CONTENTS

1

The Nature of Life and Power

The central thesis of this book is that power is a universal attribute of life and that the history of life on Earth can be meaningfully and informatively interpreted as a history of power. This claim rests on two concepts—life and power—that are represented by common everyday words but whose precise meaning deserves careful scrutiny. It is therefore essential to specify how life differs from non-life, to explore the unique properties of living entities, and to define and characterize power in the context of life.

Most of us can recognize life when we encounter it, at least when it is in the form of plants and animals. Beyond these familiar versions, however, there is a vast diversity of microscopic life, to say nothing of extinct organisms. Individual living things range over twenty-one orders of magnitude in body mass and represent millions of distinct lineages, each the product of an unbroken line of descent from the origin of life 3.8 billion years ago to the present. Despite this almost incomprehensible variety, all life shares properties that distinguish it from non-life.

To encompass the diversity of life-forms, we need a definition of life that is descriptive, incorporating its unique properties while avoiding inferences about the processes and mechanisms that explain how life works. At its most basic, life comprises particles of matter that convert free energy, reactive carbon, and other substances into structure and activity, properties that are self-sustaining thanks to chemical cycles of renewal and to the potential for the particles to replicate using information encoded in the molecular sequences of polymers. Life is an emergent state of matter because its particles possess characteristics that their non-living components do not possess. As Stuart Kauffman notes, life obeys and is consistent with the laws of physics, but it obeys additional laws that are not reducible to them.

One of those emergent properties of living things is agency. By agency I mean activity, or doing something. Agency entails expending energy and time, that is, power. To many philosophers, the concept of agency implies intentionality, or awareness of action; but this is a narrowly human-centric view of a property that characterizes all life. Agents—living things that have agency—do things with or without conscious knowledge of what they are doing. The key to the idea of agency is that organisms affect themselves and their surroundings. In J. Scott Turner's apt words, life "makes the future happen." By converting energy and matter into activity, living entitles interact with each other and affect their own and others' environment, including resources. Bacteria can climb gradients of chemical concentration. Animals move toward more favorable conditions or away from danger. Plants and fungi grow in directions that afford greater access to resources, and vines' tendrils and growing tips actively move in search of supports. Many organisms expend energy to regulate and stabilize conditions inside the body, affording them a degree of autonomy from their surroundings. For many animals, including humans, agency can become intentional, involving deliberate action with a perceived goal and purpose. There is in fact a fine line between "unconscious" activity and purposeful intention.[1]

The concept of agency as I use it in this book has a long history dating back to Aristotle, if not further. Aristotle employed what he called *psuche* to name what we might label vitality, or the force of life, an attribute that inanimate matter lacks. Although he could not characterize *psuche* and made no predictions about his concept, it was obvious to him that living beings do things, an activity that in modern terms requires the application of power.[2]

Activity that makes the future happen requires that an organism perceive and respond to its surroundings. This engagement with the environment in turn is impossible without power. Most forms of sensation—vision and light perception, hearing and related perception of mechanical vibrations and other stimuli, chemical detection, and electrical sensation—depend on either the sender or the receiver, or both, to move or to generate a signal. Animals moving through water, for example, create disturbances in the surrounding medium that are detectable by other animals.[3]

Response likewise entails the deployment of power, often in the form of movement of part or all of an organism's body. The compound leaves of members of the pea family (Fabaceae), for example, change from a horizontal orientation during the day to a more vertical one at night thanks to the metabolic activity of pulvini, structures at the base of each leaflet. The leaves can fold within minutes of being mechanically touched, again because of power generated in the pulvini.[4] In many land plants, opening and closing of the stomates by guard cells on the leaf surface regulates gas exchange and transpiration, and is a metabolically active process that differs from the more passive opening and closing of stomates in other land plants. The understory herb *Elephantopus elatum* (Asteraceae) growing beneath pines in the Florida savanna has broad, ground-hugging leaves that use forces of up to 0.058 newtons to push grasses and other competitors away. Plants with the habit of producing a basal rosette of leaves are common, raising the possibility that such behavior against competitors is widespread.[5]

Agency also characterizes developments within organisms. Motile cilia orchestrate cell movements within the developing body of most organisms, and the twisting and curving that are the hallmarks of early ontogeny in many animals, reflect the action of mechanical forces. It is far beyond the scope of this book to explore these dynamic forces. Suffice it to say that curves and deformations of growing body parts as the parts interact with one another are universal features of organisms.

