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INTRODUCTION

The World of Animal Motion

When I met my wife for the first time, she brought along a brown toy poodle named Jerry. He was a Valentine's gift from her ex-boyfriend, and he proved the perfect subject for my next scientific experiment. I spent a great deal of time putting sticky notes on Jerry's fur and filming him with a high-speed camera. Jerry did not like his stickers very much and tried to bite them off. If the stickers were on the top of his head or neck, he had another method to remove them. He shook his body and head back and forth several times, making me take a step back (Plate 1). His brown curls flew, sending dust and fleas in every direction, along with my stickers. This neat little trick, called the wet-dog shake, looked like a silly, useless act.

As I analyzed the high-speed films, I learned that Jerry's shake generated accelerations up to 12 times earth's gravity, higher than the acceleration of a Formula One race car as it turns a corner. When I gave Jerry a bath, I found his shake could remove up to 70 percent of the water contained in his fur. It took only a fraction of a second, whereas our laundry machines take minutes to perform comparably. How is the wet-dog shake so effective?

My student Andrew Dickerson and I built a wet-dog simulator, a rotating column that spun a clipping of Jerry's fur at the same rates we observed. A camera was attached to the spinning frame so we could see drops releasing from patches of fur as it was spun. It was like we had a front-row seat to the water ejection process. On our wet-dog simulator, 12 times earth's gravity was the minimal acceleration to remove the smallest drops from the fur. This regime exactly coincided with the acceleration that Jerry was generating.

To find out if Jerry was alone in his ability to shake water, I scoured Atlanta for the biggest range of animals I could find, taking trips to laboratories on campus, the local park, and the Atlanta Zoo. Over the course of the next few years, the zoo would grow accustomed to strange research requests, such as, "Can we come film your pandas shaking off water?" Ultimately, we gathered high-speed films of animals across a 10,000-fold range in body mass, from a mouse to a bear. Bears shake at four times per second, dogs at four to seven times per second, rats at 18 times per second, and mice at a dizzying 29 times per second. The blink of a human eye would miss over 10 shakes of a mouse. Why do smaller animals shake more times per second? A smaller animals has a smaller radius, which causes it to generate less centripetal force. In order to generate the same drop-releasing forces as a larger animal, it must spin faster.

Jerry's owner brought me a lifetime of love and two wonderful children, who later would also become unknowing subjects in my experiments. I'll tell you more about our adventures in the coming chapters. But I give credit to Jerry the brown toy poodle for buying me a ticket to my scientific obsession, the world of animal motion.

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Animals may look quite different, but they share one thing in common: they must move in order to survive. Movement evolved for a simple reason: the requirement for energy. It is one of the things that distinguishes animals from plants, which are generally sedentary. Plants are known as *autotrophs*, or self-nourishing, because they make their own food using sunlight. For them, large-scale movement is unnecessary, except for reproduction. In comparison, animals are *heterotrophs*, and obtain their energy by continually seeking out and consuming food. Plant-eaters move to forage, and predators move to give chase. Be it predator or prey, fast and responsive movements are one way to avoid being eaten. Yet, the more energy they expend moving, the more animals need to eat, to replenish their energy supply. Thus, animals often push the envelope in terms of speed, economy, and maneuverability.

Animal movement also involves navigating a variety of environments. It's easy to forget how difficult it is to deal with natural environments. We fly over them with ease in our airplanes, or drive miles and miles without a second thought. In contrast, consider the pigeon. A pigeon flying from A to B might encounter vortices or other turbulence in the air that can blow it off its intended course. The air it flies through is filled with obstacles such as the branches of a tree, which themselves might be rattled back and forth by the wind. You might think that such difficulties are specific to air travel, but animals on the ground have it just as hard. A salamander traveling from A to B might encounter twigs, forest litter, or mud on its way. It may even have to transition amphibiously from land to water in order to lay its eggs in a wet environment.

