Constructing Animal Locomotion from New Thermodynamics Theory

Although running, flying and swimming appear to be distinctly different types of movement, they may have underlying physics in common

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The late paleontologist and evolutionary biologist Stephen Jay Gould argued that if the clock of evolution could be rewound to the beginning and allowed to run again to the present day, the resulting animals on Earth would be very different from the ones we know now.

Gould's main point was that a high level of chance has been involved in determining which organisms have survived and evolved over the course of Earth's history. This is likely so, but still, perhaps there are some boundaries, some general design rules that would always govern the form of any animal life. An assumption behind natural selection is that some designs work better than others. But what makes some designs work better? Are there overarching guidelines?

On this topic, biology might be able to take a cue from engineering, specifically from thermodynamics. One of the basic goals of any design—whether it's an animal, a building or a machine—is to get maximum output for minimum energy. This type of design optimization can be seen, for example, in the tree-shaped flows of river basins, hung structure or the cracking pattern of drying mud flats; in the tube shape of pipes; or in the height-versus-depth proportionality in the cross sections of rivers. All of these designs allow for the maximum throughput of material with the least amount of resistance.

The thought that the maximization of flow access could also be a mechanism that is responsible for constructing the configurations of natural flow systems—both animate and inanimate—is a principle that one of us (Bejan) has developed and termed constructal theory.

Simply stated, constructal theory says that for any finite-sized system to persist over time, it must evolve in such a way that it provides easier and easier access for the currents that flow through it.

A flow is an equilibrium of areas with high and low resistivities. This is achieved by an optimal distribution of imperfections, so that the maximum number of points of the area are stressed as equally as possible. To get this optimal balance of the various resistivities, the material must be distributed in certain ways.

For example, a river basin configures and reconfigures itself so that the water is discharged with less and less resistance through the mouth of the river. The tree shape of a mature river is the easiest-access configuration that connects an infinite number of points (the drainage basin) with one point.

Optimization is an old idea and an even older natural phenomenon. Our contribution is the streamlining of its study into a single principle. This could mostly have been done a half century ago. Instead, modern physics embarked on a course tailored to the principle that all things are built up from infinitesimal local effects, such as particle physics. Constructal theory is a jolt the other way, a means to rationalize macroscopic features, objectives and behaviors.

The Flow of Animals

Constructal theory may seem like a simple idea. But it has the potential to influence diverse areas outside of physics, including biology. For instance, locomotion can be considered to be a flow of mass from one location to another. Animals move on the surface of Earth in the same way as rivers, winds and oceanic currents. They seek and find paths and rhythms that allow them to move their mass the greatest distance per expenditure of useful energy while minimizing thermodynamic imperfections such as friction. Animals move in different ways for different purposes, but effective use of energy is important over a lifetime, and the basic design of most animals should evolve toward locomotion systems that optimize distance per cost.

There have been many analyses of animal locomotion, but most have

Figure 1. Nature appears to have evolved three distinctly different forms of locomotion in flying, running and swimming. If evolution began all over again, there's no telling if these particular animals would turn out as the end products of natural selection. However, there might be general design rules that would still govern animal development, should these mechanisms of locomotion evolve once more from the beginning. Taking a cue from thermodynamics, locomotion can be considered as a flow of mass from one location to another. And like other flow systems, movement can be optimized so that an animal's mass is moved the greatest distance per expenditure of useful energy. Using these basic guidelines, formulas have been derived that are shown to govern these types of movement.

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been based on empirical relations—working backward from observations to find a model that fits the results. Constructal theory is a different approach because it works from theories based in physics to deduce and predict structure and function. It not only predicts maximum-range speeds, but also simultaneously predicts stride/stroke frequencies and net force output.

This theory is not intended to account for all forms of biological variation. It does not maintain that animals must act or be designed in a predictable fashion, only that over large size ranges and diverse species, predictable central tendencies should emerge. Ecological factors will often favor species that move in ways other than that which optimizes distance per cost, such as where energy is abundant and the risk of being captured by active predators is high. Evolutionary history and the chance nature of mutation can also restrict the range of trait variation that has been available for selection. These and other factors should act primarily to increase the variation around predicted central tendencies.

