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CHAPTER 2

THE ECONOMY OF NATURE

[T]he study of the regulation of animal numbers forms about half the subject of ecology, although it has hitherto been almost untouched.

—CHARLES ELTON

The charge was a bluff. The elephant took only a few steps, just enough to let us know which mammal was boss of that hilltop.

Once our heartbeats returned to normal, and after he worked his way down the slope, we ventured back outside to survey the aftermath of the night's raid. There was a wake of broken trees, naked branches, and the lingering aroma of dung (theirs, not ours). Elephants are prodigious producers of the latter: their hundred-foot-long intestines manufacture up to 200 pounds of manure per day to keep up with the more than 200 pounds of food and fifty gallons of water they consume.

Given the absence of any natural predators, and their enormous appetites, one might ask why East Africa is not overrun with, or stripped bare by, elephants? Perhaps it is because African elephants, the largest of all land animals, reproduce very slowly? Females do not mature until their teens, they give birth to just a few young in their lifetimes, and it takes twenty-two months of gestation for a 250-pound baby elephant to develop.

It was Charles Darwin who famously dispelled that explanation in *On the Origin of Species*:

The elephant is reckoned the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase; it will be safest to assume that it begins breeding when thirty years old, and goes on breeding till ninety years old, bringing forth six young in the interval, and surviving till one hundred years old; if this be so, after a period of from 740 to 750 years there would be nearly nineteen million elephants alive, descended from the first pair. Indeed, in fewer than 50 generations or about 2500 years, the total *volume* of elephants would exceed that of the planet.

That figure is ridiculous. But consider the other end of the size spectrum. A typical bacterium, such as the *Escherichia coli* that populates our intestines, weighs about one-trillionth of a gram (one trillion bacteria weigh one gram; an elephant weighs about four million grams). Based on a maximum doubling time of twenty minutes, one can calculate how long it would take for one bacterium to give rise to enough bacteria to equal the weight of the Earth. The answer: just two days.

But the world is not made of solid elephants or bacteria.

Why? Because there are limits to the growth and numbers of all creatures.

Darwin recognized that. And he understood it because Reverend Thomas Malthus stated it long before in his landmark *Essay on the Principle of Populations* (1798):

Population, when unchecked, increases in a geometrical ratio. . . . The germs of existence contained in this spot of earth, with ample food, and ample room to expand in, would fill millions of worlds in the course of a few thousand years. Necessity, that imperious all pervading law of nature, restrains them within the prescribed bounds. The race of plants and the race of animals shrink under this great restrictive law.

But just how are these “bounds” set? And how are they set differently for different creatures? Darwin did not know. These questions were

not pursued in earnest until another young English naturalist went on an expedition to some other remote islands, also encountered an odd assortment of creatures, became gripped by a mystery, had an epiphany (or several) during his adventures, wrote a great book, and founded a new field of science. Charles Elton is nowhere near as famous as Darwin or Malthus, but he is known to biologists as the founder of modern ecology, and the central mystery that gripped him was how the numbers of animals are regulated.

A JOURNEY TO THE ARCTIC

The *Terningen* pitched and rolled on the heaving, icy Barents Sea, and twenty-one-year-old Oxford University zoology student Charles Elton heaved right along with it. The two-masted schooner had left Tromsø two days earlier under the June midnight sun, bound for Bear Island, a desolate, rocky island well above the Arctic Circle, whose most prominent feature was aptly named Mount Misery.

Elton was part of a small advance party of the first so-called Oxford University Expedition to Spitsbergen, a team of twenty students and faculty from various disciplines—ornithology, botany, geology, and zoology—who aimed to carry out an extensive geographic and biological survey of the largest island in the Arctic archipelago northwest of mainland Norway. It was a bold and ambitious undertaking to venture far into storm-tossed and ice-strewn waters, to go ashore and traverse largely uninhabited and partly snow- and ice-covered islands, while risking the whims of some of the most intense weather on the planet; not to mention the fact that none of the team had any prior experience in the Arctic. But it was just the sort of adventure, and personal test, that the select group of Oxford men sought.

The voyage to Bear Island was a bit less than 300 miles and a severe test for Elton, who had never even left England before. The ship was a converted sealing boat whose sleeping quarters previously served to hold blubber, the smell of which could not be removed. That combined with the rough seas spelled utter misery.

