Why Big Fierce Animals Are Rare

Animals come in different sizes, and the little ones are much more common than the big.

A typical small patch of woodland in any of the temperate lands of the North will contain hosts of insects and then nothing larger running about until we get to the size of small birds, which are much less numerous. Another size jump brings us to foxes, hawks, and owls, of which there may be only one or two. A fox is ten times the size of a songbird, which is ten times the size of an insect. If the insect is one of the predacious ground beetles of the forest floor, which hunt among the leaves like the wolf spiders, then it, in turn, is ten times bigger than the mites and other tiny things that they both hunt.

The animals in this system of living do indeed come in very distinct sizes. There are, of course, some in-between ones, but not many. Squirrels in the upper size range seem obvious, but I am hard put to find something between an insect and a small bird unless it is a newt or lizard, neither of them very prominent denizens of a temperate woodland. Slugs and snails are toward the size of caterpillars. Shrews and toads are near the size of songbirds. Even a snake can be thought of as an odd-shaped hawk.

In the wood as elsewhere there are distinctly different sizes, and the little ones are the most common. The same sort of thing exists in the sea in even odder form, for in the open sea the really tiny things are plants, the

microscopic diatoms and other algae. Ten times bigger than these (give or take a few times) are the animals of the plankton, the copepods, and the like. Bigger still are the shrimps and fish that hunt those copepods. Then another jump brings us to herrings, then to sharks, or killer whales. In any one place in the sea, this clumping of life into different sizes is the normal thing.

In the sea the rarity of the large is also most clearly shown. Great white sharks are extremely rare, and the other kinds of shark are scattered pretty thinly over the seas too. Fish of the herring size are vastly more common than sharks, but even so, the number that are seen in a casual dive in the sea is seldom immense. If you drift, and focus your eyes just outside the facemask, however, myriad darting specks of the smaller animals may become visible. If you later take some of that same water and spin it in a centrifuge, there is likely to be a thin green scum in the bottom made up of an almost uncountable multitude of independent, tiny plants.

The tiny things of woodland and sea are immensely common; bigger things are a whole jump bigger and a whole jump less common; and so on until we reach the largest and rarest animals of all. A like pattern can be found in tropical forests, Irish bogs, or just about anywhere else. It is an extraordinary thing but true that life comes in size fractions which, for all the blending and exceptions that can be found by careful scrutiny, are remarkably distinct. Animals in the larger sizes are comparatively rare.

Charles Elton of Oxford pointed out this strange reality half a century ago. Elton went adventuring on Spitsbergen, an Arctic island covered with treeless tundra, where the animals move about in the open and where particularly he could follow an arctic fox as it went about its daily affairs. Arctic foxes can be delightfully tame. On Saint George Island in the Bering Sea one tried to take sandwiches from my pocket as I sat upon a rock. Elton followed his foxes and pondered their activities through a summer that was to be one of the most important an ecologist ever spent.

The foxes caught the summer birds of the tundra—the ptarmigan, sandpipers, and buntings; and these birds were at once a size jump smaller than the foxes and much more numerous. The ptarmigan ate the fruit and leaves of tundra plants, but the sandpipers and buntings ate insects and worms, which were again a size jump smaller as well as more numerous. The foxes also ate seagulls and eider ducks, smaller and more numerous than the foxes, and these birds ate the tiny abundant life of the sea. Elton not only

saw all this but, as Sherlock Holmes often lectured Watson, he *observed* it also. That small things are common and large things rare has been known by everybody since the dawn of thought, but Elton pondered it as Newton once pondered a falling apple, and knew he was watching something odd. Why should large animals be so remarkably rare? And why should life come in discrete sizes?

Elton's summer on Spitsbergen gave him the answer to the second of these questions even as he posed it. The discrete sizes came about from the mechanics of eating and being eaten. He had seen a fox eat a sandpiper and a sandpiper eat a worm. These animals of different sizes were linked together by invisible chains of eating and being eaten. Foxes had to be big enough, and active enough, to catch and eat the birds on which they preyed; and the birds likewise must overpower, and engulf at a single swallow, the animals on which they fed. The normal lot of an animal was to be big enough to vanquish its living food with ease, and usually to be able to stuff it down its throat whole or nearly so. As one moves from link to link of a food chain the animals get roughly ten times bigger. Life comes in discrete sizes because each kind must evolve to be much bigger than the thing it eats.

