Foreword to Chapter One

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Chapter 1 describes seven invasions that, as Elton says, illustrate what nonnative introductions can do in seas, estuaries, rivers, lakes, shores, tropical and temperate forests, farmlands, and towns. Each has become a classic example in the invasion literature, and most have seen subsequent developments in understanding spread, impacts, or management. Elton intended to discuss several of these developments in his second edition.

First was the invasion by the African malaria-transmitting mosquito *Anopheles gambiae* in northeastern Brazil. The three-year iconic eradication project by the Brazilian government and the Rockefeller Foundation is widely cited as a model of planning and execution.[IX] Elton emphasized how basic research and surveys were critical to the success of the effort and how the project initiated the practice of quarantine aircraft inspection. The methods, based on larval control, were later used successfully in Egypt and Zambia to suppress malaria, but the advent of DDT and use of broadcast sprays moved the focus instead to adults.[XX] In 1944, Elton had reviewed a monograph on this eradication, recounting the muskrat eradication in Great Britain (discussed below and in Chap. 6)

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and a few other eradications, calling them "major engagements in a violent struggle against the spread of undesirable plants and animals that is affecting every country" and referring to invasions as a "zoological catastrophe."[XIII]

Elton's second example, the chestnut blight in North America and Europe, is an ongoing disaster a century after its advent, particularly in North America, with enormous ecological, economic, and sociological consequences.[XVI] In Europe, the invasion was partly stemmed by a hypovirulent form of the blight fungus caused by a naturally occurring virus that was then deliberately distributed. This development spurred optimism that the virus could serve in North America as an effective biological control.[XXVIII] This has not happened, however, except to a limited extent in Michigan, where the American chestnut is introduced. One reason may be that the European chestnut (itself a Roman introduction from Asia Minor) is somewhat resistant to the blight, and another may be that the ecology of both natural and cultivated stands of European chestnut impedes virus transmission.[XXVIII] In North America, much effort has gone into hybridizing American chestnut with resistant Chinese chestnut, with occasional announcements of new resistant genotypes that seem always ultimately to prove susceptible. Recently, a transgenic American chestnut with a wheat oxalate oxidase gene has greatly increased resistance,[XXXI] and a current crowd-funding campaign supports creating a forest for research on restoration using this transgenic form.[II] Elton predicted the blight would eventually reach Britain; it did so in 2011 and now infests several sites in southern England.[XV]

Elton's third example was the European starling invasion of North America, for which he described the spread from an 1891 introduction in Central Park, New York through 1954, when it was not quite established in the American West. It is now distributed throughout North America at least from southern Alaska to southern Mexico.[XXIV] He noted that several previous attempts to introduce the starling to North America had failed, introducing a theme that he explored in detail in Chap. 6. Aside from being one of the most common birds in North America, a cause of enormous economic damage, and competing with native cavity-nesters for nest sites,[XXIV] the starling is perhaps best known as having been brought by a wealthy North American birder aiming to introduce all birds mentioned by Shakespeare.[XXIX]

Elton combined the starling invasion with his fourth example, the North American muskrat invasion of Europe, to exemplify the speed and, to some extent, the regularity with which invasions spread, describing both as spreading in concentric circles from an initial establishment by a small

propagule. Versions of the striking figure of concentric rings for the muskrat, which Elton credits to Ulbrich,[XLI] have been published by many authors, sometimes credited to Elton.[XXXIV] Theory predicting initial concentric circles through diffusion traces to the early 1950s,[XXXVI] but Elton was not enthusiastic about mathematical theory and did not refer to such theory in *Invasions* or his later community ecology monograph.[XIV] Development of mathematical theory for the spread of invasions continues to be a major part of invasion science,[XXII, XXXIV, XXXIX] with particular focus on the shape of the range as the circles are increasingly deformed and beachheads are established beyond the main invasion front.

