

Good, Better, Best: How Evolution Optimizes Anatomy and
Action

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Abstract

Review of

How Animals Work (Schmidt-Neilsen, 1972)

and

Optima for Animals (Alexander, 1996).

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Good Design

You need to transfer heat from one fluid at 100° C to another at 0° C without mixing them. Given some tubing, you could wrap one length around another. Then, with enough wound tubing, pumping both in at one end, at the nether end you would find that both fluids came out at about 50°. Good.

Can you do better? Can Nature? This is the nut of one (and thereafter many) of the problems Knut Schmidt-Nielsen (of Norwegian lineage, if you wondered; with a statue of him gazing at a camel on the Duke campus, if you wanted to wonder) was driven to by a sojourn in my Arizona Sonoran desert half a century ago. There his naturalist's eyes found surprisingly abundant wildlife given the rigor of the environment. Consider the lowly Kangaroo Rat. It never drinks water and has less appetite for moisture-rich greens than do some presidents. But like all of us, the rat must breathe, and that means exhaling air saturated with moisture that he can scarce afford to lose. Warm air carries more water than does cool. Perhaps those clever little rodents used your tubing architecture to pass incoming and outgoing air by each other, so the outgoing air wasn't so warm, and with a few snuffles of the condensing cooler air the rat could regain some drops of what would be lost. That would be good. But Nature invented a way, and re-invented it dozens of times, that does better.

Switch the input of one of your tubes to the nether end. Hot air coming in would then meet outgoing air just a little less hot than it, and raise temperature a bit more, and so on down the tubes, till at the end, the now relatively cold incoming air would meet the almost equally cold outgoing, and the transfer of heat would be almost perfect. 100° is squandered heating 0°; but is

well spent on 90°. This is called *counter-current* exchange (CCE); here counter-current heat exchange. I shall be mentioning a number of neat ideas that have some generality in this review. I call them *cachets*¹. They are terms of art that compress an intriguing idea into a simple expression. Words that you can drop at a party². You can think with them. Knut plots the temperature of exhalation from a dozen species of birds, and it is a linear function of ambient temperature--but always significantly below body temperature. Those little Kangaroo Rats do it even better than the birds, and he shows why with cross-sections of their sinuses. Knut is smarter than I, as he can generate a mathematical model of the process, which performs quite well. He is also wiser than I, as he does not write the equations of the model, just describes how it works.

What these littlest of nature's mammals do, the biggest can too. How do whales not lose all their core heat through those fins and flukes, which are perfect radiators fanning frigid waters? CCE: They warm the incoming blood with the outgoing, so when the blood gets to the fins it is at about their chilly temperature, and the blood returning from the fins is warmed to about core temperature. This clever design is no fluke; evolution work miracles!

The brain needs stable temperatures. How do you keep a cool head in hot times? You've already guessed it: CCE, as the carotids spread out in a mesh (called a *rete*) passing its blood against the flow of venous blood coming in from the nasal sinuses, which cools it as necessary, before sending it on to the brain. Farther down a man's body another organ needs to be kept cool despite how hot he is; CCE to the rescue!

Fireplaces are romantic, but most of the heat that is not made on the couch goes up the chimney. The Franklin stove is more efficient, as the stove box and chimney-pipe radiate heat

¹ I chose the word because you were not quite sure of what it meant, and this is as good a use for it as any.

² For geeks.

into the room. But while heating your front, it chills your back, as it must draw in cold air to feed the flames, and that comes from outside your house. A psychology graduate student improved the situation with counter-current heat exchange. Close your eyes now before reading on, and see if you can figure out how. ... OK, now open them³.

Hot Dogs

Counter-current exchange works great to preserve the *milieu intérieur*. But what if you want to move some of that *milieu extérieur*? Suppose that, unlike the whales, you need to lose heat? Breathing in and out through the nose would tend to conserve your bodily heat; thanks a lot, CCE! If you were a dog, what would you do? (About heat.) Perhaps find another way for the hot air to exit than the same one used by the cooler air coming in. In my Sonoran desert my Lucy spends a lot of her time panting. The nose is the primary cooler, inhaling; that long dripping tongue is merely a secondary heat exchange, designed primarily to amuse and bemuse you, as it exhales through the mouth.