It has been thought that intrinsic differences exist among the main types of locomotion—running, flying and swimming. Runners and fliers have weight, whereas swimmers are neutrally buoyant. The wings of birds are structurally different from the limbs of antelopes and the tails of fish. The flapping motion of wings is unlike the hopping legs of a running animal and the undulating body of a swimmer. Birds and fish in cruising mode are at constant altitude and depth, whereas runners are constantly on a hopping (cycloidal) trajectory. Hitting the ground during running is far different from rubbing against air and

Figure 2. Constructal theory states that for any finite-sized system to persist over time, it must evolve to provide easier and easier access for the currents that flow through it. An optimization seen in many systems is a tree shape, as it is often the easiest-access configuration that connects an infinite number of points with one source point. A false-color satellite image of the Lena River delta in Russia (top) takes on a fan shape similar to that of certain types of branching coral. A computer simulation of the flow of electrons through a two-dimensional landscape of varying electric potential (bottom) is reminiscent of the tracks that snowmelt creates as it follows the paths of least resistance down the sides of a mountain. (Top photograph courtesy of NASA Landsat Project Science Office and USGS National Center for EROS.)
water. Complicating the picture even further is the great diversity of body sizes, shapes and speeds found in even a single form of locomotion (for example, flying birds and insects).

Despite all these differences, numerous investigators have found that there are strong convergences in certain functional characteristics of runners, swimmers and fliers. The stride frequency of running vertebrates scales with approximately the same relation to body mass \(M\) as the swimming frequency of fish, \(M^{0.17}\). The velocity of running animals scales with approximately the same relation to mass as the speed of flying birds, \(M^{0.17}\). And the force output of the muscles of runners, swimmers and fliers conforms with surprisingly little variation to a value of about 60 newtons per kilogram. There are other correlations, such as that between body size and breathing rate.

In an attempt to explain these consistent features of animal design, biologists have concentrated on potentially common constraining factors, such as muscle contraction-speed or structural-failure limits. However, constructal theory allows us to take a different approach, not of starting with constraints, but beginning with general design goals that can be used to deduce principles for optimized locomotion systems. We have found that constructal theory can unite all of these various forms of locomotion by showing the underlying physical parameters that they have in common. The theory is not mutually exclusive of other hypotheses such as common constraints; perhaps constructal theory can provide a design framework and an explanation for the nature of these constraints. It can predict, explain and organize a body of knowledge that was growing empirically, by bringing the cruising speeds, frequencies and force outputs of running, flying and swimming under one theory.

**Flying**

A bird in flight spends useful energy in two ways. One is vertical loss: The body has weight, so it falls incrementally and the bird performs work to lift itself back to cruising altitude. The other is horizontal loss: The bird performs work in order to advance horizontally against air friction. Both losses are needed for flying; neither can be avoided completely. However, they can be balanced against each other so that their sum is minimal. This optimal distribution of imperfection is flight itself.

Flight is not a steady movement at a constant altitude. Its trajectory is a saw-toothed horizontal line with a tooth size dictated by the flapping stroke. It is an optimized rhythm in which the work of repositioning the body vertically is matched by the work of advancing the body horizontally. The balance is achieved by two competing trends: the vertical loss decreases and the horizontal loss increases as the flying speed increases. Balance is achieved by flapping such that the flying speed is just right.

With these parameters in mind, constructal theory predicts that flying speeds should be distributed in proportion to the body mass raised to the power 0.17. Flapping frequencies should be proportional to the body mass raised to the power -0.17. These predictions agree reasonably well with observations over the entire range of flying bodies.

We derived this formula algebraically, in a process that involved numerous substitutions for equitable terms. In addition, all constants within one order of magnitude of the value of 1 (0.1 to 10) were dropped for the sake of mathematical simplicity.

To give an example of how we arrived at this formula for speed, we consider that constructal theory calls for the minimization of the total work losses for the distance traveled. The distance is equal to velocity multiplied by time, but time is equivalent to the distance the body falls under the control of gravity, raised to the 0.5 power. The distance the body falls scales with body length or height, which is in turn equal to the body mass divided by the body density, raised to the 0.33 power. Body density has been approximated for all animals as 1,000 kilograms per cubic meter. The horizontal losses are largely a factor of air friction, which is itself dependent on air density, approximated as one kilogram per cubic meter. Solving all of these factors for optimal velocity, we arrive at a formula where the only non-constant variable is body mass \(M^{0.17}\). We have similarly shown that the net force an animal produces to move at optimal velocity is a multiple, typically about two times, of its body weight.