Elton's conclusions were obviously true in a very general way. The communities of woodland and ocean on which his thinking was based seemed to conform very nicely. Life in those communities did come in different sizes, and it seemed that the sizes had grown discrete because each kind had evolved to be much bigger than the thing it ate. But many exceptions to the general principle of food size come to mind: wolves, lions, internal parasites, elephants, and baleen whales. There are many animals that are either smaller than their food, such as wolves or parasites, or else absurdly bigger, like whales. But a closer look at any of these animals shows them to be instructive exceptions, if true exceptions to the rule all the same.

Land herbivores do not fit the Eltonian model, at least not completely, because land plants provide different-sized mouthfuls for different sizes of animals. You do not have to kill an entire land plant in order to eat it; you just tear off a suitable piece, a shoot, some grass blades, a berry, a bite out of a leaf. Food chains based on vegetation could start with many different sizes of plant-eating animal because squirrels, caterpillars, and elephants share the same food. Even so, there does not seem to be a complete continuum of sizes amongst vegetarians, at least in any one place. Both big and

little plant-eaters exist in a forest or a prairie and there is not much difficulty in sorting them into sizes. This is because the predators of plant eaters do have to be size conscious when they look for food. A selection pressure acts downward along the food chains, as herbivores evolve sizes that let them escape even as carnivores evolve sizes that enable them to catch skillfully. It is as important to be of a size that does not fit in someone else's mouth as it is to have a mouth suited to the size of one's own prey. So natural selection tends to preserve size classes even when food chains start with a pabulum of meadow-forage or forest.

Wolves sometimes obey Eltonian principles, as when they hunt singly for rodents and small game, but they have evolved the trick of packing up to haul down bigger prey in winter, when they are freed from family cares and can go out in gangs. Other pack-hunting animals work variants on this method. And all large carnivores have had their sizes adjusted to the needs of killing, rather than of engulfing, so that a lion needs to be big enough to pull down an ailing zebra, but no bigger.

Parasites are smaller than their food, for obvious reasons, but their activities still tend to separate the animals on parasite food chains into different sizes with every link, as was described before the coming of ecology in a jingle by Jonathan Swift:

> Big fleas have little fleas
> Upon their backs to bite 'em
> And little fleas have lesser fleas
> And so *ad infinitum.*

Very special sea animals, such as whales, are even more instructive, and we discuss them at the end of this chapter. But otherwise in the sea the pattern of size tends to conform very well to the simplest interpretation of the workings of food size. This is because the sea plants are tiny, individual, and have to be hunted and killed by those who would live off them (seaweeds of the coasts are of trivial importance in the wide oceans). So in the sea a rather complete set of steps runs up the food chains from the smallest plants, through crustaceans and fish, to great white sharks.

Thinking these Eltonian thoughts brings up another of nature's conundrums, "Why are land plants big but sea plants small?" But that must wait for another chapter.

Now there was the matter of rarity. Elton showed that there had to be size jumps as one went up food chains and that the animals on the upper end had to be big. But why should the big be so rare? And very rare they are. One only has to compare the number of sharks to the number of herrings, or warblers to caterpillars, to see this. With every jump in size an even mightier loss occurs in numbers. Elton coined a term to describe this fact of life; he called it "the pyramid of numbers." He saw in his mind's eye a mighty host of tiny animals supporting on their backs a much smaller army of animals ten times as big. And this array supported, in turn, other animals ten times bigger still, but these were a select few. It was a graph of life he imagined with numbers of individuals along the horizontal axis, and position in the chain of eating, together with size, on the vertical. His vision saw the functioning of animal communities like the profile of Zoser's step pyramid at Saqqara, a triangular edifice built of stacked square-ended layers so that the summit could be reached by four or five giant steps. When ecologists forgather they call this result the "Eltonian pyramid." Now, why should there be pyramids of numbers in nature wherever we look, from the Arctic tundras to tropical forests and the open spaces of the sea? Why should large animals, particularly large hunting animals, always be so amazingly rare?

It is tempting to say that no problem exists, that it stands to reason that there cannot be as many big things as little. But this claim suggests that the Eltonian pyramid reflects no more than the elementary facts of spatial geometry. There is clearly no shortage of actual space to hold more big animals. On Spitsbergen, for instance, each fox had acres and acres to run around in, and the world oceans could hold mind-boggling quantities of the large sharks and killer whales who are the top carnivores of the sea. Large plants are crammed together on the earth in astounding numbers, so that we call the result a "forest." Only the large animals are discriminated against.