A changing world creates changing conditions for animals as they move. Animal movement must change from night to day, and from season to season. Animals face rain, sleet, and snow. Starting in spring, bees gather pollen, and they can become completely covered in it, as they go from flower to flower. In addition to being covered by inanimate materials, animals must deal with crowding by fellow members of their species. Consider a dense flock of pigeons or a school of fish: like us, they face traffic jams on the search for food.

Although moving from A to B is important, another type of movement occurs on a smaller scale, and is equally important for survival. Animals transport matter into and out of themselves, a critical part of eating and waste production. We don't often think about such movements because we live in a built world, having designed tools like spoons and shovels to transport matter. In nature, animals manipulate matter with their own body parts. A dog laps water using its soft tongue and an elephant picks up fruit using its long flexible trunk. Animals live in a world of parasites, such as ticks and fleas, and grooming can be a matter of life and death. One way to combat these parasites is through animal movement, often with body parts. The cat tongue is like a hairbrush, but it is also much more. It is covered in an array of sharp spikes containing a U-shaped cavity at the tip that can spontaneously imbibe saliva and release it on contact with the individual hairs that it encounters.

Animal motion is all around us. It is the principal way animals get things done in the world. How did such a diversity of animal movements come about?

The variety of animal motion is made possible by a single common thread, evolution. Evolution functions as a deceptively simple but powerful algorithm. Organisms reproduce, making imperfect copies of themselves—that is, offspring that are different from their parents. If some of this variation improves an organism's ability to survive or reproduce, and if this variation can be passed on to that organism's offspring, then over time the population will evolve and adapt. It's a simple idea, yet few imagine the sheer variety evolution has created over the 3.5 billion years it has been at work.

All types of animal movement, no matter how bizarre, emerged through the process of evolution. Walking on water is one fascinating example. Insects evolved around 400 million years ago, and 300 million years later, terrestrial insects and spiders began to colonize the water surface. This migration helped them to avoid predators, to find new sources of food and safe places to hatch their young. The most primitive surviving water-walkers, the *Velia* or water treaders, look quite similar to the bugs from which they evolved. Like many land insects, they use their six legs to walk in a manner similar to an ant, on the tips of their feet. This motion is not very effective on water, and they move frantically and with little progress, as if perpetually slipping on ice. Moreover, their slow gait restricts them to being close to shore. These primitive water-walkers inhabit shallows where duckweed and other emerging vegetation gives them areas to climb onto for safety.

Over time, the middle legs of the water-walkers evolved to be longer, conferring on the water-walkers a distinct advantage over walking on the tips of their feet. Eventually their legs became so long that they could act like oars. This new species, called the water strider, can row like a rowboat, balancing on its remaining legs as pontoons for support. It's a highly effective gait, and such insects are nearly impossible to catch by hand. In turn, the water striders became so specialized at moving on the water surface that they move slowly on land, awkwardly dragging their canoe-like legs behind them. There is no turning back for the water striders. The water surface has become their permanent home.

Invertebrates were not alone in evolving the ability to walk on water. The Jesus Christ lizard, or basilisk lizard, is green with white dots, and large yellow eyes. It moves like a normal lizard except that it can run on water in short bursts if frightened. It has long fringed toes that it uses to slap the water surface and support its weight. Similarly, the western grebe, a black and white bird with red eyes, also runs on water, despite weighing up to ten times as much as a basilisk lizard. In elaborate mating displays called "rushing," males run across water distances up to 50 meters in order to attract females. Even after mates are selected, male and female birds will run across water together to reinforce pair bonding. Both the lizards and the birds are constrained by their evolutionary origins. While the smallest vertebrates are insect-sized, the basilisk lizards and western grebes have internal bones, making them too large and heavy to walk on water effortlessly like water striders, which have exoskeletons.