Whichever form it takes, agency provides the potential for a living thing to survive long enough to leave offspring. In other words, it is the means to achieve success, as indicated by survival and reproduction. Persistence and perpetuation, in turn, depend on performance, that is, on how well life translates resources into agency and agency into resources.

The phrase "how well" implies a comparison, in particular a comparison with the performance of other living things.

Put another way, performance is a measure of, or at least reflects, competitiveness. Polymers compete for their monomeric components in a prebiotic world; parts of the brain compete for space in the head; and organisms compete for all sorts of resources. Whenever there is more than one living particle or part of one tapping a resource, there is competition for that resource on a local scale. Trees compete with other plants for light, water, and nutrients, as well as with insects and mammals that eat their leaves. Lions vie with each other for prey and with hyenas that steal hard-won quarry, and with the parasites in their digestive systems that tap some of the nutrients acquired by the lions' efforts. Swallows compete for holes in cliffs or riverbanks, so that they can build nests where their eggs can develop and hatch in relative safety.

Animals that practice internal fertilization, in which one individual mates with another internally or in a controlled space where eggs and sperm meet outside the body, compete fiercely with, and choose among, potential partners. Flowering plants compete for pollinators, which act as surrogate vectors for sperm, by attracting them with nectar and other benefits. In its many forms, including working with others cooperatively and mutualistically as larger units, competition for locally scarce resources is a fundamental activity of living things.

The structure of organisms is to a large extent specified by their genomes, comprising molecular sequences (genes) of DNA and RNA that encode and regulate the formation of proteins, which in turn are long chains of amino acids. Whereas agency makes the future happen, the genome is a record of past success. Replication of genes inevitably introduces errors, which create genetic variation that in turn affects performance. As living things compete for locally scarce resources, some are better at it than others. They acquire more of the necessities of life, defend resources and their own bodies more effectively, and convert energy and matter into structure and activity so that survival and reproduction are more likely. Competition implies agency, but in self-replicating organisms its outcome is also affected by genes. For this reason, competition is the economic foundation of natural selection, the genes-based process that, through differential survival and reproduction, maintains or improves adaptation, the good fit between a living thing and its environment. Natural selection operates at the level of genes, but it is the whole organism that has agency, and it is the living whole that does or does not survive and reproduce. Natural selection therefore acts on the whole agent. Together with activity, natural selection is the basis of adaptive evolution—descent with adaptive modification—which is yet another fundamental property of living organisms. The good fit between an organism and its circumstances is thus the consequence of two distinct processes, natural selection and agency.[6]

It is important to make a distinction between evolution in general—descent with modification—and adaptive evolution. The former is a property of all systems, living as well as non-living. These systems change over time but not necessarily in adaptive ways and not necessarily involving replication. Galaxies, stars, climates, Earth's crust and atmosphere, and the universe as a whole can meaningfully be said to evolve, even in directions that are predictable, but they do not maintain or improve a good fit with, or accommodate, their environment. Adaptive evolution is therefore a property unique to life, arising from natural selection among replicators and from life's agency.[7]

To see how both agency and natural selection are necessary for adaptation, consider the case of camouflage, the close visual resemblance between an animal and its surroundings. The trait that makes the animal hard to see is controlled by genes, but if the animal found itself in an environment where the camouflage does not work, it will be quickly found and consumed by a predator. The animal must therefore use its agency to locate and remain in an environment where it will be least conspicuous to its enemies. This requires sensory capacity as well as mobility on the part of the animal. Although these traits are certainly also influenced by genes, their realization requires a combination of stimulus and suitable response or agency.

Adaptation is rarely if ever perfect. It persists because it works well enough under the circumstances, not because it is optimal. A visually cryptic moth on a tree trunk need not perfectly match its background, but it must fool a potential predator long enough to avoid being eaten.

An orchid flower need not precisely mimic a female wasp, but the resemblance must be good enough to entice a male wasp to visit, attempt to mate, and thereby pollinate the flower. There is thus always room for improvement, depending on how intense competition and natural selection are.

The more agency an organism has—that is, the more power it wields as it interacts with other life-forms—the greater is its capacity to influence and respond to its surroundings. Performance is power, and adaptive evolution is the long-term outcome of short-term interactions between living entities.

Watt Is Power?