A second tempting argument is to say that there is a finite amount of flesh (what ecologists call biomass) to go round and that this chunk of flesh could be used either to make a few big bodies or to make very many little ones. The big are rare because they take large slices from their cake. This assertion is true as far as it goes, but it does not go nearly far enough. If, instead of counting the animals in the different size levels of the pyramid, one weighed them, one finds that there is vastly more flesh in the smaller classes, a greater standing crop of life as well as more numerous individuals. All the insects in a woodlot weigh many times as much as all the birds;

and all the songbirds, squirrels, and mice combined weigh vastly more than all the foxes, hawks, and owls combined. The pyramid of numbers is also a pyramid of mass, and the problem remains unsolved. Why is there so little living tissue in the larger animal sizes?

Elton did not have the answer. He thought it might be because little animals reproduced very quickly (true, they do—compare the egg output of butterflies with that of the birds that eat caterpillars) and that rapid reproduction was the key to vast populations. But this is to fall into the age-old error of biologists and theologians alike, the error that says numbers are set by breeding strategy.

. . . Numbers are set by the opportunities for one's way of life, not by the way one breeds. Professorships set the limit to the population of professors, not the productive output of graduate schools. The fact that large animals are rare cannot have anything to do with their reproductive drives. Elton's explanation will not do.

It took nearly twenty years for the corporate body of science to come up with the answer to the question Elton posed in 1927. Raymond Lindeman and Evelyn Hutchinson did so at Yale by thinking of food and bodies as calories rather than as flesh.

A unit of biomass, or flesh, represents a unit of potential energy that is measured in calories. If we burn a chunk of protein we liberate so many calories of heat, and if we burn a chunk of fat we get more calories still. This is now common knowledge to the affluent peoples of the West who worry about the calories in their food lest they become obese. In the 1930s and 1940s even illiterate Hollywood starlets knew this, but biologists wakened to the idea of the calorie rather more slowly. Yet in the use of food as calories lay the answer to the rarity of the large and fierce.

Measuring an animal's flesh in calories also alerts one's mind to the vital fact that bodies represent fuel as well as vessels for the soul. An animal continually burns up its fuel supply to do the work of living, puffing the exhaust gases out of the smokestacks of its mouth and nostrils and sending the calories off to outer space as radiant heat. The animal uses up its flesh, replacing the lost substance by eating more food, then burning most of this up too. This process of consuming matter by the fires of life goes on in every level of the Eltonian pyramids, and the fires are continually fresh stoked by the plants on which the animal pyramids rest. At each successive level in the pyramids, the animals have to make do with the fuel (food) that can be

extorted from the level below. But they can only extort some fraction of what the level below had not itself used up, and with this tithe the denizens of the upper layers must both make their own bodies and fuel their lives. Which is why their numbers are only a fraction of the numbers below, which is to say why they are rare.

The ultimate furnace of life is the sun, streaming down calories of heat with never-fainting ray. On every usable scrap of the earth's surface a plant is staked out to catch the light, its green array of energy receptors and transducers tuned and directed to the glowing source like the gold-plated cells on the arms of a satellite. In those green transducers we call leaves, the plants synthesize fuel, taking a constant allotment of the streaming energy of the sun. Some of this fuel they use to build their bodies, but some they burn to do the work of living. Animals eat those plants, but they do not get all the plant tissue, as we know because the earth is carpeted brown with rotting debris that has not been part of an animal's dinner. Nor can the animals ever get the fuel the plants have already burned. So there cannot be as much animal flesh on the earth as there is plant flesh. It is possible for large plants to be vastly abundant and ranked side by side, but animals of the same size would have to be thinly spread out because they can only be a tenth as abundant.

This would be true even if all animals were vegetarian. But they are not. For flesh eaters, the largest possible supply of food calories they can obtain is a fraction of the bodies of their plant-eating prey, and they must use this fraction both to make bodies and as a fuel supply. Moreover, their bodies must be the big active bodies that let them hunt for a living. If one is higher still on the food chain, an eater of a flesh eater's flesh, one has yet a smaller fraction to support even bigger and fiercer bodies. Which is why large fierce animals are so astonishingly (or pleasingly) rare.

Thus was the grandest pattern of rarity and abundance in the world explained by two men at Yale in the 1940s. Ways of life were bumping against that most fundamental of physical restraints, the supply of energy.

As the realization of what Lindeman and Hutchinson had done for natural history percolated through the consciousness of biology in the fifties and sixties a thrill of self-respect began to throb in its younger practitioners. Here the pattern of field experience was linked to the fundamental laws of physics. We were talking of energy degraded step by step as it flowed down food chains, losing its power to do work and pouring steadily away to the

sink of heat. The grand pattern of life that Elton had seen on Spitsbergen and that countless naturalists had intuitively known before was clearly and directly a consequence of the second law of thermodynamics.