Humans cannot overcome their evolutionary origins either: our feet are simply too small to support our weight upon the water surface. Leonardo da Vinci conceived of kayak-sized floats that could be worn on one's feet. With the aid of poles with floats at their tips, one could carefully cross-country ski on water. Even with the aid of such tools, however, we could never run across water like the basilisk lizard. Our muscles simply do not generate enough power to push the water fast enough to support our weight. Evolution is both a blessing and a curse: it causes many animals to specialize their locomotion in particular media, such as air, land, or water. Evolution, for example, has made us extremely energy-conserving when walking on land, but quite awkward when walking on water. Water striders have the opposite problem—elegant on water, and clumsy on land.

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The study of animal motion is not new—in fact it has at least a four-hundred-year history. Questions about animal propulsion were around long before we had the equipment to carefully study them. One of the first to ask these questions was Leonardo da Vinci, who dissected animals and humans in secret. Leonardo's sketchbooks are filled with equal parts drills and helicopters and anatomical drawings of animals, as if they too were machines. At the time, many people believed in vitalism, that living things had a soul, which had never been observed or measured, yet made them inherently alive. In contrast, Leonardo took a logical rather than mysterious view of the world. His big idea was that the scientific method could make sense of anything around him, no matter how mysterious.

A book that is credited with drawing mathematicians and non-biologists to animal motion was *On Growth and Form*, written in 1915, but delayed in publication till 1917 due to the First World War. Its author was D'Arcy Thompson, a Scottish biologist and pioneer of mathematical biology. His thesis was that biologists had not sufficiently emphasized the influence of mechanics and physical laws on the shapes and growth of organisms. His book provided mathematical descriptions of the shape of fish, birds, and mammals. The book was flawed because Thompson had not accepted Darwin's theory of natural selection. Nevertheless, it inspired generations of artists and scientists to cross disciplines, to begin using mathematics to describe the shapes of animals. A new take on animal morphology began, where biologists used mathematics to describe the shape of animals such as fish, which evolved into shapes as different as an elongated pike and a flat flounder. Describing these shapes was an important first step to understanding animal motion because the shapes of animals greatly influence the forces they feel and create as they move through fluids.

Biologists continued to use mechanics, giving rise to a new discipline called *biomechanics*. Cambridge zoologist Sir James Gray is arguably the father of modern biomechanics, the study of the physics of animal movement and shape. Today, biomechanics is not as clear-cut an area as it was then, as it now intersects with studies of microscopic things such as the biophysics of the cell and with human-centered topics such as exercise physiology. But for the purpose of this book, the biomechanics of animals is a field that indeed began with Gray. In the 1930s, Gray conducted the first studies of the swimming of fish and dolphins. In calculating the power that a dolphin would need to swim, he came to the startling conclusion that dolphins should not be able to swim. This controversy, which became known as Gray's Paradox, continued to draw non-biologists to the study of animal motion. It drew mathematicians, such as Sir James Lighthill, who were interested in understanding the body motions that made fish swim quickly or with low energy use.

The study of animal motion was energized by the advent of technology that enabled sharper images of animals. In the 1930s, electrical engineer Harold Edgerton popularized the use of strobe photography to capture high-speed motion. Decades later the commercialization of computers led to the use of high-speed cameras and computer algorithms that could automatically track fish and the fluid flows behind them. The digital era led to further progress in robotics, and new manufacturing technologies like 3D printing. The latter is an especially important tool that is becoming widespread among scientists studying animal movement. We will discuss 3D printing in the context of artificial shark scales in Chapter 4.

Today, the gradual merging of scientific disciplines has been a key part of progress in animal motion research. Fluid mechanics students eagerly take courses in fish anatomy. Roboticists designing robotic climbers read the classical work of German physiologists who first studied how insects grip surfaces. Material scientists bring biomaterials like oyster shells into their labs to crush them and examine them with microscopes. In many ways, biological techniques and practices are becoming more widely accepted and of greater interest to other fields. These fields in turn are infusing biology with new ideas and high-tech tools, leading to ways of doing science that were not possible just twenty years ago. In my mind, this marks a turning point in how animal motion is studied.