From an early age, Elton had been captivated by wildlife. He spent countless days walking through the English countryside, watching birds, catching insects, collecting pond animals, and examining



FIGURE 2.1 The First Oxford University Spitsbergen Expedition team, 1921. Charles Elton is fifth from the right in the turtleneck sweater, Vincent Summerhayes is to the immediate left of Elton.

Photo from account by C. S. Elton written in 1978–1983. Courtesy of Norsk Polarinstitutt Library, Tromsø, Norway.

flowers. He began a diary of all of his wanderings and observations at age thirteen. Elton had been invited on the expedition by his tutor, the eminent zoologist and writer Julian Huxley (grandson of close Darwin ally Thomas Huxley), who was impressed with his student's passion for and command of natural history. He had relatively little time to prepare, as his slot on the expedition was confirmed just one month before sailing. His father provided some money, his brother lent him his Army boots and other gear, and his mother helped him put together clothes for the two-month voyage. Elton was, by his own account "very inexperienced, very raw indeed," and had only previously done some rough camping. Huxley encouraged Elton and reassured his parents, "Please assume that there is no danger in the expedition further than that involved, say, in elementary Swiss climbing, certainly much less than difficult mountaineering and indeed negligible."

By just the third day of the voyage, that pledge had crumbled. Forty-six-year-old medical officer and accomplished mountaineer

Tom Longstaff was the most seasoned voyager aboard. Seeing Elton suffering, he said, "I must do something for that poor boy," and proceeded to medicate him with large doses of brandy. With nothing in his stomach, Elton was so drunk when the landing party of seven finally went ashore at Walrus Bay on the island's southeast coast that he arrived sitting on top of a load of baggage in the whale boat, singing at the top of his lungs.

Once sober, Elton set up camp with his companions inside the ruins of an old whaling station near the shore, where the ground outside was littered with whale bones, walrus skeletons, a polar bear's skull, and a couple of arctic fox skulls. The plan was for the party to spend a week exploring the southern portion of the twelve-mile-long island before rejoining the full team and sailing on to Spitsbergen, about 120 miles to the north. The four ornithologists in the group were to focus on the birdlife, while Elton and botanist Vincent Summerhayes would survey all plants and other animals.

The birders were a bit zealous about their mission, especially F.C.R. Jourdain, the leader of the expedition. At 2:30 a.m. of the first "night" on shore (there were twenty-four hours of daylight), Jourdain awakened Elton, Summerhayes, and Longstaff with the command to get up and get to work, as there was no time to lose. Longstaff replied, "I must have my eight hours sleep," and the veteran explorer whispered to Elton and Summerhayes, "Don't take any notice." Elton soon appreciated Longstaff's wisdom, as the birders were completely exhausted by evening. Elton learned to pay close attention to Longstaff's sage advice whenever offered.

After a good night's rest, Elton and Summerhayes went out to explore and collect. Elton dreamed of one day knowing what animals "are doing behind the curtain of cover." Now he would have a chance to peer into an alien world that few had ever visited, let alone studied.

Situated where the cold polar current meets the Gulf Stream from the west, the island was constantly shrouded in fog, when it was not pounded by sleet or blizzards. Largely flat and dotted with dozens of lakes throughout its interior, and marked by a barren almost moon-like landscape in the north, the island was not without its wonders. On the southern end stood several tall cliffs overlooking the sea, populated by hundreds of thousands of seabirds. Among

the most numerous were black and white Common and Brunnich's guillemots, black-legged kittiwakes, and gray fulmar petrels; Elton also saw little auks, Norwegian puffins, and glaucous gulls.

Elton and Summerhayes started their surveys near the camp, then eventually fanned out to various lakes and other features. Elton quickly discovered that he had an excellent, determined partner in the small, slightly-built botanist. Just three years older, Summerhayes had seen more of the world, including fighting in the battle of the Somme (1916). Summerhayes was as keen to identify all the Arctic plants as Elton was to discover the animals, and in the course of their wanderings he taught Elton a great deal of botany.

Despite the weather and the shortness of time, the two men were able to survey all the island's various habitats for plant and animal life. The task was made easier by the relative sparsity of species. For instance, throughout the island, there were no butterflies, moths, beetles, ants, bees, or wasps whatsoever; the insect life consisted mostly of flies and primitive bugs known as springtails.