The concept of power as used in this book has a specific meaning, one borrowed from physics and engineering: Power is energy per unit time, expressed in watts. Energy, or the molecule harnessing it in organisms, is a currency, or means of exchange. Raw materials necessary for the construction of living things, together with free energy, must be both available and accessible to organisms. Like money in human society, energy by itself has no value to a living entity unless it is spent, that is, unless it performs work. Without energy, nothing happens and nothing gets done. The value of energy—and money—lies in its being put to use, and that entails time and therefore power.

Power can be wielded not just by cells and individual organisms, but also by organized groups, ranging from populations and communities to ecosystems and the global biosphere. The potential to grow—still another trait common to living things though not unique to them—is one way, but not the only way, in which living entities at all scales of inclusion can increase their power. Whether that potential is realized, and whether power in general exhibits trends over time, depends on external circumstances, internal technology and innovation, and the feedbacks between what economists call supply and demand, or what an evolutionary biologist might call opportunity and constraint. I deal with these issues in chapter 2. How power and the factors controlling it change over time is the central question examined in this book.

Table 1.1. Equations for power and its components

Power: energy per unit time (watts)

$P = mv^2t^{-1} = md^2t^{-3}$

Energy: force times distance (joules)

$E = mv^2 = mad$

Force: mass times acceleration

$F = ma$

Symbols

a = acceleration, in meters per second squared
d = distance, in meters
m = mass, in kilograms
t = time, in seconds
v = velocity, in meters per second

The dimensions of power offer a guide to the many ways in which organisms can increase their power or diminish the power of others. The equations in table 1.1 express power in distinct but equivalent ways, each emphasizing a different variable that competition and natural selection can target. There are thus many pathways toward greater power and toward a denial of power, and living things have explored them all.

From the perspective of a living entity, then, power might increase because of greater mass (m), greater force (F), higher velocity (v), faster acceleration (a), greater distance traveled (d), larger area covered (A), and a shorter time (t) in which a given reaction or activity takes place. Moreover, living biomass can be divided among multiple entities; therefore, power can increase as the number of entities increases in a fixed space. Put another way, abundance of living things is a component of power at the group level.

Of all the dimensions of power, time is most important, because it appears with an exponent of negative 3 in equation 1 in the table, whereas other variables have exponents of 1 or 2. A change in time therefore has a greater effect on power than change in variables such as mass, area, distance, and velocity, in which time either does not appear at all (mass, area, and distance) or has an exponent of negative 1 or negative 2. In short, the dimensionality of power tells us which adaptive possibilities for increasing or thwarting power are available to competing life-forms.

An interesting example of how a plant manipulates the time and power of its insect adversaries comes from hairy leaves and stems. I had known for years that the hairs of many plants are oriented in such a way that they point toward the tip, or apex, of a leaf. In the same plant, hairs on the stem often point toward the ground. It occurred to me that one possible function of asymmetrical leaf hairs might be to direct the movements of a caterpillar or other insect toward the leaf's tip, so that the insect spends less time chewing the leaf as the plant shepherds the intruder off. Downward-pointing stem hairs, by contrast, discourage climbing insects from ascending the plant, increasing the time it would take a caterpillar or aphid to reach the palatable parts of the plant. In experiments with oats (*Avena barbata*) and the small caterpillar *Heliothus virescens,* we found that the insect crawled preferentially toward the leaf tip as expected from the apex-pointing hairs; but the larger caterpillar *Arctia virginalis* did not show this behavior.[8]

Different names are assigned to power according to which aspects of power are being measured and which kind of living entity is involved. For individual organisms, metabolic rate (the amount of energy acquired to deployed per unit time) or fitness (the number of offspring produced per unit time or over a lifetime) are suitable measures of power. For populations, ecosystems, or human-economic units, power might be expressed as productivity, the rate at which biomass (or economic activity) is produced per unit time. Other variations might include the rate of growth, the rate of predation, the rate at which the environment is being modified, and influence, the effect that one entity has on the activity of another. The important point is that all these measures have in common their expression in units of power. Performance is power; and energy is currency.

Life is a perpetual struggle against disruption and chaos. In its many manifestations, life can be thought of as an ordered concentration of power, a local and temporary violation of the increasing entropy that physicists assure us characterizes the universe as we know it.[9] Life flies in the face of static equilibrium; the greater its power, the farther from stability life strays. Moreover, as its collective power expands, the scale at which life concentrates power also increases, spreading its influence and, as I shall argue, diminishing the destructive effects of external disruptions.