The goal of this book is to introduce readers to the world of animal movement and to the scientists who study it. I pay particular attention to key concepts that scientists use to understand the diversity of animal movement, showing that just a few physical concepts can give an intuitive understanding of a number of animal shapes and movements. Along the way, I hope to show that studying animal movement will lead to solutions to difficult problems of societal importance, such as designing more effective propellers or building robots to care for the elderly.

Most books on animal movement characterize animals according to the media that they live in, such as air, water, or land. Others separate animals into gait types such as walking, jumping, swimming, or flying. I've avoided these approaches, and instead focus on the broad physical principles at work. By focusing on principles, I can group seemingly disparate animals together. This is the rationale behind grouping sharks and eyelashes together in Chapter 4: they both involve fine surface textures that affect flows. Focusing on physical principles allows me to group animals and robots together. This is the rationale for putting walking robots and swimming fish together in Chapter 5: they both transfer energy in ways that reduce their energy use in propulsion. Another way to say this is that they have high fuel economy or gas mileage. However, I will avoid using the word “efficiency” in this text because engineers considering efficiency to only be non-zero if an animal is climbing a hill. Only then is an animal doing work against a force, in this case gravity. Going on flat ground at constant speed can’t be described by efficiency because it doesn’t actually require doing any work. Although this idea may be against your intuition, I will discuss how Newton’s laws make it the case in Chapter 5. I believe a focus on principles rather than appearance will lead to thinking about animals in new and useful ways.

As you will see, this book is heavily focused on fluid mechanics, the physics of fluid motion such as the motion of air and water. Water constitutes more than 70 percent of the surface of our planet. As a result, a good number of animals have adapted to move through it. At the same time, many animals are composed of 70 percent water and must consume water on a daily basis. As a result, animals possess a number of internal bodily processes to facilitate the motion of fluids on their insides. Animals produce fluids such as saliva to moisten their food, or urine to excrete wastes. We’ll discuss urination in Chapter 3 when we talk certain body and organ shapes that are effective at driving fluid flow.

I have also structured this book such that each chapter focuses on the stories of several key scientists. My goal is to convey the scientific process as if it were a mystery story. When I was younger, I loved reading mystery books by Agatha Christie because I could follow her logic as she presented the details of each case. I also enjoyed reading about the strange characters that brought the case to life. As we follow the scientists, we'll encounter a number of characters. Sometimes these characters are the machines the scientists are working with, the wind tunnels and high-speed cameras. Other times, they are the team that is at work, with members from biology, engineering, and physics. I've done my best to showcase the team effort that is necessary to make science happen, but I often leave the spotlight on the main character for the sake of story. I've chosen studies that were done early in a scientist's career, so you can see what it's like to embark on new territory. Since I've featured studies published in the years 2000 to 2018, a good number of these scientists may still be actively working, depending on when you are reading this book. Of course, no book on animal movement would be complete without the animals themselves, which are sometimes not so cooperative in revealing their secrets.

American astronomer Carl Sagan once said, "Science is a way of thinking much more than it is a body of knowledge." I hope that by following the journeys of a few select scientists, I can convey how they approach problems in animal motion. The details of this journey and the moment of discovery are often not contained in the scientists' journal papers, which are cited in the bibliography. Instead, I came upon the material over a series of interviews I conducted with the scientists from 2015 to 2017. Moreover, all the material in this book has been read and verified by the featured scientists themselves. For them, the scientific process involves a number of key steps. They conceive of the idea that they want to test, and work to hone their idea into a well-defined question. Then they design and perform an experiment that answers this question. When possible, they follow up by building a device that tests the original concept. Headway is made by a combination of logical thinking, help from team members, hard work, and serendipity. How much of their success in making discoveries is indeed luck? The answer is, less than you would think. Louis Pasteur said, "In the fields of observation, chance favors only the prepared mind." I try to slow down the moment of discovery as much as possible, so that you can see the logical steps that led to this aha! moment. This moment of discovery is not so much a moment of genius, but a series of logical steps that led to a conclusion.