Whereas you may have watched your Lucy pant, have you noticed that she does not increase the frequency of panting as she gets hotter? This is what the engineers call bang-bang control⁴: It is either on or off. Why is frequency not a smooth function of temperature? Think about it for a moment before reading the answer suggested by a student of Knut's⁵. Mammals

³ I hide the answer here from your unclosed eyes to increase the response cost of peeking. The student fashioned a stovepipe with another inside. One passageway exhausted the smoke (and heat); the other drew cold air from the roof down to feed the fire, heating it on the way down, so that it added hot air to the firebox, and did not draw cold air over you to that box.

Take-home problem: Would you send the hot air up the outer donut of chimney or up the inner hole?

⁴ Antonym: self-control.

⁵ Dogs pant at resonant frequencies of their lung/throat mouth system. If they were to do other, they could easily generate more heat by panting than dispel by it. Not all birds pant at resonant frequency, but my favorite, *Columba*

cannot make use of CCE to increase the oxygenation of their blood from the air they breath, but birds can, and fish breathing through gills use CCE to extract 80-90% of the oxygen that flows over them. “It was during the work with the ostrich that the need for further understanding of bird respiration became acute” is the type of sentence that regularly charms you in *How Animals Work*. Dogs pant at resonant frequencies; do large birds tune their breathing tracts and wingbeat so that breathing and flying are synchronized?

A colleague designed a charter school decades ago, in which he used CCE for knowledge exchange, having more advanced students tutor less advanced, throughout the grades. It is still in operation. To what novel uses might you put CCE?

There is a mechanism similar to CCEs, called *counter-current multipliers*, where a solution must be concentrated “up-hill”, as the kidneys must concentrate urine. I shall let you turn to Knut for explication of this and other questions. But, before you turn, ponder how you might design a *CCM*; and for what else it might be a cachet.

Splat

In looking through the book you will come across many straight lines, often in double-log coordinates. These are *scaling laws*. The cost of running in animals ranging from the white mouse to a horse is a near perfect power function (slope -0.40) of their body weight. There are many such scaling laws in biology, typically power functions, and often their observed slope can be derived rationally (West et al., 1997), or readily interpreted. A fascinating recent book about such laws is *Scale: The universal laws of life, growth, and death in organisms, cities, and companies* (West, 2017). He delivers on the promise of the sub-title. Question: Do psychologists’

livia, does. Try the experiment yourself: Pant at different frequencies. First alert your partner that it is an experiment. Then sit down.

favorite power functions, the psychophysicist's sensory scaling laws, and the behaviorist's generalized matching law, fit into any of these schemes?

An early observation of scaling laws at work was given by the biologist JBS Haldane: "You can drop a mouse down a thousand-yard mine shaft and, on arriving at the bottom, it gets a slight shock and walks away. A rat is killed, a man is broken, a horse splashes." As the length of an animal doubles, its surface is squared and its mass is cubed. Your cachet: *square-cube law*. The mass, and thus the kinetic energy that must be dissipated by the animal, increases as the cube of its length, but its landing/impact surface increases only as its square. The strength of bones increases as their cross-section area, whereas the mass they must support increases with the volume of the animal. Thus, ants can have very skinny legs, but elephants must have huge columns of legs. Gullivers just can't travel. *Square-cube law*. HO-scale model trains are $1/87^{\text{th}}$ the length of a real train. Their mass is thus 87^{-3} that of the real train. Less weight to hold them on the track, so they more readily flip at just a few feet per second, with linearly proportional wheel flanges of little help.

Gas exchange is a surface phenomenon and so varies as the square of the length of an animal, but the mass it needs to service grows as the cube of the length. What are the design features of our lungs that help deal with his disparity? Drugs are absorbed as the area they come in contact with, about the square of body length, but the mass that they must serve as its cube; good dosing requires knowledge of the square-cube law. But metabolic rate is another factor, and that decreases uniformly with the body weight; drugs will be slower to clear in a large animal, as Knut's story about dosing an elephant⁶ revealed. Because of this metabolic scaling, all species

⁶ With LSD. Strange story. Don't ask.

live for the same number of heartbeats⁷. In prescribing a novel drug, my physician looked it up in the pharmacopeia, looked at me up and down, and asked: “I need to dose this in proportion to your skin area—do you know what that is, Peter?” I just grinned and shook my head, and “No” was all I said.