The property of self-perpetuation sets life apart from non-life. The biosphere has persisted for at least 3.8 billion years despite great crises as well as profound environmental changes of life's own making. This is possible only if resource supply is regenerated. This regeneration involves cycles of production and consumption, implying a degree of cooperation among competing entities. The result is what we call an economy, or ecosystem, comprising entities that compete and collaborate, establishing relationships that stabilize and potentially increase the flow of material necessities. The power of global life derives from the feedbacks between resources and living entities and on the capacity to renew and replenish what is used up.

Where Do Agency and Power Come From?

Ultimately, all of life's agency derives from energy and raw materials from inorganic sources. In the simplest case, energy is taken up passively, and work is accomplished with minimal effort by the organism. The ascent of water from the roots through the stem to the leaves of plants, for example, is due to transpiration, the loss of water vapor through pores (stomates) in the leaves. This is an inevitable consequence of photosynthesis.[10] Passive filter-feeders such as sea lilies (crinoid echinoderms) extend their food-collecting structures so that they intercept food-laden water currents.[11] Evaporation and the resulting air flow beneath the cap of a mushroom are responsible for catapulting spores, which are on average 10 micrometers in diameter, away from the mushroom.[12] Seeds with extended hairs, feathery plumes, or stiff wings disperse passively in the wind. Many plants rely on the wind to disperse spores or pollen.[13] One of the few examples of wind as the motive agency for animals comes from the pelagic hydrozoan *Velella,* which floats and moves over the ocean surface with the aid of a sail.[14] Most seaweeds, which must acquire nutrients passively from the surrounding water, grow more quickly in wave-swept environments, because they intercept more water per unit time than they would under calm conditions.[15]

A particularly intriguing example of harnessing the wind to adaptive ends is furnished by poplars and aspens, trees of the genus *Populus*. Their vertically held leaves tremble in the slightest breeze, collectively making a very characteristic hissing sound that can be heard at a distance of tens of meters from the tree. As the leaves flutter in the wind, their smooth surfaces cause small insects to lose their grip and fall to the ground.[16] I have wondered whether a similar antiherbivore effect might explain the clattering sound that the fronds of coconut palms (*Cocos nucifera*) make in the wind. In Dutch, the coconut palm is known as the klapperboom, an apt description. One problem with using power from wind or water currents is that it cannot easily be stored. For effective use, it must be reliable, reasonably consistent, and not so intense that organisms are swept away in uncontrolled ways.

These examples make clear that, even when the acquisition of resources is passive, organisms must nonetheless put energy into the appropriate structure, molecular machinery, and physiology to take advantage of those resources. This investment requires metabolism, a universal capacity of living things that entails the ability to harness external sources, store them in molecules as chemical energy (mostly chlorophyll and adenosine triphosphate, or ATP), and release them in a controlled way. The rate of metabolism—a measure of power—affects how much force, work, and power an organism can produce. The energy content of an organism is that organism's energy budget; the rate of metabolism, or perhaps more accurately the metabolic scope, is the organism's power budget. By scope I mean the difference between the basal metabolic rate, the rate of energy use when the organism is at rest and not engaged in strenuous or expensive activity, and the maximum rate, which can be achieved for short periods of intense activity. For this reason and for others, an individual's metabolic rate is not constant; it varies according to life stage, time of day, temperature, and frequency and intensity of costly activity. Most organisms exercise substantial internal control over metabolism, just as they do over such other functions as growth, locomotion, digestion, respiration, and reproduction.[17]

Movement of part or all of the body is a widespread way in which organisms exert power. It involves motors: the molecules that drive stiff flagella in bacteria, cilia in animals and single-celled protistans, contractile muscles in animals, and the pulvini of plants. Scientists working at the intersection of biology and physics have discovered surprising regularities in the scaling of power and force of motors with mass, either of the motor itself or of the body it powers. Maximum speed of locomotion, for example, scales with body mass to the 1/6 power, regardless of whether the moving structure is an animal or a human-made vehicle weighing less than 35,000 kilograms. Organisms ranging over nineteen orders of magnitude in body mass have maximum speeds averaging ten body lengths per second, all else being equal.[18]

These scaling relationships reflect central tendencies, but they obscure large variations. To a physicist, these variations might simply reflect unwanted noise, but to an evolutionary biologist they indicate that organisms have considerable adaptive scope. In other words, the regularities are not so strict that they constrain the adaptive options available to organisms faced with particular challenges. The variations in actual force and power therefore show how basic rules can be bent or even broken in the course of adaptive evolution.

