13. Allometry & Skew (2025)

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If there is one generalization about the evolution of life on this planet, it is that successive living forms kept getting bigger. And because of simple geometric and physical laws, not all properties of these entities could grow bigger in proportion. This disproportionality is called **allometry** and it played a very important role in how organisms have evolved.

A second general pattern in the evolution of earth's life is that organisms almost always got bigger by teaming up together. Each new and higher-level collaboration became a major transition, creating an explosive expansion and diversification of new life forms (Bozdag et al. 2024; Hein et al. 2017; Maynard Smith and Szathmary 1995; Robin et al. 2021). And each new collaboration raised the issue of which parties paid the costs, and which parties enjoyed the benefits (Bourke 2011). Where overall benefits were not equally distributed among the members of the collaboration, we say the system had **skew**.

In essay 11, I argued that the current political turmoil in the United States is a conflict between those promoting the allometric benefits of collaboration and those seeking to maximize economic skew. I thought it might be instructive to take a quick tour through the evolution of life and see how this particular battle has been raging for billions of years.

What is Allometry

Consider two properties, **A** and **B** of an entity. If increasing or decreasing the value of **A** causes a proportionate change in **B**, we say that **A** and **B** are **isometric.** But if the change in one of the properties is associated with a disproportionate change in the other, we say the properties are **allometric**. As an example, consider a sphere. If I increase the radius of the sphere, the circumference of the sphere goes up proportionately, and is therefore isometric with the radius. However, the surface area of the sphere increases with the square of the radius, and thus the surface area is allometric to both the radius and the circumference. And the volume of the sphere, which increases with the cube of the radius is allometric to the radius, the circumference, and the area.

So, who cares? Well, *you* should! You are not a sphere, but the same issues apply. As you grew bigger from childhood, your surface area grew more slowly than your volume. Your surface area determines how quickly you lose heat; your volume determines how much tissue you have to produce heat. It is easier to stay warm when you are big then when you are small. Because of this allometry, large size confers an energetic benefit.

Because of these allometric benefits, large herbivores, such as the African buffalo, get all the energy they need by eating very low-quality forage. Since low-quality forage tends to be common and occurs in big patches, African buffalos can happily forage in large groups. This provides opportunities for polygynous males to compete for the many available females. In contrast, the small dik-dik antelope must seek out high-quality buds, fruits, and new leaves. This resource tends to be widely scattered in tiny amounts, so dik-diks forage solitarily or in pairs. Given the wide dispersion of dik-dik females, this species is usually monogamous.

The point is that simple allometry can have profound effects on many properties of a species. In this case, it affects diet, spatial dispersion, and mating system. Who would've guessed?!

What About Skew?

As noted above, living things got bigger over evolutionary time by forming collaborations. An obvious option in any collaboration is a division of labor. In both human economics and evolutionary biology, a division of labor is favored when increases in task specialization produce a disproportionately larger increase in productivity (Cooper et al. 2021; Michod et al. 2006; Yenni et al. 2020). This is just another way of saying that there are allometric benefits to divisions of labor.

In biological systems, the relevant productivity is how many replicas an organism can produce in its lifetime. This will depend on how long it lives (survival) and its rate of offspring production (fecundity). Since organisms only have limited resources and are vulnerable to predators, there is usually a trade-off between investing in survival and investing in fecundity. If the organisms are members of a collaboration that has adopted a division of labor, it is only natural that some members may focus on ensuring survival for the collaboration while others focus on reproduction. The risk is that the former will end up producing fewer offspring than the latter. This is called skew.

Why join a collaboration if you will be the victim of skew? One possibility is that collaborative efforts are so productive that the skewed participant still does better than if they were on their own. Another possibility is that participants that begin at low status gradually ascend to the upper ranks so that on a lifetime basis, everyone does the same. Status can also change over time as a result of direct conflict between collaboration members. A third reason to accept a low status is that there is no other place to go: you either join a collaboration, or you die. Finally, if the other members of your collaboration are closely related to you genetically, their offspring are almost as good in an evolutionary sense as your own.