Better Design

As the Lion by its Claw; The Brachistochrone Problem

Someone challenges you to draw a curve from point A to point B below it and to its right, so that a frictionless ball rolling from A to B would get there faster than along any other curve. (Hint: This is a situation where CCE won't help). What would you draw? A straight ramp? A semicircle? A catenary? This optimization problem had bemused good mathematicians for several years. Galileo thought, but couldn't prove (as the calculus was not yet invented) that it was a parabola (close but wrong). In 1696 Johann Bernoulli, one of a clan of gifted Swiss mathematicians, posed it as a challenge to the world (that small world of 17th century mathematicians). Johann had the correct answer (but with a flawed derivation), which took him weeks to arrive at, in his back pocket; yet had to extend the deadline because of the paucity of returns. In the end, six great mathematicians provided answers: Johann Bernoulli, Newton, Jakob⁸ Bernoulli, Leibniz, Tschirnhaus, and l'Hôpital. When Newton eventually found the problem in his post, he completed his proof overnight (taking longer than he would have in his

⁷ In answer to your surgent question, no, I feel I shouldn't tell you what that number is, to keep you from counting down. But do exercise to lower your resting metabolic rate, is my advice.

⁸ Whose correct derivation Johann tried to steal; this was not the last intellectual property theft amongst the clan; the next lead, as you know, to the St. Petersburg Paradox.

prime) and submitted it anonymously⁹. When Bernoulli saw it, he said he knew it surely to be Newton's solution, just "as one knows the lion by its claw". The correct answer was a segment of a cycloid, the curve traced by a point on a circle rolling along a line. One of the solutions evolved into the calculus of variations, which tells us what kinds of functions, or curves, satisfy a minimum or maximum—a big brother to the simple calculus that you may have met in high school.

Optima for Animals

Alexander (1996) uses the calculus of variations to prove that the shortest distance between two points is a straight line. Why prove the obvious? To sharpen our pencils. But he starts simpler, first reviewing that high-school calculus using homely examples, such as the optimal shape for a can to minimize the metal used to contain a particular volume. Any guesses?¹⁰ He wryly notes that most of the cans in his grocery store do not satisfy this solution: "they may have been applying some other optimization criterion". This, the "optimal for what?" question, is a recurrent issue in optimality theory. What is the optimal speed for an airplane? Given the relation between power used and air resistance and lift, Alexander provides a solution for minimal power between two airports. Then he derives another for minimal fuel—if you fly a bit faster, using more power, you get there sooner, using less fuel. What is optimal depends on what variables you are talking about. What is the optimal lifestyle—fast and furious and everything goes, or calm, centered, and—academic? Husband the candle, or burn it at both ends? "Optimal for what?" is the question that you are starting to learn to ask.

⁹ Whilst complaining that he "didn't like to be pestered by foreigners about mathematical things".

¹⁰ Its height should equal its diameter.

As Alexander (1996) explains, calculus is the tool of choice for optimization, and typically involves some variant of taking the derivative of a function and setting it to zero. That, however, gives you an extremum, which could be either a maximum or a minimum. You need to check which, and there are several straightforward techniques to do so (e.g., take the second derivative at that point. If it is positive, the curve is going up from there, and you are at a minimum; negative, at a maximum). If you are sometimes embarrassed by your mathematical mistakes, join the crowd. Some designers of an early flying wing aircraft, precursor to the B2, concluded that you maximized range if all of the weight of the craft was in the wings. Eventually the contract was cancelled because of inadequate range (“insufficient funds” is what the press release originally said after 15 aircraft were built). A subsequent investigator found that the extremum in this case was a minimum, not a maximum—the designers had apparently failed to check the second derivative, and designed the worst, not best, possible configuration! They were “embarrassed” by their mistake, but refused to step back from the design, on which the B2 was based (Biddle, 1989). They redesigned their claim instead, arguing that it optimized other objectives. (It didn’t.) The B2 incurred billions of dollars in redesign. Clearly those designers were optimizing their claims over objectives other than the best aircraft design to maximize range¹¹.