Elton had brought various means for collecting and preserving such treasures. He caught flying insects in a butterfly net, and shook other bugs out of plants and leaves onto a white sheet, or uncovered them by flipping over stones. The insects were killed with cyanide, and Elton put them inside tissue paper with labels and packed them into cigar boxes. For aquatic creatures Elton used a series of nets with different mesh sizes. He preserved some aquatic animals inside glass tubes containing alcohol or formalin, which he then corked and sealed with wax.

Elton paid particular notice to what enabled each species to survive in the generally barren and harsh conditions. For example, it was obvious that the seabirds lived off the sea and that the vast quantities of manure they dropped from the cliffs fertilized the lush vegetation growing below. Other birds Elton found inland, such as the snow bunting, dined on sawflies, while the arctic skua lived off other birds, stealing their food and eggs.

As the days wore on and food supplies began to dwindle, the skua weren't the only creatures living off the birds. The ornithologists collected many eggs and birds. The egg shells were preserved by blowing out their contents (Jourdain once blew so many that he fainted),

which were then made into omelettes. And after skinning, the bird carcasses were put in cooking pots. Elton and the team were surprised at how many species were edible, and he jovially wrote home about having guillemot eggs for breakfast and “stew of fulmar, eider duck, long-tailed duck, purple sandpiper, snow bunting, vegetables & rice!”

Toward the end of their planned week on the island, a gale blew in that would make it impossible for the ship to approach the island safely. Longstaff realized that they would have to stay longer and needed to get a message to the *Terningen*, which was waiting in Tromsø. He asked Elton to walk with him to the northeastern corner of the island (an expeditionary rule was to always go out in pairs for safety) to a coal mine with a wireless station. It was a brutal seven-mile, four-hour hike in driving snow and sleet to reach the mine, and then another four hours back again across knife-edge stones and slushy ground.

Despite the storms, running low on bread, being out of margarine for cooking, and having nearly worn through his Army boots in just a week, Elton declared that life on Bear Island “is rather fun.”

After four days of battling strong gales, the ship was able to return to Bear Island and to retrieve Elton and his comrades just a few days behind schedule. The entire expedition team then headed farther north toward Spitsbergen—and straight into another gale that pushed “growlers” (chunks of dangerous, greenish sea ice) into their path.

Once that storm subsided, the *Terningen* made its way up the west coast of Spitsbergen. About halfway up the 280-mile-long island, the ship turned toward the azure waters of Ice Fjord, and the clouds parted. The team was treated to a stunning panorama of jagged, snow-capped mountain peaks and shimmering glaciers that crept down pure white valleys to the sea. A whale’s spout and then a pod of porpoises broke the glassy surface, while strings of petrels and auks darted just above the water.

More than 200 miles wide, Spitsbergen presented a vast opportunity, and challenge, for exploration. Elton landed first on a smaller island west of the main island called Prince Charles Foreland, where he would spend about ten days surveying with Summerhayes. Longstaff helped Elton establish a campsite on the scabbles near a large, several-mile-long lagoon that was half covered with ice, on which many seals lounged. Before returning to the ship, Longstaff cautioned

Elton not to walk across the lagoon ice. Elton had learned that Longstaff only gave advice once, and if one forgot it, well, that was one's own mistake.

After nine fruitful days on the island collecting and observing the animals, Elton made that mistake. He was out walking with geologist R. W. Segnit on the ice attached to the shoreline of the lagoon. He stepped on a weak spot created by runoff from the shore and broke through into the frigid water. He was saved from going under only by his ruck-sack, which held him up a bit, and was able to climb carefully back up on the ice. However, freezing cold, momentarily stunned, and wearing sun-goggles, Elton did not realize that he had been turned around and almost stepped right back into the hole. Only a shout from Segnit stopped him from another mis-step that would have likely drowned him. Shivering with hypothermia, Elton was able to return to camp to dry out; he left the island two days later for a longer stay at Klaas Billen Bay in the interior of the main island.