We can now understand why there are not fiercer dragons on the earth than there are; it is because the energy supply will not stretch to the support of superdragons. Great white sharks or killer whales in the sea, and lions and tigers on the land, are apparently the most formidable animals the contemporary earth can support. Even these are very thinly spread. One may swim many lifetimes in the world oceans without encountering a great white shark, and an ancient Chinese proverb asserts that a hill shelters only one tiger. Evolutionary principle tells us that the existence of these animals creates a theoretical possibility for other animals to evolve to eat them, but the food calories to be won from the careers, or niches, of hunting great white sharks and tigers are too few to support a minimum population of animals as large and horribly ferocious as these would have to be. Such animals, therefore, have never evolved. Great white sharks and tigers represent the largest predators that the laws of physics allow the contemporary earth to support.

But here we run into what seems to be the first real difficulty of the argument. There are living animals that are much larger than tigers and sharks, and there have been some very big ones in the past. How does their existence square with our interpretation of the second law of thermodynamics?

Elephants and the big, cloven-hoofed animals are larger than tigers. In the past there have been even bigger mammals, such as giant ground-sloths and *Titanotherium*, a beast like an overgrown elephant and the largest land mammal ever. There have also been the largest reptiles of the Mesozoic, the ponderous dinosaurs: *Stegosaurus, Brontosaurus, Iguanodon.* None of these animals poses any difficulty for the model. They have all been plant eaters. In the strict Eltonian model the plant eaters are small, and indeed in life most of them actually are. In the open sea this rule that plant eaters must be small is strictly enforced because the drifting plants are so tiny that only very small animals can make a successful living by eating them. But on land, plants often appear as continuous mats of leaves, which we call vegetation, and it is possible for enormous sluggish animals to slurp them up without much nicety in the hunting. Masses of energy are available in the plant-eating niches at the bottom of the Eltonian pyramids, with the result that viable populations of even enormous animals can be supported. The

brontosaur and the elephant alike, therefore, leave both our belief in the energy-flow model and the second law of thermodynamics intact.

That leaves two trickier kinds of animals to explain away: the great baleen whales of the contemporary oceans, which are the largest animals ever to have lived, and the flesh-eating dinosaurs such as *Tyrannosaurus rex.* These are both meat-eating animals, and they are impressively bigger than great white sharks or tigers.

The baleen whales have learned to cheat, hunting their food in non-Eltonian ways. Essential to the normal structure of the Eltonian pyramid was that every carnivorous animal should have a direct relationship to the size of its food, being big enough to catch and eat it but not so big that the food item should prove a trivial mouthful not worth the effort of hunting. On this model, the food of a blue or right whale should be several feet long. But it is not. The whales cheat with their sieves of baleen, which let them strain from the surface of the sea the tiny shrimps called krill in huge numbers and with little effort. The whales have cut out the middlemen, avoiding all the energy losses that would have accrued if the krill had been passed to a fish and that fish passed to a bigger fish before the whale had its chance at it like any other Eltonian feeder. So the whales, although not plant eaters, feed very low on food chains where the energy supply is still comparatively large. Floating as they do in the sea, they use little energy in their sluggish hunting, paddling quietly along with their mouths open, straining the meat out of the oceanic soup. So the apparent exception of the whales is no exception at all, and our model may stand.

Tyrannosaurus rex is more difficult for the argument. Tyrannosaurs were huge carnivorous dinosaurs, often pictured as a great green kangaroo-like form with a hideous toadlike head, nightmare teeth, and a pair of useless little flapping arms dangling below the ugly neck. An animal of this size answering to the name of *Tyrannosaurus* certainly existed, for we have specimens of all his bones. He was several times larger than lions or tigers, or indeed of any other recorded predator. What enabled it to escape the constraints apparently placed on all its successors by the second law of thermodynamics?

It is useful to note first that the tyrannosaur fed at the same level as its modern successors, the big cats, and at the same level as the baleen whales in the sea. It fed on plant eaters relatively low in the food chain, close to the bottom of the Eltonian pyramid, where there was still much energy to be

won. A large body, therefore, does not seem hopelessly out of the question. We know that there were many kinds of very large herbivores about in the tyrannosaur's time, animals that, in the absence of pack-hunting predators such as dogs, could be overcome only by very powerful attackers. So we might conclude that the necessity for Mesozoic predators to be large and ferociously active is self-evident. There was nothing else to get at the meat so massively on the hoof, so natural selection provided *Tyrannosaurus rex*.