Optimal behavior

After analyzing optimized structures such as bones and eggshells, Alexander turns to motion—walking, running, flying and leaping. He shows the utility of catastrophe theory, at least qualitatively, in the analysis of gaits. He slowly ponders the order in which tortoises should move their feet. Of most interest to this audience is his review of optimal foraging. The

¹¹ Like, their reputations.

questions addressed include: In selecting prey, should a bird eat only the biggest worms, or anything it comes to? How long should a carnivore pick over a carcass before moving on? When should a challenged stag fight and when should it run. You have already just now, I am sure, mused over the relevant variables, dear reader. Alexander does too, and puts a fine point on them with reasonable math models, many from the literature. Alexander is not just a theoretical modeler; he brings data to bear on his models wherever they are available. How long should a bird sample concurrent probabilistic schedules (the “two-armed bandit” problem) before settling on the best one? Alexander recounts the work of Krebs and associates in collecting relevant data and providing a Bayesian analysis showing that their birds came close to optimal performance (Krebs et al., 1978). But you needn’t travel to Oxford to forage; a different Bayesian analysis of pigeon foraging under concurrent probabilistic schedules is in a closer patch in the Sonoran desert (Killeen et al., 1996). A related problem confronts the bird choosing between two patches, one historically better than the other—but with more conspecifics there that he will have to elbow out of his way. A solution to this problem is called the *ideal free distribution*. Is it relevant to humans choosing careers, restaurants, or dating bars?

George Price was a brilliant and troubled man who turned to biology later in life (Harman, 2011). He was active in the field for only a few years, but his handful of articles has had a profound impact (Baum, 2017; Gardner, 2008). The *Price Equation* formalized Hamilton’s analysis of altruism: Why, in this Darwinian world, be altruistic, and what is the best tradeoff between altruism and selfishness? Like great art, that equation is both apparently simple yet profoundly subtle. Price introduced his mentor, Maynard Smith, to game theory and its potential role in biology, and together they wrote *The Logic of Animal Conflict* (Smith & Price, 1973), cited over 6000 times. It introduced a different kind of optimum, an evolutionary stable strategy

(ESS)—an equilibrium that once reached, resisted perturbation (ESS—a new cachet; e.g., “have you reached an ESS with your partner?”). The original article, or Alexander’s rendition of it, is one of those intellectual gems that all students of behavior should know. It contains another cachet: Hawk-Dove Strategy. The apt title of Harman’s biography is *The Price of Altruism*. Bemused, perhaps, by his equation for altruism, Price gave away all of his possessions in random acts of kindness. He burnt his candle at both ends, and then his bridges; and when he was bereft, he lived under a bridge, and soon died there.

Let’s talk about something happy for a change. Babies. Should you have lots of babies (but no time for them), or a few (so you can invest heavily in their growth)? If you (your species) adopted the first strategy the population would grow exponentially fast at a rate r . But that cannot last forever; it would slow down and stop when it hit the carrying capacity of the environment, K . The simplest model of this process gives a logistic growth curve that fits many data (and which may, surprisingly, have chaotic properties: May, 1974). In unstable environments where resources come and go, the r strategy of high reproductive rate works well. Fruit flies that eat only dead saguaro cactuses (my Sonoran desert, if you couldn’t guess), dung beetles, and germs are such “ r selected” species who put everything into reproduction. Others that live in stable environments have stable populations near its carrying capacity. Great apes, humans and a few other animals exemplify “ K selected” species, investing heavily in a small number of offspring to elevate the K of their niche. Like many of the concepts found in this book, this distinction has applicability outside the realm of population dynamics: Should you aim for many quick publications in B journals, allowing no time to make them excellent, or for fewer more difficult ones in A journals? Is there an optimal mix? Should you write book reviews that are unlikely to have any offspring (citations)? Do the answers depend on your life stage? Do you

recognize that *r-vs-K strategy* is another cachet that you now can drop at that party when someone else says *counter-current?*)

While I have your mind on sex, should you (your species) have more girls than boys, or the reverse? Fisher showed that the sex ratio typically should find an equilibrium near equality. Alexander shows why. But that is not the case for social insects that have an intriguingly different genetic system, one that explains the mystery that Darwin could not solve, how so many units in those colonies would slave away for the colony with no chance of reproducing. Alexander computes a different ratio for them, and reports work of biologists that brilliantly confirms it.