Despite being farther north, and more snow- and ice-covered than Bear Island, the summer temperatures on Spitsbergen were much warmer (some days over fifty degrees Fahrenheit) and more comfortable, at least when it was not snowing. Elton took advantage of the conditions to conduct some actual experiments on the adaptations of Arctic animals. To learn more about how they survived in the climate and which habitats they could live in, he tested the tolerance of crustaceans and their eggs to freezing and thawing, and to different concentrations of sea water. [Figure 2.2]



FIGURE 2.2 Charles Elton studying pond life at Bruce City, Spitsbergen, 1921.

Photo from account by C. S. Elton written in 1978–1983. Courtesy of Norsk Polarinstitutt Library, Tromsø, Norway.

Elton found very similar birdlife, vegetation, and insect life on Spitsbergen as on Bear Island but saw more evidence of larger mammals, including two species of arctic foxes, reindeer (in the form of shed horns), and seals. Then, one morning while the breakfast bacon was frying, a shout came up from below the campsite: “Polar bear!”

No one knew how the unwelcome visitor had reached the bay over the glaciers and valleys. But now that it had found their camp, there was sadly no alternative but to shoot it. Elton, ever the zoologist, did a very thorough inspection of the body, both outside and in, and was disappointed not to find any hitchhiking parasites for his collections.

After more than two months of collecting and living on the tundra, the now-veteran Arctic explorer assembled his thirty-three boxes and bundles of gear and specimens, loaded them all onto the ship himself, and sailed home.

UP AND DOWN AN ARCTIC FOOD CHAIN

Once safely back at Oxford, Elton and Summerhayes assembled the data they had gathered from their surveys. Many naturalists, especially those with a collector’s bent, might have been disappointed at the meager pickings on the Arctic islands. But Elton realized that the relative scarcity of species presented a rare opportunity to describe all the transactions and relationships among an entire community of organisms—to peel back the curtain on animal life.

While previous naturalists had seen a community as one entity, or as a collection of species, Elton took a novel, functional approach. It was obvious to Elton that in the economy of Arctic islands, the precious commodity was food. So he traced where every creature’s food came from.

Food was extremely scarce on land, but it was plentiful in the sea, so he started there. He knew that marine animals (plankton, fish) were eaten by the seabirds and by the seals. The seabirds were eaten in turn by the arctic fox (as well as by the skua and glaucous gull), while the seals were eaten by polar bears. These relationships formed what he dubbed “food chains.”

But the connections among the inhabitants of the tundra extended far beyond a few animals. The droppings from the seabirds

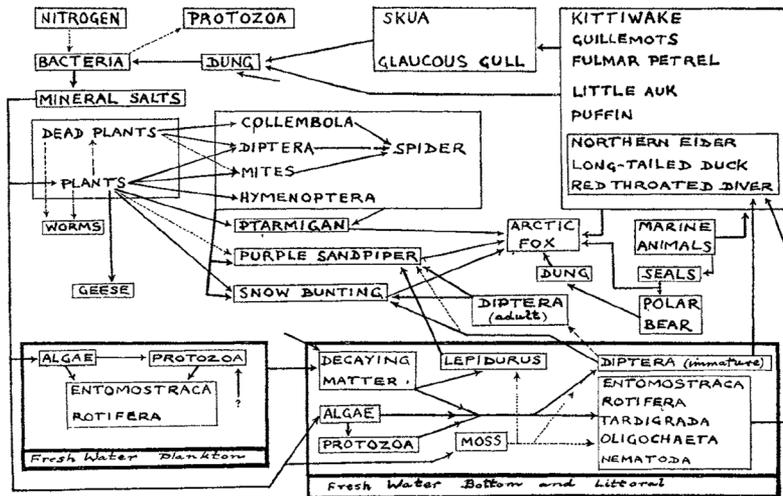


FIGURE 2.3 The food chain on Bear Island. The first food web drawn by Charles Elton. To follow the food chain on land, start with the nitrogen and bacteria at upper left and trace the links all the way to the arctic fox.

From Summerhayes and Elton (1923).

contained nitrogen, which was used by bacteria, which nourished plants, which produced food for insects, both of which were consumed by land birds (ptarmigan, sandpiper), which in turn were food for the arctic fox. In this manner, the food chains in a community were connected into larger networks that Elton dubbed “food-cycles,” later called food “webs.” Elton drew a schematic of these chains and webs, the first of its kind, in a paper published with Summerhayes in 1923. [Figure 2.3]

LEMMINGS AND LYNX

Elton himself moved quickly up the academic food chain, as well as the ranks of the Oxford University Expeditions. After receiving his undergraduate degree in 1922, he was appointed to a departmental lectureship in 1923, and named chief scientist for a new expedition to Spitsbergen.