The muskrat invasion of Europe began with only five individuals introduced at a site in Czechoslovakia, and this is depicted as the center of the circles, but, as Elton noted, new centers quickly formed as individuals escaped from fur farms established beyond the front. Muskrats have also been introduced to Russia, China, Japan, and Tierra del Fuego.[XXV] In Tierra del Fuego, they benefit from the presence of introduced beaver,[VIII] a form of "invasional meltdown" (see Chap. 4 Foreword). In Chap. 6, Elton detailed the eradication of the muskrat from Britain, and in Chap. 1 he probably intended in the second edition to elaborate on their impact, as he had inserted in the proof copy the abstract of a paper detailing their impact in the Soviet Union.[XXX]

Elton's fifth example was a cordgrass he called *Spartina townsendii*, now known as *Spartina anglica*. As he noted, it is a hybrid between native British *S. maritima* and eastern North American *S. alterniflora*. His observation that it did not increase much for decades but spread rapidly in the 20th century is now explained by the fact that the initial hybrid, which arose repeatedly, is sterile. This is now called *S. townsendii*. A spontaneous doubling of chromosome number instantly created a fertile "new polyploid hybrid species" (p. 16),[XXXVIII] which Elton noted had been introduced to North and South America, Australia, and New Zealand. Elton viewed it as "on the whole a rather useful plant, because it stabilizes previously bare and mobile mud between tide-marks" (p. 16). Today it is deplored for the same reason, among others,[VII] and is even listed among 100 of the world's worst invaders.[XXVI] Elton had intended to update the *Spartina* story; in the proof copy, he had inserted copies of two more recent papers, one on the cytological basis of the hybrids and several beneficial uses of it, with a caution that, in certain cases, it chokes channels, invades swimming beaches, and can also eliminate native plants.[XXI] *Spartina alterniflora* has also hybridized with native *S. foliosa* in California to produce a new invasive species.[XXXVIII]

Elton's sixth example was the sea lamprey invasion of the Laurentian Great Lakes. As with *Spartina anglica*, he noted a puzzling lag, in this case in reaching Lake Erie after the completion of the Welland Canal. But the lag ended with "explosive violence" as the lamprey invaded Lakes Huron, Michigan, and Superior. Elton focused on the gruesome manner in which the lamprey dispatches its prey and detailed the rapid decline of the lake trout. He intended to elaborate on this invasion. In addition to detailed notes from the references he cited on the lake trout decline,[X, XVII] he had tucked into the proof copy a note from a 1964 reference to the effect that selective poisoning in streams was aiding recovery of lake trout food fish.[III] In fact, further development of chemical controls has subsequently produced substantial lamprey control,[XXXVII] albeit with some nontarget impacts.[XXXII] Current development of both pheromonal attractants and barriers promises improved lamprey management.[XXXVII] However, the Great Lakes have been so thoroughly transformed by introductions of nearly 200 nonnative species (among notable examples are zebra and quagga mussels, alewives, round gobies, and Pacific salmon) as well as pollution and various habitat changes that even complete elimination of lampreys would not recreate a semblance of their status two centuries ago, even if feared Asian carp do not reach the lakes.[XI,XXXII]

The seventh example was the Chinese mitten crab, about which Elton had written in 1936, reviewing a book about its invasion in Germany one year after it was first recorded in Britain.[XII] This remarkable review presaged the 1958 book, detailing the German invasion and closing with a ringing statement about the wave of invasives assaulting Britain, including the muskrat and *Spartina townsendii* (*anglica*). The book review predicted the crab would spread in Britain. In *EIAP* Elton wrote that the crab had not yet "taken hold" in Britain but that it was very likely to do so. He was prescient, and he doubtless intended to document its spread in the second edition, as he had placed in the proof copy a short 1986 article[IV] describing its spread to the River Ouse, River Humber, and the Thames. By 2006 it had occupied several other rivers and estuaries.[V]

Elton probably aimed to include the American mink in this chapter in the second edition, as he had inserted here in the proof copy an article on its spread and impact in Britain[XL] and had noted another[XXIII] in the "Addenda to Invasions" at the beginning of the proof copy. The American mink has proven to be a scourge to the water vole in Scotland,[I] affects many native species on the Continent,[VI] threatens European mink with extinction,[XIX,XXXIII] and is established in Argentina and Chile.[VIII,XVIII] In Spain its impact on native species is exacerbated by large populations of the

introduced Louisiana red swamp crayfish as prey, another example of "invasional meltdown."[XXVII]

Elton ended Chap. 1 thus: "We must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora" (p. 22), and he urged ecologists to begin to study them, in order to understand their mechanisms, impacts, and how to manage them. In short, he called for the founding of the discipline we now call invasion science. This call was not answered until the 1980s,[XXXV] but the field is now a large, burgeoning enterprise dealing with the many questions Elton had raised and posing others he had not envisioned.

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