OK, you have had sex, and your female has laid her eggs. You have a vape while you consider: Should the female, or the male, or both, or neither hang around to guard them? Depends. Alexander writes a simple ESS model for what it depends on, and identifies four species that adopt each of the possibilities, each making apparent sense in that ecological niche. Where there is sex, of course, there is often cheating, and Alexander devotes a brief section to it. Should you cheat? Should you be a “parental” or a “cuckolder”? Once again, the ESS is a model of choice. For so salient a problem nature has devised many solutions, mate guarding (which takes time away from cuckolding) among them. Evolution is all about trade-offs, and optimality theory is one way to understand what is getting optimized by the tradeoffs that nature has settled on. That is the beauty of evolutionary biology; evolution has proceeded long enough to settle on good solutions that often astound in their clever adaptation to strange niches; and in that adaptation, create new niches for others.

Best Design?

Alexander concludes with the chapter *Dangers and Difficulties*. The first difficulty is to decide what to optimize. You might think the answer is simple: fitness. But that is very difficult to compute. In the book he had analyzed how to optimize resolution of the ommatidia of a fly's eyes. It is clear that better resolution will improve fitness, but that comes with other tradeoffs; how to model its impact on fitness would complicate the math and introduce too many hypotheticals.

A second difficulty is to understand the constraints that bear on optimization. In modeling, as in poetry, constraints are a necessary part of the creation, else optimal bones would be weightless and unbreakable. One of the reasons for optimality modeling is to better understand those constraints.

Optimization theory is not an answer; it is a frame for questions, a way to generate hypotheses to be tested. It can go wrong in several ways he lists. But he cautions against the danger of mending those errors by curve-fitting: "one should be careful about tinkering with models to fit existing data. It is always dangerous unless the modification is theoretically plausible and the modified hypothesis is tested by further observation or experiment" (p. 147). This is a caution pertinent to all psychologists, who often stop thinking once they find a curve that fits. Alexander addresses critics' misunderstanding, acknowledging that there may be many local optima (another cachet!) in the evolutionary landscape, from which further progress toward a higher optimum is impossible because it would incur a short-term fitness disadvantage. Squid will never swim as efficiently as fish, because their jet propulsion works well enough, and offspring with proto-tails to beat would not compete effectively with standard squid offspring¹².

¹² This is why reproductive and competitive isolation will often let a deviant form get a leg up, so to speak.

Finally, Alexander notes that the goal of optimality theory is not to prove that an animal or some aspect of their behavior is optimal; that is nonsensical. It is to generate hypotheses in a principled way about the constraints, quantities optimized, and tradeoffs. Just as physicists are often happy when predictions fail: “Ahhaa, an opportunity for new physics!”, biologists are not dismayed by the failure of an optimality prediction. It shows that they had been understanding a situation incorrectly, and now had an opportunity to solve the new puzzle: Just why didn’t the beasts do it that (obvious, but now obviously not right) way; what had the biologist overlooked? He gives examples.

What are the constraints on our own behavior that have made such sensible approaches so rare in our science? Is it simply the difficulty of the endeavor, and the creativity that it requires, or is it something else? Do we avoid solutions that invoke final causes, such as optimization? I hope not; for even light waves optimize their path so that it is the shortest and fastest of those available. Ancient Greeks posited this, and now all the laws of mechanics can be written as equations (“Hamiltonians”) where action is minimized, another kind of calculus of variations. If photons optimize, why not pigeons?

These books are both good, neither better than the other, written by the best experts in their fields. Both were Fellows of the Royal Society and other prestigious academies, and both were CBEs (similar to a Presidential Medal of Honor, and perhaps in our times, the better). They were the authors of many books and papers. *How Animals Work* is an easier read with minimal math in it. You will leave it with an enhanced admiration of the beauty and adaptability of animals, the cleverness of their solutions, and the dogged curiosity of a scientist. *Optima* is harder work. To get value from it, it is best if you give some thought to how Alexander sets up the math for the numerous problems he addresses (although you needn’t study the equations

deeply, or even pick up a pencil). You will come away from it with a much better appreciation of the approach, and some ideas and proto-tools for your own work. Which is best for you? It depends on constraints, such as your comfort with quantitative arguments—and, of course, on just what it is that you are optimizing over. While you are making up your mind, check out West's *Scale*; less academic, no less authoritative, and possibly provocative of your designing a cachet or two of your own.

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