It was extraordinary responsibility for a 23-year-old, but it was par for the Oxford enterprise. Polar exploration was largely a young man's game, and Elton was in what proved to be remarkable company, as many expedition members subsequently distinguished themselves in other endeavors or perished trying. The organizer of the first expedition was George Binney, who was just a twenty-year-old undergraduate at the time. Binney would also organize the 1923 expedition and a much more ambitious and complex 1924 expedition. He was later knighted for his exploits during World War II, in which he organized operations to run through the German blockade of Sweden. The 1923 expedition added twenty-one-year-old Sandy Irvine, who would attempt to climb Mount Everest the next year and disappeared with George Mallory just a few hundred meters from its summit. Medical officer Longstaff was the first person to summit a mountain over 7,000 meters and would later climb peaks all over the world. The medical officer on the 1924 expedition, and Elton's sometimes tent-mate, was twenty-five-year-old Australian Rhodes Scholar Howard Florey, who would develop penicillin into a drug during World War II and share the 1945 Nobel Prize in Physiology or Medicine.

The 1923 expedition had a new make-up and destination. Binney sought a leaner, more efficient enterprise and trimmed the team to fourteen: seven scientists and seven "henchmen" who were able hunters, rowers, and mechanics. The *Terningen* steered this time for Spitsbergen's little-explored sister island North East Land (Nordaustlandet). Despite its proximity to Spitsbergen, the island proved much less accessible. The ship was thwarted by thick belts of ice that surrounded the island and broke its propeller while trying to force its way through a strait. Partially crippled, the ship was pushed about by the ice floes, and the plans to explore the island had to be abandoned.

But for Elton, the journey was not a bust. On the way back to England, the ship stopped as usual at Tromsø. Elton went browsing in a bookstore and happened across a large tome on Norwegian mammals titled *Norges Pattedyr* by a Robert Collett. Although Elton did not read Norwegian, he was intrigued enough to plunk down one of the remaining three British pounds he had left in his pocket for the journey home for a book that Elton later declared "changed my whole life."

Back in Oxford, Elton obtained a Norwegian dictionary and laboriously worked out a word-by-word translation of one part of the book. There were fifty or so pages on lemmings that, although he had never seen one of the small guinea pig-like animals, enthralled Elton. He was captivated by Collett's descriptions of so-called lemming years, when the rodents swarmed out of Scandinavian mountainsides and tundra in such massive numbers in the autumn that citizens had taken note of the extraordinary phenomenon for centuries.

Elton drew up charts of the reported events and found that they occurred with a fairly regular periodicity of three to four years. He made maps and noticed that migrations involving different lemming species in different parts of Scandinavia seemed to occur mostly in the same years. He stared for hours at the maps spread around the floor of his cubicle in an old building at Oxford, thinking there must be something important he was missing. Then, sitting on a seat in the lavatory, it came to him "in a flash." Like Archimedes in his bathtub, Elton on his toilet got the idea that the lemmings were the "overflowing" of a periodically increasing population. At the time, zoologists had assumed that animal numbers largely remained steady. But Elton now realized that they could fluctuate dramatically.

Digging further, Elton wondered how general the phenomenon was. Even though there were no direct reports of lemming migrations in Canada, Elton was able to infer those events by thinking about food chains. He had previously read a book by a Canadian naturalist that described fluctuations in the populations of other mammals, including the arctic fox. Knowing that the foxes eat Canadian lemmings, Elton located a table of the number of fox skins taken by the fur-trading Hudson Bay Company and, sure enough, found a good correlation between a spike in the number of fox skins and the timing of lemming years in Norway.

The implications for Elton's food chain concept multiplied. Lemmings were also preyed on by birds. Elton noted that short-eared owls gathered in numbers in lemming years in southern Norway, as did peregrine falcons that preyed on the owls.