The bottom line is that divisions of labor and skew are common in collaborative systems.

The First Living Things

The Earth was formed about 4.5 billion years ago. By at least 3.8 billion years ago, the first living cells had appeared. "Living" means they had achieved two key requirements: first, they had mechanisms to promote their s**urvival,** and second, they could **reproduce** themselves. Interestingly, all current life on the planet has descended from the same common ancestor. Soon, this ancestor had branched into two groups, the Bacteria and the Archaea, (collectively called **Prokaryotes)**. While sharing some structural properties (e.g., a protective wall around the cell, their DNA floating around the cell contents, and their energy-producing machinery mounted on the outer cell membrane), the two groups differed in details of their chemical composition.

Most members of both groups initially made a living by metabolizing chemicals they encountered in their environment. One group of bacteria, the cyanobacteria, figured out how to use light to combine water and carbon dioxide into carbohydrates that could later be used as an energy source. This process released oxygen as a waste product, and this was the reason that atmospheric oxygen went from almost 0 to about 1% of current levels by 2 billion years ago. It took another billion years to oxygenate the deep oceans and get atmospheric oxygen to 10% of current levels.

Even the initially low amounts of atmospheric oxygen opened up new metabolic opportunities for prokaryotes. Oxygen loves to gobble up electrons and when exposed to other compounds, both inorganic and organic, it grabs the electrons holding those compounds together, breaking them into pieces and releasing energy. Once oxygen in the atmosphere reached sufficient levels, members of both prokaryotic groups evolved metabolisms based on oxidation.

Prokaryotic cells are full of oxidizable fuel. It cannot have been very long before prokaryotes began eating each other. Some even invaded another prokaryote and became a parasite. One way to avoid being eaten is to be bigger than your predator. Or, if you were big enough, it would be much easier to eat other prokaryotes. Being big clearly has advantages! But here, prokaryotes hit an allometric wall set by their basic structure: as they got larger, their ability to produce energy could only increase with the surface area of the cell membrane, whereas the energetic needs of the cell contents increased with the cell volume. At some point, the cell would become too large to feed itself.

Eukaryotes

Then about 2.5 billion years ago, a large archaeal cell which had either engulfed or been parasitized by an oxidative bacterial cell, failed to digest or expel the bacterium, and instead let it live within its cell contents. So began a symbiosis between the two cells with the archaeal cell absorbing nutrients through its cell membrane and the bacterium oxidizing them to provide energy for both cells.

Over the next billion years, descendants of this early symbiosis refined the collaboration with a division of labor. The host archaeal partner gave up any energy production on its cell membrane, and multiple copies of the bacterium in the cell contents, now called mitochondria, took over making energy. The genes that both parties had brought to the relationship were combined into a central "government" with its own protective membrane, called the nucleus. A few genes were left in each mitochondrion to create the necessary proteins there for energy production. When the new partner cell reproduced, both the combined nuclear genes and entire mitochondria were present in each of the progeny.

These new combined organisms, called **Eukaryotes**, broke through the prokaryotes' size ceiling since mitochondria could be produced in any number and scattered throughout the volume of the cell. Much bigger cells could be created without starving! Getting rid of the prokaryotic cell wall allowed them to extend portions of the cell, like the pseudopodia on an amoeba, and become highly mobile. To keep cell contents in proper positions as the cell changed shape, eukaryotes evolved a much more structured cytoskeleton. All of this new structure required new proteins, and this required new genes to produce the proteins. As a result, eukaryotes have four times as many genes as prokaryotes. Eukaryotes also have longer genes because of segments called introns that do not themselves code for proteins but instead allow a single gene to produce a number of alternative proteins (Muro et al. 2025).