I have always been unhappy about this reasoning. If natural selection could fashion a tyrannosaur at that time, why not in all subsequent times? Why in particular was there nothing like a tyrannosaur in the great age of mammals, that later part of the Tertiary epoch when all the plains lands of the earth held herds of game that make the herds of modern Africa seem trivial by comparison? I have felt compelled to conclude that the constraints on the size of ferociously active predators that have been applied throughout the age of mammals ought to have applied to the reptiles of the Mesozoic era also. By thinking thus I maneuver myself into the position of saying that, on ecological grounds, the *Tyrannosaurus rex* did not exist. And yet there the bones are, indubitably the bones of a large, flesh-eating animal of the size claimed. It was with a sense of inward peace that I saw a drawing of a recent attempt to put the bones together differently.

The classic picture of the hopping, predacious tyrant lizard is derived from nineteenth-century reconstructions of the animal. The new reconstruction, first published in *Nature* in 1968, shows the animal to be a waddling, slow-moving beast, not at all the sort one can imagine dashing after a herd of galloping brontosauri. But it probably got them all the same, picking out the sick and the dying, often getting them only as carrion. The tyrannosaur was not a ferociously active predator. It did not stand upright, nor did it hop. It held that massive body horizontally, perhaps able to move swiftly for short periods as it balanced its motion with the long tail. But most of its days were spent lying on its belly, a prostration that conserved energy and from which it periodically roused itself, lifting its great bulk on those two little arms in front until it could balance on the thick walking legs. The tyrannosaur did indeed support a large mass by meat eating, but it escaped the energy-consuming price of being active in order to overcome prime specimens of the giant prey it ate. It managed on land essentially the same stratagem that the baleen whales manage in the sea; it found a non-Eltonian way of getting the meat of plant eaters without having to hunt them properly. Nothing like

it has been seen since because the true active predators of the age of mammals were able to clean up the meat supplies before a sluggish beast such as a tyrannosaur could get to them. And active predators might even have eaten the tyrannosaur itself.

Tyrannosaurus rex, as popularly portrayed, is a myth. But it is probably safe to say that it will be as durable as any other myth in our culture. The size and ferocity of real-life predators is restricted to the scale of a tiger, and even these must always be rare. The second law of thermodynamics says so.

Content Questions

1. How, specifically, did his fieldwork of following and observing the arctic fox lead Charles Elton to his conclusions about why large animals are rare? (224–225)
2. Why did Elton conclude that animals' differing sizes are related to "the mechanics of eating and being eaten"? (225)
3. Why is it that "natural selection tends to preserve size classes even when food chains start with a pabulum of meadow-forage or forest"? (226)
4. What "fact of life" does Elton's "pyramid of numbers" describe? (227)
5. Why are the explanations of lack of physical space, limitations of biomass, and the rapid reproduction of smaller creatures inadequate to answer the question of why large animals are rare? (227–228)
6. How did Raymond Lindeman and Evelyn Hutchinson, by thinking of food and flesh as calories, finally furnish a satisfying explanation of the rarity of large animals? (228)
7. In what way did the conclusions of Lindeman and Hutchinson change the way in which biologists view the regulation of population composition and size within a community? (229–230)
8. How does fierceness, as well as size, contribute to an animal's rarity? (229)
9. In the 1950s and 1960s, what relationship did some biologists articulate between Lindeman and Hutchinson's conclusions and the second law of thermodynamics? (229–230)
10. According to Colinvaux, why don't elephants or whales prove Lindeman and Hutchinson's hypothesis wrong? (230–231)

Application Questions

1. Currently, there is considerable debate among paleontologists about whether *Tyrannosaurus rex* was a predator or a scavenger. Would Colinvaux's argument favor one of these ecological roles over the other? Why?
2. Using examples from sources other than Colinvaux, how do we explain the fact that the pyramid of biomass and the pyramid of numbers do not apply to all communities?

Discussion Questions

1. In describing how Lindeman and Hutchinson modified Elton's conclusions, what point is Colinvaux making about the scientific process?
2. Is the force of Colinvaux's argument harmed by his mistaken assumptions about *Tyrannosaurus rex?* How would you modify his argument by taking into account newer findings about this dinosaur?
3. Based on Colinvaux's explanations of how animals evolve in relation to their sources of food, what conclusions can you draw about humankind's evolution as it relates to the food we eat?
4. Does Colinvaux's point of view alter the presumptions that we make about human beings? If so, how?