology over population cycles during the 1950s. In 1949, Finnish zoologist Pontus Palmgren fired the opening salvo when he asked, "Are the fluctuations periodic in the matemathical [*sic*] sense of the word, or can they be considered as random variables?" (Palmgren, 1949, p. 116). After examining the voluminous published data, Palmgren concluded that he doubted the existence of well-defined periodic population fluctuations such as the 10-year snowshoe hare cycle that Elton and Green had established. Rather, he argued, these fluctuations occurred at more random periodicities and reflected natural oscillations. Palmgren's article touched off a flurry of debate in the literature. A succinct summary of the many tensions and entanglements is beyond the scope of this article but some observations will be helpful here. Commentators at the time (and historians much later) have tried to bring order to the complexity of these debates by setting up opposing "camps": mathematicians versus ecologists; historicists versus ahistoricists; or those using a priori methods versus the advocates of an a posteriori approach, for example (Hewitt, 1954; Kingsland, 1985). Upon further consideration, these "camps" can better be characterized as overlapping networks of allegiance to methods and concepts. Two convergence points – a "Symposium on Population Cycles" published in the *Journal of Wildlife Management* (1954) and the 1957 Cold Spring Harbor Symposium on Quantitative Biology – provide the best windows into the differences that created these networks of allegiance.

Ornithologist Oliver Hewitt, editor of the *Journal of Wildlife Management*, identified some of the controversies in his introduction to the 1954 Symposium on Population Cycles: whether questions about causation of cycles should be abandoned; the role played by chance or randomness; and the magnitude and degree of regular periodicity required of population fluctuations in order to label them "cycles" (Hewitt, 1954). This last debate – how to determine if a fluctuation was a true "cycle" – overlapped with the distinctions between mathematical and ecological methods. Mathematicians, wrote Hewitt, "count all the peaks, and demand an exact periodicity or none at all." Ecologists, on the other hand, tended to "look at cyclic behavior subjectively, select dominant peaks to indicate the ten-year cycle, and allow considerable variation in both periodicity and amplitude" (Hewitt, 1954).

However, a close reading demonstrates that the Symposium's contributors defied easy categorization and certainly did not reflect antagonistic "camps" by discipline. For example, zoologist LaMont C. Cole, who advocated mathematical modeling, selected peaks in the data and felt that causation questions were still pertinent, while suggesting that "first consideration [to explain the peaks] should be given to the possibility that the fluctuations occur at random" (Cole, 1954, p. 22). Australian statistician and mathematician P.A. Moran disagreed with Cole's definition of what counted as "cyclic" fluctuations and was suspicious of randomness, despite the importance of quantifying it in models (Moran, 1954, p. 65). Field ecologist Paul Errington, who collaborated with statistician colleagues at Iowa State University, expressed an interest in what statistical analysis could contribute to questions about the role of animal behavior in contributing to population fluctuations (Errington, 1954). Thus some field biologists (such as Errington) advocated statistical methods (while others eschewed them); and some model-oriented biologists and mathematicians (such as Cole and Moran) adopted a more a priori method of selecting variables and "peaks" in the data than did others. Each had complex intellectual allegiances that informed this debate and others during the 1954 Symposium.