In this book, and in the field of animal movement, we take a departure from much modern biology, which is focused on cellular and molecular science and model organisms, such as yeast, fruit flies, and mice. These animals are used because much is known about them, making tightly controlled studies possible. In contrast, scientists in this book study animals for the opposite reason, because so little is known about them. The flying snake must be captured in the rain forests of Singapore, the humble cockroach must be raised in the lab and fed like a pet. Be it an obscure animal or a disgusting one, these animals can reveal physical principles that can lead to broader claims about movement, relevant not just to animals but also to robots.

The word *robota*—in Czech, literally, “forced laborer”—was introduced in 1920 by Czech playwright Karel Čapek. Since the computer era, the field of robotics has expanded rapidly, and has been tasked with working beyond the factory floor. Automation is particularly difficult on rugged terrain, which covers much of our planet. Even the insides of our houses are filled with a variety of terrain, including carpet, hardwood floors, piles of clothes, and children’s toys. These places are too unpredictable, too ridden with obstacles for wheels to work. Instead, some believe a legged robot might be the best strategy for movement. And if we are looking to legs, studies of animals can be of great use.

Studying animals can also teach us about the importance of body size, which can in turn influence how we design machines. In physics, bigger is different. As animals grow, certain forces that were previously negligible become important. For example, large animals simply cannot afford to fall down because they will be easily hurt. But as animals get smaller, their bones appear to be effectively stronger due to the physics of scaling. This is why fleas can jump 120 times their body length without being injured. Such invincibility at small sizes gives small animals a wider range of behaviors. Small animals are naturally more robust, so much so that they regularly crash into objects without damage. These fundamental issues of animal movement apply to machines as well. By understanding how animals of different sizes move differently, we can gain intuition into how to design machines of different size.

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I start this book with my own beginning in the study of animal motion, investigating how insects can walk on water, the subject of my doctoral thesis. For this book, this seemed like a good place to start because such insects are so common. Across ponds, lakes, and streams, they leisurely stand on the water surface. We don't give them a second thought, but clearly they are a feat of nature. To understand the water striders, I learned to use a high-speed camera, a tool important to the study of animal movement that captures movements too fast for the human eye to see. I'll introduce the concept of surface tension, a tendency of a fluid surface to minimize its surface area. Surface tension is responsible for forming the shape of a water drop and supporting an insect's weight as it walks on water. I'll also introduce the concept of surface texture, in examining the hairy coating on the water strider's legs that makes the water strider water-repellent. Along the way to understanding these insects, I met a talented mechanical engineer, who built a robotic water strider. Chapter 1 sets the stage for the rest of the book in that it begins with a simple question about animal movement, and finishes with a proof-of-concept, here the construction of a device that can walk on water. It also shows how welcoming the field of animal motion can be to those with no training in biology.

Chapter 2 begins after my doctoral thesis, when I went to New York City to spend my postdoctoral years studying the motion of snakes. There, I learned about how solid surfaces can interact with each other in surprising ways. It is this frictional interaction that permits a snake to slither effortlessly over carpet and other seemingly uniform surfaces. Other animals can slither through sand and soil, as if they are swimming through water. I placed this chapter after walking on water because moving through soil is just as incredible as walking on water. It takes us hours to dig a hole in soil just a few feet deep. However, animals with long, streamlined bodies can easily dive down through sand. In this chapter, we will also learn about another tool, X-ray high-speed video, that can image animals underground.

One of the important concepts in Chapter 2 is the idea of optimality, that certain body shapes are well suited for moving through a particular medium. This streamlined body shape makes motion through sand and mud possible. In Chapter 3, we dig deeper into optimality, discussing three animals with particular body shapes that are best for performing some desired function. Of course, the process of evolution is not goal-directed, and animals carry with them a number of constraints that make it impossible to achieve perfection, also known as a *global optimum*. However, in the examples presented, we find that animals are good at dealing with the cards that they have been dealt.