Lemmings were not the only prey whose numbers fluctuated wildly. Elton learned that the populations of Canadian rabbit (or "varying hare") also oscillated, spiking enormously about every ten

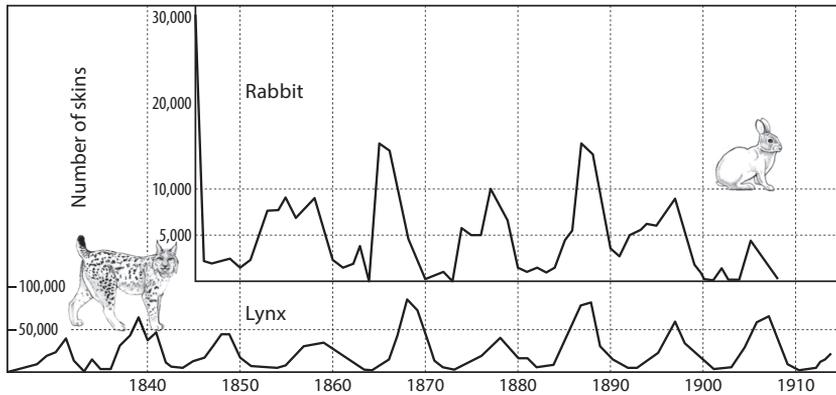


FIGURE 2.4 The ten-year cycles of lynx and rabbits in the Canadian north. Elton studied the records of the Hudson Bay company to determine that the populations of lynx and rabbits surge and crash with a ten-year periodicity.

From Elton (1924).

years before plummeting. The rabbits are the favorite prey of the Canadian lynx. “It lives on Rabbits, follows the Rabbits, thinks Rabbits, tastes like Rabbits, increases with them, and on their failure dies of starvation in the unrabbitted woods,” wrote one naturalist. The cat’s fur meanwhile was the favorite quarry of fur trappers for the Hudson Bay Company. The company, it turned out, kept careful records of furs taken every year from about 1821 on. When plotted, the number of furs taken also showed a striking ten-year cycle that correlated with the rabbit cycle. [Figure 2.4]

Elton thought these cycles offered valuable glimpses into the workings of animal communities. They demonstrated the remarkable power of populations to increase dramatically, particularly if unchecked. By the same token, the abrupt crash in lemmings and rabbits showed that there were also forces, such as epidemic disease, that could rapidly eliminate a large proportion of animals. And these cycles showed how the numbers of one species can influence the numbers of other species through food chains.

In short, the cycles demonstrated that the numbers of animals are regulated in a variety of ways. Elton documented these “Periodic Fluctuations in Numbers of Animals” in a forty-five-page paper he

crafted in 1924. He did not know it at the time, but he was laying a cornerstone of the new science of ecology. The young naturalist would next lay the foundation.

LIFE IS ALL ABOUT FOOD

In 1926, Elton's former tutor Julian Huxley was putting together a series of short books on biology. He was keen to have each one written by leading thinkers that would focus on new and emerging principles. Although Elton was just twenty-six, Huxley respected his extensive Arctic experience (three expeditions by that time) and admired the original thinking evident in his published work. Huxley proposed, and Elton accepted to write, a short book on animal ecology.

Elton hurled himself into the project. He wrote like a fiend, most every night from 10 p.m. to 1 a.m. in his flat near Oxford's University Museum and completed the book in just eighty-five days! Despite the breakneck pace, the resulting *Animal Ecology* was a classic in terms of both style and substance. The 200-page book had an engaging, conversational tone, with many handy analogies. Its chapters were logically organized around key ideas that introduced and set the agenda for major facets of what Elton saw as the new science of ecology.

Elton explained that his book was "chiefly concerned with what may be called the sociology and economics of animals." The analogy to human society and economics was deliberate. "It is clear that animals are organized into a complex society, as complex and as fascinating to study as human society," and "subject to economic laws," Elton wrote. The analogy had deep roots in biology. The concept of an "economy of nature" had been embraced by the great naturalist Carl Linnaeus in the eighteenth and by Darwin in the nineteenth century. The connotation was that like human society, animal communities were composed of interacting creatures with different places and roles.

"At first sight we might despair of discovering any general principles regarding animal communities," Elton said. "But careful study of simple communities," as he had performed in the Arctic, "shows that there are several principles which enable us to analyse an animal community into its parts, and in the light of which much of the apparent complication disappears."