The issue of randomness versus certainty in animal population data became an enduring source of debate, and this issue dominated the 1957 Cold Spring Harbor Symposium, "Population Studies: Animal Ecology and Demography." Again, the dynamic was complex. Ecologists such as the Australian entomologist A.J. Nicholson believed that animal populations were regulated around a natural balance or equilibrium that reflected certainty in natural patterns (Kingsland, 1985, 119). Nicholson, who had visited the BAP in the early 1950s, advocated density-dependent models and asserted that competition determined population dynamics (McIntosh, 1986, pp. 189–190). Australian zoologist Herbert George Andrewartha and his former student L.C. Birch disagreed. Birch had worked with George Leslie at the BAP in 1947, learning mathematical modeling techniques that he applied to insect populations (Kingsland, 1985, p. 117). Andrewartha and Birch had worked during the 1930s and 1940s on the population dynamics of various insects, most importantly for our purposes *Thrips imaginis*, a pest of apple trees. Andrewartha was also an expert on the phenomenon of diapause, during which an insect paused its life cycle and lingered in the egg in order to survive during harsh weather. Their observations and analyses showed that environmental factors (such as temperature) sometimes regulated populations without feedback from the populations themselves (a so-called "density independent" model); but they nonetheless argued that all factors "at least have a component of density-dependence in them" (Andrewartha, 1957, p. 236). Thus Andrewartha and Birch could not be easily classified as advocates of either density-dependent or density-independent models. What happened in any particular case depended on the *probabilities* of various conditions being present – and those probabilities were unpredictable and even *random*.

Andrewartha valued statistics and probability as the method of analysis that would best "explain the actual counts or estimates" made by an ecologist in the field, thus situating himself in empirical field ecology; and he also made it clear that ecologists had to discard "the classical idea of cause and effect" pursued by Elton and the other early animal ecologists (Andrewartha, 1957, pp. 219, 230). Elton's method of a priori thinking rankled Andrewartha so much that he wrote an extended treatise on what he viewed as the proper roles of induction and deduction in scientific thinking, incorporated into his later book written with Birch, *The Ecological Web* (1984). The environment, Andrewartha explained, could not be divided up into "factors" pitted against each other by the ecologist in order to determine an ultimate cause of population variations; in nature, there were no ultimate causes.

In the end, these debates expose underlying disagreements about how ''nature'' worked and how scientists could most authentically access knowledge about it. For some, including Charles Elton, the brutal randomness of exogenous control as a basic organizational principle of nature was inconceivable. In his review of Andrewartha and Birch's book *Distribution of Animals*, Elton wrote: ''I cannot believe that the natural communities of the world will be found to have evolved solely 'by guess and by chaos' or that the interrelations of animal populations have not introduced a gradual order into the structure of animal communities'' (Elton, 1955). Elton had set up the method of inquiry into population cycles in the 1920s on the basis of the idea that ecologists needed to identify the underlying patterns and causes of natural phenomena. However, by moving on to the more dynamic models dependent on the interactions of abundance with external factors – and phenomena such as disease – Elton and his co-workers expanded the inquiry into population cycles and (inadvertently) invited subsequent work in ecology to proceed from basic conceptions of how ''nature'' worked that made some of them very uncomfortable indeed.

Conclusion

Focusing on Charles Elton and the BAP allows us to capture some important factors that shaped Anglo-American animal ecology in the early to mid-twentieth century.

First, some of the most serious controversies in animal ecology developed over time due to Elton (and the BAP's) early focus on population cycles. As we have seen, both the wildlife management and quantitative biology communities hotly debated the details of population cycling during major symposia in the 1950s. Controversy developed even from within Elton's inner circle. This is best illustrated by the career of Dennis Chitty, an internationally influential ecologist who spent 26 years at the BAP working under Elton. Chitty (a potential successor of Elton as BAP director upon Elton's retirement), vigorously pursued the question of what caused population cycles. He studied food supply, predation and disease as regulators of cycling field vole populations from the 1930s until after World War II, but he could not find definitive evidence that these factors accounted for population decreases. Chitty's wife, scientist Helen M. (Stevens) Chitty, took over analysis of the Hudson's Bay Company records and also could not come to definite conclusions from those data.