**Running**

If we treat running in the same way as flying—as an optimized intermittency

![Figure 3. A simple diagram of the periodic trajectory of a flying animal showing the factors considered in estimating animal locomotion from constructal theory. The sawtooth pattern results because flying velocity \(V\) is composed of alternating work done to overcome vertical loss \(W_v\) and work done to overcome horizontal loss \(W_h\). \(W_v\) is found by multiplying body mass \(M\), gravity \(g\) and the height the body falls during the cycle \(H\), the latter of which scales with body length \(l\). \(W_h\) is the product of the force of air drag \(F_d\) and the distance traveled per cycle \(D\).](image)

![Figure 4. In the periodic trajectory of a running animal, the distance of each stride is a multiple of the animal's velocity \(V\) multiplied by the time \(t\) of frictionless fall from the height of the run \(H\). Therefore, \(t\) is equivalent to \(H\) divided by gravity \(g\), raised to the 0.5 power. The stride length \(l\) both scale with the body length, and the body mass \(M\) is approximated by the body density multiplied by the body length cubed.](image)
in the Earth’s gravitational field—we can also predict the speeds and stride frequencies of all runners. Running is a succession of cycles involving two losses. One loss is the lifting of the body weight to a height that can be generalized as the body length (approximately the length of the limbs). This work is the vertical loss, because when the body lands, its gravitational potential energy is destroyed in the legs and the ground. (For simplicity, we ignore elastic storage during landing.) The second is horizontal loss: the work performed to overcome friction against the ground, the surrounding air and internal body parts (although again for simplicity, we consider all friction to be external).

The vertical and horizontal losses compete, and when they are in balance their sum is minimal. The optimized intermittency called running is again found to be characterized by a speed proportional to \( M^{0.17} \) and a stride frequency proportional to \( M^{0.17} \), using a similar derivation as was described in the previous section for the process of flying.

The predictions from this theory of running are quite robust: The horizontal loss may be dominated by dry friction against a hard surface, permanent deformation of a soft surface such as sand, mud or snow, or air drag. All these effects influence the speed and frequency, but they influence them in almost the same way. If air drag is the dominant horizontal loss mechanism, the speed and frequency deviate by only a factor of 10 from what they would be for runners with dry friction and ground deformation.

Another surprise came from the calculation of the work spent on lifting the body off the ground. For both runners and fliers, the average force exerted over the stride or stroke cycle should be twice the body weight. This agrees with the force-weight measurements across all body sizes, for all animals that fly and run. So far we have seen that as an optimized intermittency, running is similar to flying.

Swimming

Is swimming like running and flying? The obvious answer is no, because the movements of the neutrally buoyant bodies of fish seem to have nothing to do with gravity. This view has until now prevented the emergence of a physical theory of locomotion that includes swimming.

The reason why running is no different from swimming or flying (in spite of the fact that swimmers and fliers do not touch the ground) is that the ground supports the weight of every body that exists above it. The same ground serves as a reference against which all moving bodies push, and without it no locomotion is possible.

In swimming, because the bottom of a body of water is immense and stationary, a fish can push and move its body relative to the ground by performing work against gravity and friction, just like a bird or an antelope.

To advance horizontally by one body length, a swimmer’s body must do work equivalent to lifting a parcel of water of its own size to a height approximately equal to its body length. This body of water must be lifted because a net vertical displacement is the only way that water can flow around an animal, or any object. Wa-
ter is incompressible, and the ground under the water does not move, so only the free surface is deformable. This is readily visible as a bow wave lifted in front of a body moving along a water surface, but what has not been appreciated previously is that this vertical work is nonnegligible and is fundamental to the physics of swimming at all depths.

Why don't we see this free-surface deformation caused by every fish that lifts water over itself in order to progress horizontally? Because most fish are small and swim deep. The lifted water is equal to the volume displaced by the free surface as it rises over a very large area—all the larger when the fish is deeper. The lifting of the free surface is visible when the fish is large and near the surface. Elevation of the water surface also has been demonstrated and used in the field of naval warfare, where certain radar systems are able to detect a moving submarine by the change in the surface water height as it passes.

With this, constructal theory accounts for swimming. Its predictions of speed and stroke frequency are the same as those for running on deformable ground, and they agree with much data.