As might be expected, many eukaryotes took advantage of their larger size and mobility by eating prokaryotes and other eukaryotes. Serendipitously, this led to even further symbioses and collaborations. For example, a predatory eukaryote consumed a cyanobacterium which it retained in a new partnership. The bacterium eventually became the chloroplasts of photosynthetic eukaryotes including plants. Red algae were created in this way. Then later, another eukaryote consumed a red algal cell, formed a new secondary symbiosis, and this combination gave rise to the brown algae and dinoflagellates.

The Evolution of Sex

Over time, the world changes: what was a good adaptation last year may not be so good in the next. And other species are constantly evolving; suddenly a new predator shows up that wasn't there before. Producing multiple kinds of descendants is often a good way to avoid extinction. Mutation is slow and has random effects. If there were some way to incorporate genes that provided new features already tested by selection, that could be quite advantageous.

Most prokaryotic cells have a single chromosome, but also small circular pieces of DNA called plasmids. When a prokaryotic cell dies, or is consumed by another, some of the victim's plasmids can be taken up by nearby prokaryotes and even incorporated into their chromosomal genes. Adjacent cells of some prokaryote species can connect with a tube and exchange plasmids and chromosomal genes. Finally, prokaryotes, like everything else, can be infected by viruses, and these can transfer plasmids or chromosomal genes between species.

While all of this can enhance prokaryote diversity, it is chancy and ad hoc. Eukaryotes evolved a much more deterministic process**: sex**. At some stage in their lives, all eukaryotes are diploid. That is, all of their chromosomes are present as similar (homologous) pairs. Genes in equivalent locations on the two members of a chromosome pair have the same function, although they may differ in how they do it. At some point, the organism undergoes meiosis in which it divides up each homologous pair of chromosomes and puts one or the other copy into a reproductive cell called a gamete. Before they are separated, the two members of each homologous pair are brought so close together that they "swap" some homologous genes. If they do, neither chromosome in the pair is identical with the parental chromosomes. The genes have been mixed, increasing offspring diversity! The gametes are then sent off into the environment to mix and find gametes from other parents.

Eventually, two unrelated gametes meet and fuse their cytoplasmic contents to form a zygote. This mixing of chromosomes from different parents greatly increases descendent diversity. But note that the zygote is in fact a collaboration. And as so often happens, skew raises its ugly head! While each gamete's chromosomes make it into the new nucleus, the DNA-bearing mitochondria and chloroplasts are not so cooperative. In almost all eukaryotes, the organelles from only one gamete survive the resulting competition (Chung 2025; Kuroiwa 210; Munaasinghe and Agren 2023). In humans for example, sperm mitochondria enter the egg at fertilization but are quickly digested by the egg cytoplasm.

Multicellularity

For a billion years after they first appeared, eukaryotes diversified and spread worldwide. However, except for some colonial chains and sheets of cells, most eukaryotes remained single-celled independence. While forming larger associations might have created a size advantage, the costs of cell adhesion, cell coordination, and early development were apparently two prohibitive to promote early multi cellularity (Lynch 2024; Muñoz-Gómez 2024).

Then just after 0.8 billion years ago, for reason still debated, the entire earth was covered with ice and snow (Simpson 2021; Crockett, et al. 2023). There was even thick ice on the equatorial oceans. This "snowball earth" lasted about 70 million years before conditions changed, the ice melted, and tropical oceans went back to being warm. However, the ice age lasted long enough to impose major selective pressures on living things. Ocean temperatures dropped to -4 C. This drastically reduced the rate of diffusion of nutrients in water and greatly increased its viscosity. In addition, light that was needed by marine photosynthetic life was reflected back into space by the ice covering the water's surface.

Most prokaryotes count on diffusion to obtain their nutrients from the surrounding medium. The only way they could afford to live under snowball conditions was to increase their surface area to volume ratio by becoming smaller. Many eukaryotes had evolved flagella or cilia that allowed them to move through the water to find new nutrient patches. However, the higher viscosity of the water made it difficult for a single cell to go fast enough.