By the end of the 1950s, the Chittys had disavowed exogenous and population-level causes of cycles, focusing instead on physiological and behavioral attributes of individuals within the population – an idea that Elton had previously discounted in favor of density-dependent population-level influences. Dennis Chitty developed a competing hypothesis of population regulation: populations were self-regulating based on individual attributes, and unlimited population growth was halted by the natural selection of ever-more aggressive individuals that eliminated competitors within the population (Chitty, 1960). Chitty's most prominent student, Charles J. Krebs, remembers Chitty having "little use for the dominant paradigm of the density dependent regulation of populations" that had guided Elton's research group at the BAP (Krebs, 2015). Chitty and Elton clashed, each stubbornly entrenched in his own explanation for population cycling. Chitty later recalled in his memoir that Elton chided him in a 1956 letter: "you will more and more sit back into a team-world of your own…with people around you that agree with everything you say" (Chitty, 1996, p. 121). Although Dennis Chitty later wrote that his strong disagreements with Elton did not affect his career decisions, the Chittys departed for Canada in 1961. With no obvious successor to Elton and lacking support from Oxford, the BAP was shut down after Elton's retirement in 1967. Its influence, however, continued – even when some younger scientists (such as the Chittys) moved off in different directions – through animal ecologists' continuing concerns with questions about natural selection, population control and regulation, and the relative influences of local conditions and universal forces.

These were central questions of interest not just to ecologists, but also to mathematicians, epidemiologists, economists, and many other natural and social scientists who sought to model natural phenomena (Murphy, 2013; Connelly, 2010; Mitman, 1992).[27] Studies of wildlife cycles stimulated efforts to quantify population data and brought animal ecology into conversation with other disciplines. This was one important strategy for transforming "natural history" into "scientific" animal ecology (as Elton defined it). This is not to say that Elton's vision was uncontested. He quarreled openly with his next-door Oxford colleague, evolutionary ecologist David Lack, who was also interested in population ecology and density-dependent regulation. Lack derided Elton's ecological surveys as "natural history on punch cards," and

[27] I thank an anonymous reviewer for suggesting some of this literature.

literally the door that separated the two rivals' institutes remained locked until Elton retired (Chitty, 1996, p. 122; Crowcroft, 1991, p. 137). The close quarters may have exacerbated the two ambitious scientists' differences of opinion (Anderson, 2013), but both considered the pursuit of questions about animal populations to be central to the enterprise of reforming natural history during the early and middle decades of the twentieth century.

Finally, by focusing on disease as a local population regulator that could interact with global climatic influences, Elton facilitated an interdisciplinary network of researchers whose ideas and practices became integrated into animal ecology. Although many of these people (such as Robert Gladding Green) identified professionally with fields other than ecology, their work nonetheless shaped the young discipline. The BAP's success depended on Elton's ability to design research programs, gain patronage, and build interdisciplinary networks of field scientists and collectors, laboratory workers, and mathematicians from around the world. Elton enlisted these allies as essential contributors to his richly complex inquiry into basic questions about life on earth, such as the role of stability and instability in natural systems. Allies provided new tools (such as the punch-card system suggested by Green) and helped institutionally, too (especially in sending talented scientists to work at the BAP). The BAP's central place in animal ecology (and even its eventual survival) thus depended heavily on Elton's personal and professional networks and his ability to mobilize these resources, and this helps to explain why his retirement signaled its end.[28] However, through the dozens of ecologists who had worked at the BAP over the years (and their students), questions about population cycles outlived the institution. Particularly important (and controversial) were the concepts of abundance and density dependence, which steered later generations of animal ecologists toward investigating exogenous relationships between groups of animals, populations of microorganisms, climate, and other factors (a fruitful topic for further historical investigation).

The debate over the ecological factors responsible for population cycles continues today, and the current understanding of this phenomenon's causation integrates various external and internal factors. As one group of ecologists (including Charles J. Krebs) studying lynx population cycles recently wrote: "Our results clearly indicate that the observed 10- year cycle is the result of joint forces of both intrinsic and external factors" (Yan et al., 2013). Thus the inquiry begun by Elton

[28] I thank an anonymous reviewer for encouraging me to highlight this point.

and the BAP ecologists remains quite active. It is a testament to the wonderful complexity of population cycles, in various species around the globe, that this phenomenon continues to drive ecologists' curiosity today much as it did that of Charles Elton and Robert Gladding Green almost a century ago.

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