Thus, even though some animals do not touch the ground, they use the ground to propel themselves. The flapping of the bird's wings produces vortices of air that eventually stagnate against the ground and increase the pressure that the ground supports. The water lifted by the swimming fish induces a local elevation of the free surface and a greater pressure on the lake bottom. The ground feels, and

Figure 7. Theoretical predictions from constructal theory are compared with the velocities, frequencies of strokes or strides, and force outputs of a variety of animals. Solid lines in these log-scale graphs show the predicted velocity (a) or frequency (b) of animals based on body mass for running mammals or running animals where the ground is hard and thus the main frictional loss is due to air drag. Dashed lines show the predicted velocity (a) or frequency (b) of animals based on body mass for swimming animals or running animals where the ground is soft and thus the main frictional loss is due to ground deformation. A dotted line indicates the predicted force output, based on body mass (c). The theoretical predictions ignore constants between 0.1 and 10, and so are expected to be accurate within an order of magnitude. (Data from Bejan and Marden 2006.)
Figure 8. During flight, useful energy input into a system is destroyed completely in a distributed fashion by components that have equivalent functions in animals and machines. Constructal theory predicts that all flow-system structures result from the clash between two objectives: the need to carry substances from the core to the periphery and the need to avoid direct leakage of these substances and energy (such as heat) into the ambient surroundings. The ultimate purpose of food or fuel taken in by a bird or put into an airplane is to provide power for flight, which overcomes air friction and supports the mass of the animal or machine. In between fuel input and power output, however, energy is destroyed by various flow systems.

Figure 9. Constructal theory's predictions of velocity based on body mass extend from animals to man-made machines. The force-mass relation of engineered motors is the same as that for all types of animal locomotion. In this log-scale graph, there is a direct scaling relationship between flying animals (insects and birds) and airplanes. The solid line shows the predicted velocity from constructal theory, whereas dots show measured values of mass versus velocity for insects (green dots), birds (blue dots) and airplanes (brown dots). (Data from Bejan 2000.)

By the Numbers
We compared projected values from constructal theory for velocity, stroke/stride frequency and force output with empirical data for a wide variety of animals.

All of our predicted mass-scaling exponents are based on the assumption of geometric similarity, or in other words, we idealize animal shape to be roughly spherical. However, small and statistically significant variations from this assumption tend to be the rule rather than the exception throughout the literature on animal scaling. Wingspans of birds show a particularly large divergence from geometric similarity. Because larger fliers have relatively longer wings, they should have a more negative mass scaling of wingbeat frequency than predicted by our model.

In general, empirical scaling slopes vary because of the identity of the species sampled, taxonomic differences in the scaling of body dimensions, variations between studies in animal behavior and methodology, and statistical assumptions.

Thus, although we do not find statistical support across the board for the exact scaling slopes predicted from the theory, in all cases the scaling exponents derived from theory fit the data about as well as could be expected. The data fall within an order of magnitude of the predictions, which is the expectation for a dimensional analysis in which constants between 0.1 and 10 were ignored. This is noteworthy considering that this theory uses only density, gravity and mass, without any fitting constants, to make these predictions.

Branching Out
We have shown that a thermodynamic approach can predict complex features of animal design. We believe we have provided evidence that if evolution were rewound, and if runners, swimmers and fliers appeared again, the process should consistently produce the same types of speeds, stroke-stride frequencies and force outputs for these forms of locomotion as exist today. The theory could even be used to predict how these features would evolve on other planets with different gravita-
Humans routinely encounter different terrain and we adjust our speed and stride frequency accordingly. Consciously and unconsciously, we pay attention to the effectiveness of our movement patterns, and we may be wired to select optimal gaits. When astronauts walked on the moon, they encountered a completely different gravitational force, so it would be interesting to see how well their preferred speeds and hopping frequencies match the predictions of our theory.

The predictions of constructal theory are consistent not only for animals, but even for man-made machines. The force-mass relation of engineered motors is the same as that of runners, fliers and swimmers. The constructal theory of animal flight also predicts speeds of machine flight and unites the animate with the inanimate.

The theory can, for instance, help in the design of efficient robots to roam on other planets or in remote environments on Earth. It has general utility for the design of any novel locomotion device, or even for the improvement of existing ones, as the theory provides an objective for some of the major features that engineers need to specify. For example, automobile tires deform during each rotation, resulting in a vertical loss of energy, while also sustaining a horizontal loss from friction. It would be interesting to see if tire design has already been optimized, or if further improvement is possible. More fancifully, our predictions could be used in animation to choose the speeds and stride patterns of creatures such as dinosaurs, to accurately show how, for instance, a Tyrannosaurus Rex should look while chasing a vehicle in a movie.

Constructal theory grew out of engineering, and in fact it loops back to aid that field. By identifying the principle that accounts for geometric form in natural flows, we can improve our vision as designers and creators. A more basic understanding of what makes a design optimal and efficient can allow us to create designs that are more efficient from their first conceptualization. With constructal theory we can invent based on principle, not solely by copying from nature, and approach design as a science.

**Bibliography**


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