Now that we have zoomed out and looked at the broad form of animals, it's time to zoom back in, to the world of the small, in Chapter 4. We are not accustomed to looking at small features on large objects. For instance, a car's shape is recognizable, but how often do we hold a magnifying glass to its surface? This is where nature departs from the built world. An animal grows by the reproduction of individual cells, which generates not just the animal's overall shape, but also intricate patterns on its surface. Growth is how a shark develops the fine scales on its surface, and how you grow eyelashes to protect your eyes. I'll talk about the hydrodynamic properties of each of these fine structures.

One of the drivers of animal motion is the need to move with the highest fuel economy possible, to save energy for other activities. Escape strategies, on the other hand, have a different need: speed, as in the fast escape stroke of the water strider or the C-start, the snapping of a fish's body like a whip when it is startled. These body motions, like sprints, involve high accelerations that rapidly convert fluid motion into heat. Nevertheless, being economical is important for any animal that must travel long distances. In Chapter 5, I discuss animals that can move using very little energy. I will introduce the concept of *energy transfer*, which is the main way that animals reduce their energy consumption. We do the same when we walk: our legs act like pendulums that transfer energy from gravitational to kinetic energy. Fish push this idea to its limits by harvesting energy from their surroundings similarly to the way a kite is pushed by the wind to move.

Thus far, we had not considered animals' interactions with obstructions and other unfavorable conditions in their environment. Our built world tries to remove many of the obstructions around us to facilitate transportation; highways have been designed as smooth and straight as possible. In comparison, when a bee flies through a field to gather pollen, it is surrounded by thousands of plant stems, each of them waving in the wind. The bee's solution is hard to believe. It simply crashes into the stems over and over on its way to find pollen. Its wings have special crush-zones that store elastic energy like springs, bending without breaking. In Chapter 6, we'll also talk about other injury-preventing strategies of insects, such as how mosquitoes survive a rainstorm.

I have focused so far on adaptations we can see, but in Chapter 7 we turn to adaptations that are under the hood—the nervous system. The nervous system is put to the test in particular in insect flight, where one of the most difficult tasks is to stay motionless, or hover. It is difficult for a fruit fly to hover, because the fruit fly's body is inherently unstable. Like a sheet of paper, the fruit fly does not tend to fall straight when dropped. The fly is affected by the air currents that it itself generates as it falls. The nervous system works with the body to put hovering and other kinds of locomotion under automatic control. Automation makes animal motion repeatable and robust, with as little input from the animal as possible, like driving with cruise control.

Thus far, we have considered how individual animals move. This approach is sufficient for solitary animals, but a good number of animals live in groups, the subject of Chapter 8. Flocks of starlings, packs of wolves, and colonies of ants are all examples of groups of animals that cooperate. Cooperation is a key innovation in the evolution of animals. Cooperation is so advantageous that once it evolves in an animal, it is there to stay. We discuss cooperation of fire ants and the engineering of cooperation in a swarm of 1000 robots.

I close the book with my thoughts about the future of animal motion. We are standing at an exciting point where changes are occurring very rapidly, both within the study of animal movement and in adjoining fields. Animals can now be captured with 3D technology, capturing both their bodies and the positions of their bones. Technology is enabling robots to start to move in a lifelike manner, and at a size comparable to animals. Micro-fabrication is making possible insect-sized flying robots. Snakelike robots are being used in search-and-rescue operations. New kinds of robots called biohybrids are composed of actual rat muscle tissue, but grown into un-ratlike shapes like the manta ray. With these exciting advances going on, I'll discuss a few simple things you can do to participate in discovery and to help others better understand and appreciate the field of animal motion research.

I hope you are as excited as I am to take a bird's-eye view of animal movement. Writing about each of these areas in the book has changed me, as it has changed many of my colleagues. The German scientist Haike Vallery once told me that as soon as she started studying walking, she began to walk very slowly, considering every single move she made. I hope that as you read each chapter, it too will change the way you consider the world. Remember, science is not about answers. It is about a careful level of inquiry, a curiosity about the way the world works. Take this curiosity with you as you begin to explore the wide world of animal movement.

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