An example will illustrate the importance of variation. As I noted earlier, organisms ranging from bacteria to large vertebrates have average maximum speeds of ten body lengths per second, measured at activity temperatures typical for these organisms. Some heat-loving archaea—microorganisms that have evolved separately from bacteria at the prokaryote level of organization—have maximum speeds of 400–500 body lengths per second, propelled by flagellum-like structures called archaella.[19] These minute specks of life are thus the fastest known organisms, at least by this metric. Absolute speeds are slow, but in a world where movement of tiny organisms is dominated by viscous forces, they are remarkable.

As generators of power, motors in highly mobile animals can take up a large fraction of body mass. In tropical butterflies that are highly palatable to birds, for example, there is a premium on rapid, erratic flight to avoid being caught by the faster birds. These butterflies devote almost half of their body mass to flight muscles.[20] Pacific salmon of the genus *Oncorhynchus* weighing 0.22 kilograms and capable of burst speeds of six meters per second have 0.1 kilograms of swimming muscle mass, or almost 60% of body mass.[21] These percentages do not include the motors responsible for supplying the muscles with oxygen—in the cases discussed, the heart—or the metabolic costs associated with the brain, which must coordinate sensory and motor functions.

Energy storage in organs dedicated to that function is key to the projection of power in many organisms. Often this is in the form of chemical energy, which can be tapped during times when resources or external energy are scarce. Plant bulbs, tubers, above-ground succulent stems, and seeds rich in oil or starch are familiar examples. Fat reserves enable bears and ground squirrels to hibernate during long winters at Arctic latitudes and enable birds to migrate between wintering and breeding grounds. Bird chicks have access to abundant yolk and albumen inside the egg before they hatch.

Energy can also be built up slowly and stored as potential energy in mechanical devices such as springs before it is released in enormous bursts of power by tripping a latch. Such mechanisms are thus power amplifiers by which organisms, as well as many human-made devices, can generate huge forces, velocities, and accelerations over extremely brief time intervals.[22]

Spectacular examples come from plants that hurl their seeds away from the parent as the fruit holding the seeds fractures explosively. In the herb *Cardamine hirsuta*, a member of the cabbage family (Brassicaceae), the two-valved fruit (technically a silicle) springs open as the valves separate, releasing the seeds at speeds of more than ten meters per second over an interval of three milliseconds, enabling the seeds to travel a distance of about two meters. The stored energy that makes this release possible is due to metabolically generated turgor pressure in the valves, aided by various modifications at the cellular and structural levels in the valve walls.[23] In Panama, the tree *Hura crepitans* (Euphorbiaceae) uses similar mechanisms of explosive fracture to propel its seeds at a speed of seventy meters per second when pressures in the pod exceed ten atmospheres.[24] The spitting cucumber *Ecballium elaterium*

(Cucurbitaceae) and dwarf mistletoe *Arceuthobium* sp. (Loranthaceae) pressurize their fruits osmotically. At a critical pressure, the fruit releases a jet of liquid and mucilage-covered seeds, aided in the case of the mistletoe by metabolic heating of the fruit.[25]

Many small animals also apply amplified power to execute lightning-fast motion. The planthopper *Engela minuta* (Dictyophoridae) weighs about twenty milligrams and is less than one centimeter long, but its long hind limbs release a spring that allows the insect to jump with a velocity of 5.5 meters per second within just 1.2 millisecond.[26] Using a hammer-like finger on one of its mouth appendages, the tropical mantis shrimp (stomatopod) *Odontodactylus scyllarus* smashes the shells of prey snails with a force of up to fifteen hundred newtons at a speed as high as twenty-three meters per second once enough energy has accumulated for release by the fifteen-centimeter-long animal.[27]

A species of *Dulichiella*, a tiny amphipod crustacean found among seaweeds in North Carolina, sports an enormous claw in the male, averaging 30% of the animal's mass. This claw releases a latch so that it can close the one-millimeter-long, 184-micrometer-thick, movable finger of its claw to reach a velocity of 1.7 meters per second in as little as fifty microseconds. Although the function of this extraordinary snap is unknown, the fact that males but not females have the enlarged claw indicates a role in sexual selection, although defense also remains a possibility.[28]

At the high end of behavioral sophistication, some animals resort to storing resources outside the body. Jays, squirrels, and many smaller rodents cache seeds and nuts, and some desert ants store vast quantities of seeds underground. Bees make and store honey. A truly extreme form of external storage is agriculture, in which animals grow fungi or, in the case of humans, plant crops. I return to these remarkable enhancements later in the book.