Those principles emerged from the central importance Elton placed on food and food chains. He saw food as the “currency” of animal economies. “The primary driving force of all animals is the necessity of finding the right kind of food and enough of it. Food is the burning question in animal society, and the whole structure and activities of the community are dependent on questions of food-supply,” he asserted. Elton encapsulated each principle that flowed from this basic premise with a charming and apt Chinese proverb:

Food Chains

“The large fish eat the small fish; the small fish eat the water insects; the water insects eat plants and mud.”

Food chains formed the “economic” connections among the various members of a community. Chains of animals were linked together by food, and all were ultimately dependent on plants. In Elton’s scheme, plant-eating herbivores were “the basic class in animal society,” the carnivores that preyed upon them were the next class, and the carnivores that preyed upon them the next class and so on, until one reaches an animal “which has no enemies” at the terminus of the food chain.

According to Elton, the structure of these food chains was related to the sizes of creatures at different levels.

Size of Food

“Large fowl cannot eat small grain.”

Elton argued that size is the main determinant in the structure of the food chain. Things that were too big to subdue or too small to support an animal were off the menu: “the size of the prey of carnivorous animals is limited in the upward direction by its strength and ability to catch the prey, and in the downward direction by the feasibility of getting enough of the smaller food to satisfy its needs.”

These size parameters in turn had important consequences for the numbers of the different kinds of animals in populations and food chains.

The Pyramid of Numbers

“One hill cannot shelter two tigers.”

Elton noted that the animals at the base of a food chain are typically abundant, while those at the end, such as tigers, were relatively few in number. There was generally a progressive decrease in numbers between the two extremes. Elton called this pattern the *pyramid of numbers*.

One example he cited was an English oak wood, where one finds “vast numbers of small herbivorous insects like aphids, a large number of spiders and carnivorous ground beetles, a fair number of small warblers, and only one or two hawks.” Another example he had documented first-hand was in the Arctic, where copious numbers of crustacea are eaten by fish, the fish eaten by seals, and the seals by a smaller number of polar bears. Elton asserted that such pyramids existed in animal communities “all over the world.”

The pyramids of numbers implied that normally there was some balance of animal numbers in a given area. A fundamental question then was how such densities were maintained: How did animals regulate their numbers so that they avoided overpopulation on one hand, and extinction on the other? Elton suggested that, in general, increases in numbers were held in check by predators, pathogens, parasites, and food supply. Extinction was avoided, he explained because as a prey became scarce, predators would switch to other quarry, allowing numbers to recover.

Elton’s picture of the regulation of animal numbers, then, was somewhat akin to Cannon’s idea of homeostasis—that levels were kept within ranges by counterbalancing factors. (Elton did not use term, for Cannon had not yet popularized it, but some later ecologists did).

Elton considered the regulation of animal numbers to be of enormous fundamental as well as practical significance, and devoted almost one-quarter of his book to the subject. But, he admitted, “It has been necessary to speak in generalities, since so little is known at present about the rules governing the regulation of animal numbers.”

Indeed, ecologists were spurred by Elton’s book to search for those rules of the regulation of animal numbers, just as physiologists were motivated by Cannon to search for the rules that regulated processes within humans and other creatures.

And that is where we will head next.

But just before we do, there is one more impact of Elton's book to mention—in fostering the myth of suicidal lemmings. According to Elton's reading of Collett's book, a lemming year occurred “when a whole lot of lemmings apparently went crazy and walked downhill.” He wrote in *Animal Ecology*: “The lemmings march chiefly at night, and may traverse more than a hundred miles of country before reaching the sea, into which they plunge unhesitatingly, and continue to swim until they die.” This description, however, was based on yarns collected in Collett's book. Elton had never seen a lemming, nor a migration, let alone a mass suicide.

The myth of lemming suicide received a considerable boost from the 1958 Walt Disney film *White Wilderness*, which depicted lemmings leaping to their demise. After the narrator explained, “A kind of compulsion seizes each tiny rodent and, carried along by an unreasoning hysteria,” viewers saw lemmings leaping into the water from a high cliff. The scene was faked; the animals were flung off the cliffs by the filmmakers.

The movie won an Academy Award.