As suggested by Simpson and colleagues (citations above), the most likely eukaryotic solution was to form a hollow ball of flagellated cells (rather like contemporary *Volvox*). By beating their flagella in a synchronized way, they could propel the ball despite the viscosity. In addition, by having a large cross-section, the ball acted like a net trapping any nutrients or other organisms in its path. By keeping the ball hollow, the collaboration of cells dodged the allometric problem that increasing size increases the volume faster than the area. In fact, the bigger the ball, the faster it could move and the larger the food net. While Snowball earth might have favored reductions in prokaryotic cell size, it likely favored increased size for multicellular eukaryotes.

Although current life on the planet seems to owe its ancestry to a single original prokaryote, and later a single original eukaryote, multicellularity arose multiple times during Snowball Earth. Once the planet warmed up again, the stringent constraints on living things were relaxed. The new multicellular associations were suddenly free to exploit new ways of making a living. And they did, leading to a burst of new multicellular organisms in the subsequent Ediacaran and Cambrian periods.

As with the first eukaryotic symbioses, multicellular eukaryotes soon adopted divisions of labor with some cells focused on survival and others on reproduction. Reproductive skew was avoided in many groups such as algae, fungi, plants, and animals by starting each new individual from a single fertilized zygote that divided into multiple copies with identical genes. So, it didn't matter which cells did the reproducing: everyone benefited. Of course, this happy situation changes when cells mutate and break out of the collaboration to become cancers.

Some eukaryotes form collaborations with individuals who are not genetically identical despite consequent skew (Queller and Strassman 2009). These all seem to fit into one of the justifications listed at the beginning of this essay. For example, slime molds (*Dictystelium*) spend most of their lives as single-celled amoebae on the forest floor. When food becomes scarce and starvation is imminent, adjacent cells form a multicellular "slug" that crawls to a location where wind-dispersed spores are feasible. The slug builds a stalk and releases the spores. As many as a quarter of the participating amoebae that contributed to the stalk contribute no spores. Why did they bother? The reason has to be that they would have starved otherwise, and they cannot know when they join the collaboration whether they will be contributing spores, or not.

Sociality

By now, you get the point! Social groups of organisms, the next higher level of collaboration, follow all the same rules. For example, social insects, such as ants and bees, exhibit high degrees of division of labor, and avoid the costs of skew by being closely related genetically. Mated birds of some species recruit "helpers-at-the-nest" who guard and feed the young, but do not themselves foster offspring. Their best hope is that one or more of the parents will die and they can take over the nesting situation. Even the collaborations between mated male and female birds and mammals are vulnerable to one or the other mate having "extra-pair" copulations leaving the other parent to raise unrelated offspring. Cheating in a social collaboration is always a possibility.

Allometry and skew have had enumerable roles in our evolution. Consider adjacent tribes before humans discovered aviation. The defense of a tribe's territory is a function of its perimeter, but the number of warriors available to defend that territory increases with its area. A big tribe on a big territory has more than enough warriors do both defend its own territory and encroach on the territories of neighbors. This can generate status and economic skew based on tribal affiliation.

It seems unlikely that human societies can ever escape the risk of skew. Even simple hunter-gatherers have divisions of labor based on gender, age, and prior achievement, and this easily leads to skew in the number of wives or other benefits. As argued in essay 11, recorded history shows a recurrent alternation between low-skew and high-skew societies. The evolutionary game model presented in that essay concluded that neither type of society is long-term stable. Instead, there is an intermediate tipping point: if the fraction of skew-promoters in a cooperative society exceeds this value, it becomes increasingly optimal for everyone to switch. Similarly, in a society that is heavily skewed, if enough cooperators accumulate to exceed the tipping point, it becomes increasingly advantageous to cooperate. In both cooperative and skewed societies, there are mechanisms that can be invoked to discourage the accumulation of the opposite strategy. But if history is any guide, none of these are foolproof.

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