Why Be More Powerful?

The advantages of wielding more power are obvious and universal. In the short term, powerful agents have greater access to resources and are in a better position to survive under circumstances favorable to them, in part because they are not as threatened and constrained by rivals as are weaker agents. Dangerous and powerful predators, from octopuses and sharks to eagles and wolves, can freely roam uncluttered environments where prey are most abundant and vulnerable. Less powerful competitors are relegated to times and places where resources are less plentiful or accessible. Even for these weaker agents, however, there is an advantage to being as powerful as circumstances, including their superior competitors, allow.[29]

In competition there are always winners and losers in the sense that one party gains more or loses less power than the other. Despite this universal inequality, both parties incur costs. Predation, for example, in which one of the competitors eats part or all of another organism, is potentially expensive for the predator, which must expend power to locate, catch, and subdue its prey. The prey often survives such attempts, owing in part to its costly antipredatory adaptations. In our laboratory trials with the shell-breaking, sand-burrowing crab *Calappa hepatica* in Guam, for example, we found that more than 90% of attacks on well-armored marine snails were unsuccessful, allowing the prey to survive and to repair the shell damage inflicted by the powerful pincers of the crab.[30] All the prey species have specific crab-resistant shell features such as a narrow opening, crack-stopping ribs, and a high spire so that the head and foot can withdraw so deeply into the shell that the predator cannot reach them.

A broad survey of predators ranging from sea stars and planktonic copepods to spiders, snakes, and lions revealed that attackers almost never had a 100% success rate under field conditions. Often these predators would be effective at detecting prey, or catching mobile animals, or subduing dangerous or well-armored prey, but never in all phases of an attack. The cost of failure for predators can therefore be high, although on average not as high as for the prey that are successfully killed.[31]

Another dramatic example of the high cost of being a strong competitor comes from trees. In order to compete for light, trees must grow into the canopy, where sunlight is most plentiful. Given that a canopy already exists and that young trees typically begin life near the ground, the great height necessary to reach the canopy requires wood. In tropical forests, each hectare supports about three hundred tons of plant biomass, of which about 97.3% is wood.[32] Although this is an average based on hundreds of species, including lianas with less wood, the extraordinary allocation of trees' resources to the production of inert wood illustrates the very high cost of being a vigorous competitor in one of the world's most productive ecosystems. Understory plants that are much less productive cannot hope to match such investments.

The inequality of power between competitors has profound implications for adaptive evolution. Given that winners are more powerful than losers, there is a fundamental imbalance in agency and natural selection between the winning and losing sides. Winners have a greater evolutionary effect on losers than losers do on the winners. For predators, this means that competitors for prey exert greater influence on the characteristics and distribution of these predators than do the prey. The sharp claws of lions, for example, are effective weapons for capturing and subduing prey, but selection for sharper claws may be due to competition with hyenas, vultures, and other lions rather than to the defensive strategies of the lion's mammalian prey.[33] This asymmetry of power can be reduced but not eliminated by prey that pose a real danger to their potential predators, as occurs when the prey are venomous, toxic, or aggressive.[34]

This effect, where the more powerful agents have greater influence on the characteristics and distribution of organisms than the less powerful, results in the evolutionary process I call escalation. The idea is that enemies have greater agency and exert more intense selection than victims. It is this enemy-directed adaptive evolution that is responsible for the relentless and pervasive selection for as much power as individuals and populations can sustain.[35]

An instructive example of costs associated with competition and escalation comes from adaptive tail loss in geckos. Like many other lizards, the geckos *Mediodactylus kotschyi* and *Hemidactylus turcicus* from islands and mainland habitats in the Mediterranean region shed (or autotomize) their tails in response to danger. Autotomy enables lizards to escape despite the costs of reduced locomotion that the loss and subsequent regeneration of the tail incurs. Predatory vipers are important agents favoring autotomy, but on islands the primary culprits are members of the same gecko species.[36] Both predators and competitors of the geckos thus elicit expensive adaptations even when the target geckos are not competitive winners.

As long as there are safe places for potential victims, or limits to power of the victors, the outcomes of competition allow both parties to maintain or increase their power through adaptive evolution. There is, however, one important exception to this generality, a case where one side has evolved so much power that the victims' adaptive options disappear. I finally became aware of this possibility after the archaeologist Curtis Marean approached me with a question: why do South African shell middens, which represent the remains of early human marine shellfish diets, show a trend toward smaller shell sizes from lower to higher levels in the middens? It occurred to me that humans are unusual among animals in targeting large prey individuals of species that we hunt, fish, and gather. Reams of data show that people select larger prey over smaller ones.[37] The consequence of this deliberate selection is that the protective and competitive benefits that come with large size are effectively eliminated, leaving almost no scope for adaptation of the prey in response to us as predators. The only remaining option, which has in fact been widely adopted by heavily exploited fish species, is to mature as smaller adult sizes and to reproduce at an earlier age. This trend leads to lower per-capita fecundity, a problem exacerbated by laws that prescribe minimum sizes for harvesting. The same principle applies to the limpets, mussels, turban snails, and other shellfish in those South African middens, and to the harvesting of shore animals worldwide.[38]

This human example exposes an important point about the limits of power. In part thanks to technology and our social nature, we humans have wielded more individual and collective power than any other living or extinct species. Other top competitors have by comparison exerted limited power. This constraint, imposed by diffuse regulation from many species, permits all players to adapt regardless of their competitive status.

I shall leave the question about how humans were able to achieve such unprecedented power until later in the book, but one widespread agency that might have contributed at least to the early ascent of power in humans as well as in many other animals is mate choice. Sexual selection associated with mate choice has led to all manner of extravagant behaviors and bizarre traits, which serve to advertise to, coerce, attract, and control potential mates.[39] I suggest that selection for greater power is amplified in species in which competition for mates is important. The antics and displays are very costly, as the example of the fast-closing and very powerful claw of the small amphipod discussed earlier demonstrates. Such extreme investment indicates that individuals engaging in mate competition have power to spare and, insofar as it confers an advantage in reproduction, it indicates intense selection for greater power. The development of potent weapons like horns, antlers, and claws in animals or large showy flowers in plants testifies to the generality of these advantages in organisms engaged in mate competition.[40]

The hypothesis that mating-related displays indicate overall vigor and "good genes" has long been popular among scientists who study animal behavior.[41] Richard Prum disputes the idea that ornaments related to sexual selection are "honest" signals of overall fitness, presumably because, in his view, survival and fecundity would be higher in their absence.[42] This criticism, however, is beside the point. If displays result in mating, that is what matters, regardless of expense and what might have been. In short, the behaviors and ornaments work. They amplify activity and selection for individual power. In fact, I would turn the "good-genes" hypothesis on its head: It is mate selection and mate competition that indirectly also favor traits that expand power in other aspects of an individual's life.

This argument applies with equal force to plants. In order to attract mates, flowering plants must invest heavily in nectar and other rewards for obtaining the services of faithful pollinators. Such requirements might make selection for greater power imposed by herbivores and by neighboring plant competitors more intense. In this connection it is no accident that high rates of photosynthesis, elaborate mobile chemical defenses such as latex, and the active opening and closing of stomates and of leaves in response to environmental conditions characterize flowering plants but not other plant groups. The idea is that mate competition—in this case for pollinators—favors the increased scope for power that higher rates of production and greater investment in defense provide.

In short, selection for greater power is extremely widespread. Great power may be reserved for the tiny minority of top competitors, but the benefits of power accrue to any organism that has agency. Lineages of losers may initially decrease in power as they become specialized to live in places where organisms are relatively safe from powerful rivals and where resource supply is limited. Once they have adapted to these low-powered modes of life, however, organisms like parasites, cave-dwellers, deep-sea animals, and understory forest herbs must wield as much power as circumstances warrant because they must confront enemies even under these safer surroundings. Indeed, as I shall show in later chapters, innovations in these initially safe environments can enable some lineages to gain enough power that they make these habitats more competitive. Selection for greater power is relentless and universal. It may be more intense for some lineages than for others, and most lineages never achieve the status of top competitor, but power is the ultimate evolutionary aphrodisiac.

INDEX